Lazy Leapers: A study of the locomotor ecology of two species of saltatory nocturnal lemur in sympatry at Ampijoroa, Madagascar

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by Ruth Dorcas Warren
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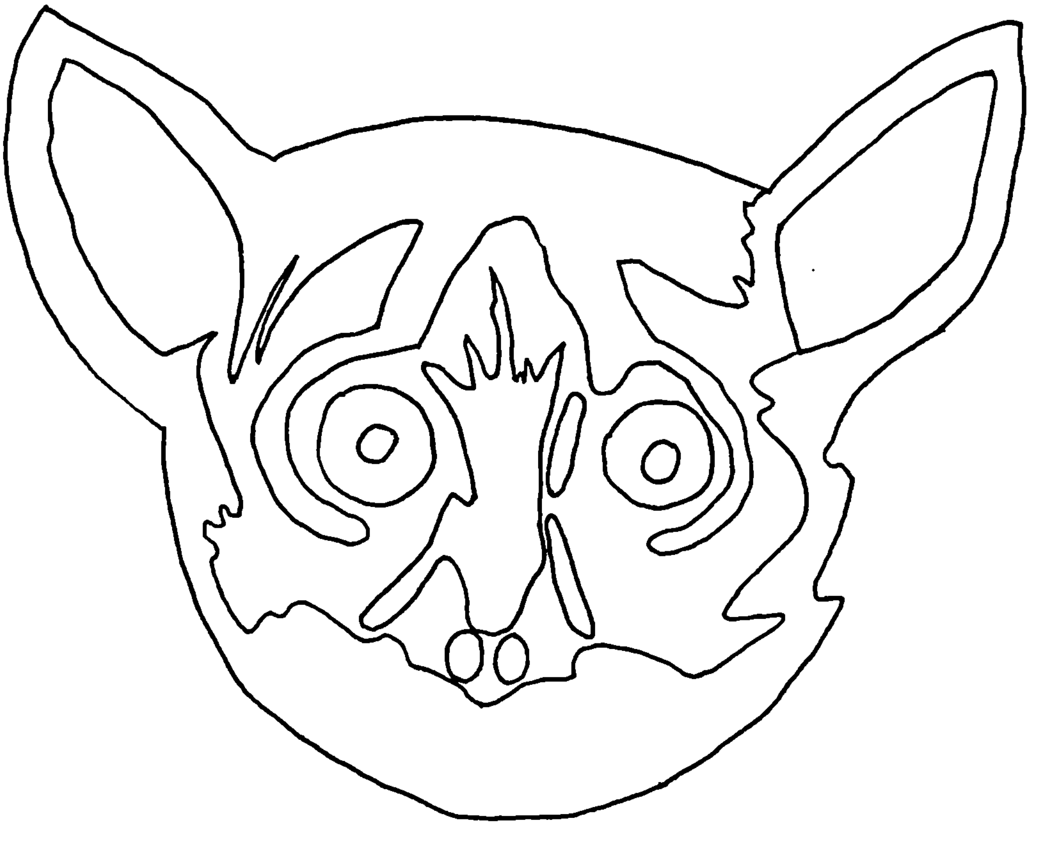

Dedicated to mum and dad,

with all my love,

always

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Abstract

This study is a comparison of the locomotor ecology of two species of lemur, *Lepilemur edwardsi* and *Avahi occidentalis.* Generally they are regarded as nocturnal, folivorous, and are vertical clingers and leapers with the same morphological adaptation for leaping. They have a similar body mass (and consequently are expected to have a similar metabolism). In at least part of their range, they can be found coexisting. The two species of lemur were studied in their natural environment of the dry deciduous forest at Ampijoroa, Madagascar.

Four animals of each species were caught and radio-tracked for complete nights over an 18 month period. Data were collected on locomotion, support use and preference, home range size, nightly distances travelled and feeding choices.

A.occidentalis and *L.edwardsi* were demonstrated to have grossly similar locomotor repertoires but with differences in emphasis. *A.occidentalis* leapt more often and further than *L.edwardsi* but *L.edwardsi* climbed more often than did *A.occidentalis.* *L.edwardsi* used a lower stratum of the forest than did *A.occidentalis* demonstrating a spatial differentiation between the two species. *L.edwardsi* used vertical and angled supports more predominantly than did *A.occidentalis.* Jacobs D preferences values were obtained to measure the ratio of support availability to support use. The two study species did not use supports at their frequency of occurrence. Overall, both species surprisingly avoided vertical and angled supports in the forest and chose to use sloping or horizontal supports.

Lepilemur edwardsi was shown to have a small home range of 1.09 ha, and there was a very high degree of overlap between individual home ranges whereas *Avahi occidentalis* had a mean home range size of 1.6 ha with only a small area of overlap between groups. Four species of plant identified were eaten by both species, which showed that food choices are not exclusive. *L.edwardsi* was less discriminating in the age of leaves eaten than *A.occidentalis.*

The energy cost of locomotion, using biomechanical principles, was calculated. Both species have locomotion costs which were extremely small but particularly this was so for *Lepilemur edwardsi.* *L.edwardsi* travelled one third of the distance travelled by *A.occidentalis* each night and it appeared to be the distance travelled by the two species which accounted for the large difference in the relative energy cost of locomotion.

1 Introduction

1.1 General Introduction

An animal needs to move in order to feed, reproduce, find shelter, defend its territory, and escape from predators. Locomotion is thus one of the basic requirements of survival. A comprehensive study of locomotor ecology therefore, concerns all these aspects of an animal's lifestyle which constitute possible selective pressures on the locomotor system. Important factors include the animal's use of supports, the structure of the environment, and the home range (and hence the distance travelled on a daily basis), the characteristics of the food eaten and its pattern of dispersal in the environment, and, associated with these factors, the energy available in potential food stuffs, and the energy used in locomotion.

Locomotor studies on extant species have, typically, three essential components. These are 'form', 'function' and 'biological role' (Bock & von Wahlert 1965). 'Form' is the physical structure of the organism, and is closely associated with the 'function' of a 'feature'. The latter is its action, 'how it works'. The 'biological role' of a feature has been defined as 'the action or the use of the faculty by the organism in the course of its life history' (Bock & von Wahlert 1965). Study of form and function alone does not predict the biological role of a feature: it indicates only the way it works. For a complete understanding of the feature under investigation, it is essential to observe the animal in its natural environment.

The first of these three components, the form, is relatively easy to ascertain; the study normally involves morphologists making discrete measurements of parts of the organism. The second component, the function, is more complicated. Its study requires an understanding of the biomechanics of the musculoskeletal system and how the latter responds biologically to the external and internal forces engendered by the animal's activity. The third component, the biological role, is notoriously inexact and time-consuming to study due to the considerable complexity of the ecosystem in which the animal exists (*e.g.* Crompton 1980). It is necessary to study function in the context of the physical characteristics of the environment in which it must perform, as well as the behavioural and adaptive role that this activity plays within the animal's *habitus.* This study, therefore, attempts to address questions relevant particularly to the biological role and lifestyle of the animals, in the overall context of the comprehensive tripartite approach outlined above.

Primates show one of the most diverse locomotor repertoires of all orders of mammals. There are no flying or burrowing primates, but within the order there are animals which amongst other modes run, walk , knuckle-walk, leap, hop bipedally, brachiate, arm-swing, climb, and use quadrumanual suspension (Jouffroy 1989). Use by primates of both the terrestrial and arboreal biotope implies considerable behavioural flexibility. Within the three-dimensional canopy, accurate and precise locomotion is a necessity. Hence, sophisticated techniques of crossing discontinuities in the canopy have evolved. They involve complex interactions of muscles within the primate limb, which latter exerts and experiences compressive and tensile forces, depending on the substrate and mode of locomotion, and which is constantly subject to gravity. Several factors are likely to effect the 'biological role' of the locomotor system in the natural environment. These are on the one hand the 'locomotor type' of the animal, its body mass and hence its food choice; and on the other, the structure of the habitat, and the available energy it can supply.

It has only been in the second half of this century that comprehensive studies relating form, function and biological role of locomotion have been undertaken. Considerable quantitative data on primate locomotion were provided by Fleagle's (1976 a,b, 1978) study of locomotion of the siamang and two sympatric leaf monkeys in Malaysia, which related locomotion to habitat use.

Other quantitative studies on locomotion and posture of primate species around this time documented *Colobus guereza* (Morbeck 1977, Rose 1978), *Papio cynocephalus* (Rose 1977), *Ateles geoffroyi* (Richard 1970, Mittermeier 1978), *Alouatta palliata* (Richard 1970) and *Ateles paniscus* (Mittermeier 1978).

In 1967, Napier and Napier published a classification of locomotor modes, and in the same year Napier and Walker defined a locomotor category called vertical clinging and leaping (VCL). This was a mode of locomotion seen typically in prosimians utilizing vertical supports, in which the body is upright, where leaping is propelled by powerful extension of the hind limbs, and where leaping involves a rotation in the vertical plane, so that the animal faces the landing substrate towards the end of flight. It has since been demonstrated that this category is an oversimplified 'umbrella' term describing various degrees and modes of leaping specialization. Oxnard *et al.* (1990), amongst others, pointed out that VCL contains three distinct morphological and behavioural groups: an indriid group including *Avahi* and *Lepilemur*, all of the Cheirogaleinae together with some galagos; and a tarsier group with *Galago alleni* and *G.senegalensis* [1]. The cheirogaleine group can be regarded as morphologically unspecialized for leaping. The indriid group is morphologically specialized, with elongation of the femur, whereas the tarsier group is specialized by an elongation of the foot. Both species in this study, *Lepilemur edwardsi* and *Avahi occidentalis*, fall into the same subgroup of the VCL category. The majority of quantitative field studies of vertical clinging and leaping have been on the African prosimians, including *Galago alleni*, *G. demidovii* and *Euoticus elegantulus*, (Charles-Dominique 1971, 1974, 1977); *G. senegalensis* and *G.crassicaudatus* (Bearder 1974, Bearder & Doyle 1974, Crompton 1980, 1984); and in South-East Asia, the tarsiers, *Tarsius bancanus*, *T. syrichta* and *T.spectrum* (Niemitz 1979 a,b,c,

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[1] While I am aware of Olson's (1981) revision of Galaginae, a more conservative taxonomy is preferred here for the sake of clarity for non-primatological readers. Hence, *Galago moholi* is considered as *Galago senegalensis* and *Otolemur crassicaudatus* is considered as *Galago crassicaudatus*.

1984 a,b, 1985; MacKinnon & MacKinnon 1980; Crompton & Andau 1986,1987). Data on the Malagasy prosimians are restricted to a broad review of *Lepilemur* (Charles-Dominique & Hladik 1971) and work by Demes on *Propithecus* (in press). **Chapter Two examines the locomotor behaviour of two of the most specialized primate leapers in Madagascar, as yet unstudied: *Avahi occidentalis*, the smallest of the Indriidae, and *Lepilemur edwardsi*.**

Body size is one of the most influential factors on locomotor morphology. Within a locomotor category, the mechanical demands on primate morphology differ according to body size. However, Demes and Günther (1989) demonstrated that a large specialized leaper, such as *Indri*, is not simply a scaled-up version of a small specialized leaper, such as a tarsier. In this study, the effect of raw body size is controlled for, since both species are of a similar body mass: 800 - 1000 g for *Lepilemur edwardsi* (Razanahoera-Rakotomalala 1988) and 700 - 900 g for *Avahi occidentalis* (Razanahoera-Rakotomalala 1981). Differences in body mass also have far reaching effects in terms of energy cost of locomotion and metabolism. Due to the allometric relationships of metabolism originally set out by Kleiber (1961), the metabolic rate changes with body mass with a power of 0.75. This power factor does vary slightly with food choice, but will be essentially similar for both species in this study since they are both folivorous. This implies that both species are using approximately the same amount of energy to sustain their base metabolism.

Considerable emphasis in this study is placed on habitat utilization and support availability (**Chapter Three**). Several previous studies have related locomotor behaviour of arboreal vertebrates, particularly primates, to habitat structure. Quantitative studies have related frequencies of locomotor behaviour to the types of substrates used, often focusing on sympatric species (Morbeck 1977; Mittermeier 1978; Fleagle 1978; Fleagle & Mittermeier 1980; MacKinnon & MacKinnon 1980; Gittins 1983; Crompton 1984; Garber 1984; Harcourt & Nash 1986b). However, while forest structure has been qualitatively described by quantifying the frequency of occurrence of trees of different sizes and by measuring tree crown diameters, most researchers have not related these variables to preferences in support use (Gautier-Hion *et al.* 1981, Whitten 1982, Crompton 1984, Ganzhorn 1989). In particular, despite Crompton's (1983) thorough examination of locomotion and support use by *Galago senegalensis* and *Galago crassicaudatus* in their natural environment, he was not able to ascertain whether the animals were using the most available support types or if they were choosing specific support categories. However, Cannon and Leighton (1994) used a quantitative method of assessing support utilization in relation to support availability when studying gibbons and macaques. This ratio is called Jacob's D after Jacob's (1974) method of quantifying food preference. While Cannon and Leighton were thus the first to take support availability into account, the present study is the first in which this parameter has been calculated for the 'vertical clinging and leaping' locomotor mode.

Comparisons of lifestyles between sympatric species are more robust than for allopatric species. Sympatry of the species studied is an important factor as it controls for the various external effects of the environment on the behaviour of the animals; the study species are exposed to the same external factors (such as habitat structure). There have been several studies on sympatric species of primates (*e.g.* Sussman 1974; MacKinnon & MacKinnon 1978; Fleagle 1978; Fleagle & Mittermeier 1980; Cannon & Leighton 1994), but only a very few studies have been done on nocturnal primates (*e.g.* Charles-Dominique 1977; Hladik *et al.* 1980; Harcourt & Nash 1986b). Hutchinson (1957) suggested that sympatry may be ecologically 'permitted' when there are interspecific differences in resource utilization. Since both *Lepilemur edwardsi* and *Avahi occidentalis* are nocturnal, at least partial temporal overlap of their niches occurs, and hence, resource utilization and/or spatial separation are the most likely modes of niche differentiation.

Most primates restrict their activity to a familiar delimited area of the environment in which they live. This utilized area has been termed the 'home range' (DeVore 1963; Jay 1965). Distances travelled in moving through the home range to new feeding sites, to defend territories, or to find mates, are a necessary prerequisite to understanding some of the energetic demands made by locomotion on the animals' energy budget. The importance of complete all night 'follows' (or at least, coverage of all hours of the night) was highlighted by Crompton (1987) who found home ranges of *Tarsius bancanus* to be much larger than those expected from partial night follows and sleeping site locations. Social behaviour will also influence distances travelled within the home range. For example, strongly territorial animals may wish to patrol the borders of their territories to protect them from incursions by other individuals or groups. There have to date been no all night 'follows' made on either *Lepilemur edwardsi* or *Avahi occidentalis* to ascertain true home range sizes and nightly travel routes. **Chapter Four of this study investigates home range size and social behaviour of these previously little known species.**

Feeding behaviour may directly influence locomotor morphology. A rare posture or locomotor behaviour used in accessing food may be critical in the animal's adaptability to the environment and hence future survival. But indirect influences may be even more important. Hladik (1978) has argued that folivory is the most specialized of all primate food choices. To begin with, digestion of cellulose is only possible through fermentation by gut bacteria (Bauchop 1978). Further, the time taken for fermentation of leaves by bacteria is assumed to be the same in primates of any size, and fermentation rate should be proportional to gut volume, and so to body mass. As metabolic rate is proportional to body mass$^{0.75}$ (Kleiber 1961) there will be a physiological threshold in body size, below which no mammal will be an obligate folivore. Kay & Hylander (1978), found that for primates this threshold appears to be 700 g. Both species in this study feed on leaves and, since their body mass is approaching Kay's threshold, it is reasonable to expect that dietary energy will be a limiting factor in the lifestyle of these animals. **Chapter Five of this study examines the food choice of both species, feeding postures, and preferences of branch type from which food acquisition takes place.**

Vertical clinging and leaping is regarded as an expensive mode of locomotion because it is non-cyclic, and there is no possibility for conservation of energy between jumps (Crompton *et al.*1993). A folivorous diet is thought to depress the metabolic rate slightly (McNab 1978) but a small body mass will limit energy gained from leaf eating (Hladik 1978). It seems highly probable that the energy cost of locomotion is a strong influencing factor on the locomotor ecology of the two small folivores in this study. **The last chapter (Chapter Six) in this study therefore combines the knowledge gained from all the previous chapters to estimate the energy cost of locomotion for the two species using biomechanical principles.**

This study, therefore, is a comparison of the locomotor ecology of two species of lemur, both of which are nocturnal, and folivorous, are vertical clingers and leapers with the same morphological adaptation for leaping, have a similar body mass (and consequently are expected to have a similar metabolism); and coexist in the same forest environment. This is the first time that such a comprehensive study has been made to ascertain comparative locomotor ecology and the influence of diet, home range, distances travelled, energy cost of locomotion, support availability and habitat utilization on the locomotor strategies of two similar species.

1.2 Biodiversity of Madagascar and the Conservation Status of Malagasy Lemurs

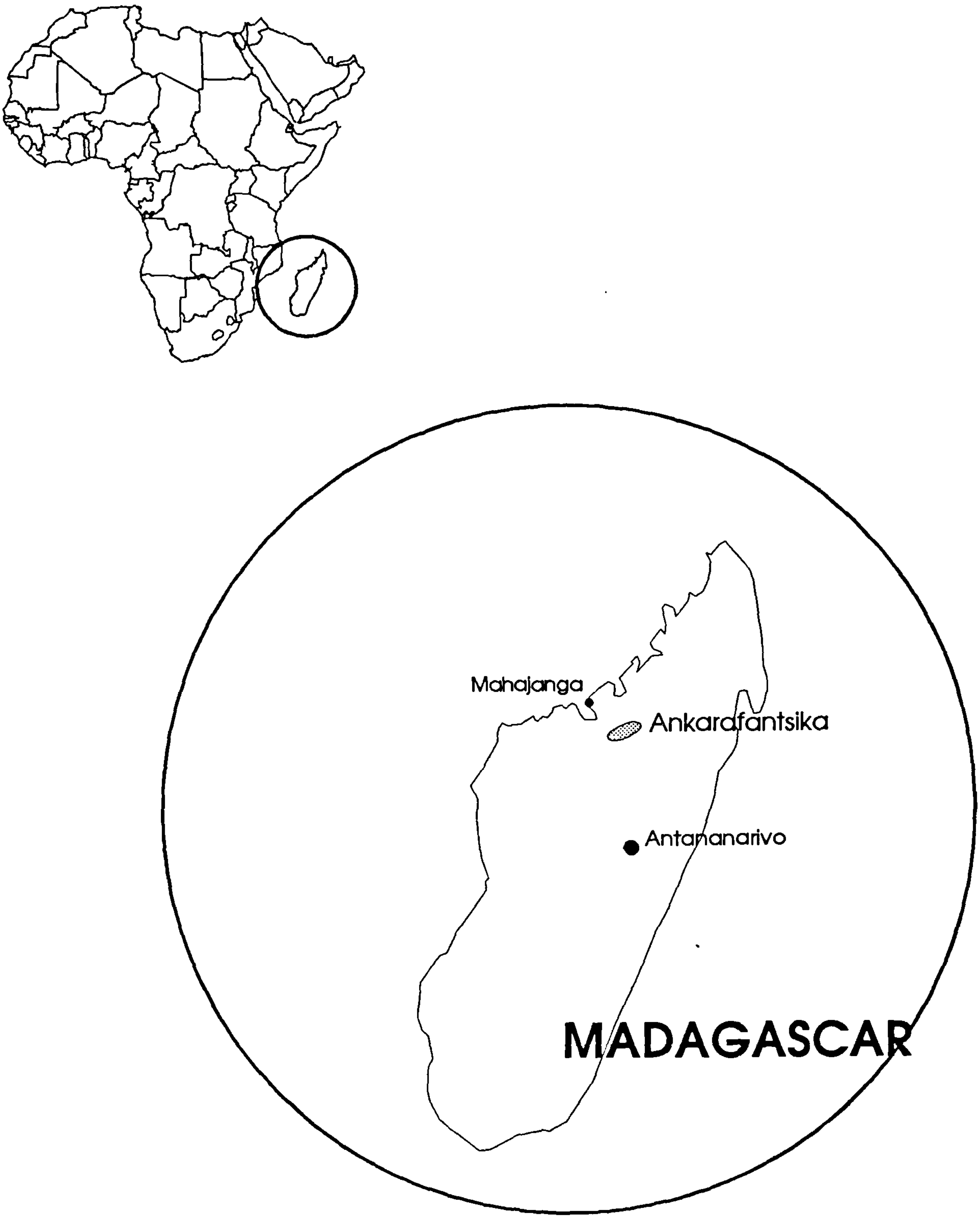
Madagascar, the fourth largest island in the world, is found off the east coast of Africa, split from the mainland by the Mozambique Channel (Fig 1.2a). The island falls into the tropical zone, but climate and habitat is very variable over the island. The country has been divided into two floristic zones, a moister eastern region with rainforest, and a dry western region which is more seasonal. Both of these zones contain a wide range of habitats (White 1983). Madagascar is thought to have broken off from mainland Africa as long as 200 million years ago and mammals may have drifted across on rafts until around 40 million years ago, when increasing width of the Mozambique Channel may have finally prevented further rafting (IUCN/UNEP/WWF 1987).

The relative isolation of Madagascar has made the flora and fauna on the island unique: for example, all nonhuman primate species and 94 % of the tree species are endemic (IUCN/UNEP/WWF 1987). The number of mammals and birds is relatively low on the island and there are only five orders exist there: Rodentia, Carnivora, Chiroptera, Insectivora and Primates. Despite this, Madagascar is fourth on the World List of primate species and its level of endemism is unsurpassed (Mittermeier *et al.* 1992). Madagascar is thus one of the world's highest primate conservation priorities, with more endangered and vulnerable primate species than any other country (Mittermeier *et al.* 1992).

The human population of Madagascar was estimated to be 11.9 million in 1992 and is predicted to rise to 31.7 million by 2025 (PRB 1993). The population is predominantly rural, and depends on agriculture for survival. The people clear forest by 'tavy' or 'slash and burn' where the forest is cleared and burnt to allow plantation of crops such as rice, manioc and maize. After one or two years, the soil becomes degraded and is left fallow for grazing cattle. However, due to the very poor nature of the soil, grazing can only be sustained for 2 or 3 years and eventually, the land is colonised by indigestible grasses or left bare. Repeated burning of grazing land to encourage tender new grass for cattle often spreads to forested areas. Slash and burn is thus a major threat to the forests of Madagascar (Harcourt & Thornback 1990). Some logging occurs, but most of the remaining forest outside protected areas is found on steep slopes and valleys which cannot be reached by machinery. Madagascar has 11 Nature Reserves, 6 National Parks, and 23 Special Reserves which cover a wide range of ecosystems throughout the country, but there is little effective protection for the reserves, and many exist essentially on paper (Nicoll & Langrand 1989).

Madagascar has lost at least 14 lemur species in the last 2000 years since the arrival of humans on the island (Mittermeier *et al.* 1992). However, two new species have been discovered in the last five years (*Propithecus tattersalli* and *Hapalemur aureus*), one has been rediscovered (*Allocebus trichotis*) and the aye-aye (*Daubentonia madagascariensis*), has been found to have a much wider distribution than was originally thought (Mittermeier *et al.* 1992). An action plan for the conservation of lemurs was proposed by Mittermeier *et al.* (1992) in an attempt to spearhead conservation priorities for the years 1993-1999. A recent political change in the country may be the key to gain the political will necessary, (given foreign aid ,and sound development projects), to turn the action plan into a reality.

Fig. 1.2a Madagascar in relation to Africa and the position of the study site, Ankarafantsika



1.3 Study Species

1.31 *Lepilemur edwardsi*

Lepilemur edwardsi, (see Fig. 1.3a), is commonly regarded as a member of the monogeneric sub-family Lepilemurinae, which along with the extinct sub-family Megaladapinae makes up family Lepilemuridae (Petter *et al.* 1977a, Tattersall 1982, Fleagle 1988). This lemur has a mean body mass of 800 - 1000 g (Razanahoera-Rakotomalala 1988) and is characterized by the lack of permanent upper incisors, an unusual articulation between the mandible and the skull (Tattersall & Schwartz 1974), large digital pads on its hands and feet, and a large caecum.

Considerable variation in karyotype within Lepilemurinae has been used to separate the genus *Lepilemur* into six (Dutrillaux 1988), or seven species (Petter *et al.* 1977a), each of which exists in a distinct geographical zone. *Lepilemur edwardsi* is found in the dry deciduous forests of western Madagascar. It has been described as nocturnal, solitary and folivorous (for review see Harcourt & Thornback 1990). Two or three individuals sleep in tree holes during the day but move separately at night (Petter *et al.* 1977a, Albignac 1981b). Albignac (1981b) reported the usual home range to be 1 ha but some home ranges are larger for particular males. He (1981b), considered that overlap occurs between individual home ranges and reported an aggressive territorial display associated with calling and branch shaking (Albignac 1981b). The predominant diet of *L.edwardsi* was thought to be leaves (young or old), flowers, fruit and fleshy seeds (Razanahoera-Rakotomalala 1981, Albignac 1981b and Ganzhorn 1988). Population density, estimated from ten transect walks along 1.7 km of trail at Ampijoroa (Ganzhorn 1988), was reported to be 57 ± 22 individuals per square kilometre. *L.edwardsi* is threatened by habitat loss, due to forest fires (usually started by the local population to clear land for cattle grazing) (Nicoll & Langrand 1989). It is classified as 'rare' in the IUCN Red Data Book (Harcourt & Thornback 1990).

1.32 *Avahi occidentalis*

The genus *Avahi* was previously considered to be represented by a single species, *Avahi laniger*, the smallest member of the family Indriidae. However, the species is distributed in two distinct areas. Individuals of each area can be distinguished morphologically, and so the species has been held to contain two sub-species, *A.laniger laniger*, the eastern form and *A.laniger occidentalis*, the western form (Hill 1953b, Petter *et al.* 1977a). Rumpler *et al.* (1990), confirmed this hypothesis by cytogenetic study of the two forms. It was shown that *A.laniger occidentalis* has a karyotype that differs from *A.laniger laniger* by three chromosomal rearrangements. Such a configuration is considered to strongly reduce male fertility, and so the former has been re-classified as a distinct species, *Avahi occidentalis* (Rumpler *et al.* 1990, see Fig. 1.3b).

The distribution of *A.occidentalis* is restricted to the north west of Madagascar. Albignac (1981a,b) reported the animals to be monogamous, living in small family groups of between two and five individuals. The groups were composed of an adult male and female and young of up to two years of age (Albignac, 1981a,b). Territory size was reported to be 3 - 4 ha with considerable overlap between the ranges of neighbouring families (Albignac 1981a,b). Very little inter-group aggression has been reported and few territorial calls have been recorded (Razanahoera-Rakotomalala 1981, Albignac 1981b). The animals eat only young leaves and buds (Razanahoera-Rakotomalala 1981, Albignac 1981a) and were recorded to eat twenty different species over an undefined time period (Razanahoera-Rakotomalala 1981). Razanahoera-Rakotomalala (1981) reported this species to feed at the beginning and end of the night with a long period of rest between 21.30 and 00.30 hours and to travel only 180 m a night. Ganzhorn (1988) estimated population densities of 67 ± 66 individuals per square kilometre at Ampijoroa. The main threat to this species is habitat destruction due to clearance of forest by fire to clear land for cattle grazing (Mittermeier *et al.* 1992). *Avahi occidentalis* is more endangered than *Lepilemur edwardsi* and is classified as 'vulnerable' in the IUCN Red Data Book

(Harcourt & Thornback 1990).

Fig. 1.3a *Lepilemur edwardsi*

Fig. 1.3b *Avahi occidentalis*

2 Locomotion

2.1 Introduction

The first studies of animal locomotion date back to the 4th century B.C. Aristotle referred to flying, swimming, quadrupedal and bipedal locomotion in his treatises (quoted in Jouffroy 1989). In the 2nd century, Galen made several dissections of macaques which were the basis for his book 'Myologie' (Sarton 1954). Galileo (1638) and Borelli (1680) initiated the study of biomechanics, during the seventeenth century, applying some physical laws and equations to animals. Borelli (1680) paid particular attention to the muscles of posture which acted to counteract gravity (Jouffroy *et al.* 1983) and also discussed the kinematics of leaping. In the eighteenth century some travelling naturalists wrote anecdotes on primate locomotion (Bosman 1704, for the potto; Seba 1734, for the loris and Buffon 1770, for the apes). In the second half of the nineteenth century, serial photography of moving objects was employed for analysis of gaits by Marey (1887) and Muybridge (1881). Later that century, and early into the next, improvements in engineering and technology allowed further study of biomechanics.

Until very recently, study of the primate anatomy in the twentieth century has been primarily concerned with the form rather than the function of animals. Nayak (1933) compared galago and loris anatomy, Jouffroy (1962) studied lemuroid limb anatomy and Uhlmann (1968) the primate hip and thigh. Attempts to classify primate locomotion were made by Mollison (1911), who used body proportions as guidelines for creation of five locomotor groups. These groups, described on the basis of notes from travellers, were runners, climbers, leapers, brachiators and bipeds. The groups' names were based on the prominent form of locomotion. Associations with function were minimal. But Pauwels, in 1949, examined anatomy explicitly in terms of biomechanics, with emphasis on the overall locomotor system. Gray (1944) integrated the mechanical properties of materials with their employment in dynamic events in reference to the locomotor system of tetrapods. But Maynard Smith and Savage (1956) were the first fully to relate locomotor anatomy and its function to biomechanics. They suggested that the physical laws of biomechanics were a strong influence on the biological variation of animals.

In the first half of this century, locomotor studies of primates in the wild were restricted entirely to descriptive work, and this information was collected as part of overall behavioural studies (Yerkes & Yerkes 1929; Carpenter 1940). It was only later that quantitative data on locomotion were collected for their own sake. Avis (1962) studied colobine locomotion in captivity, using arranged supports, and compared the results with data from pongids and atelines. Unfortunately insufficient time was allowed in the experimental enclosure to enable the animals to display their complete locomotor repertoire. Napier (1963) used slow-motion film and observation to correct the incomplete results of Avis by showing that colobines do, *contra* Avis, arm-swing. Napier's study was particularly important in that its emphasis was not on locomotor morphology but locomotor behaviour. During the Second World War multivariate statistics were considerably developed and in 1958 Ashton and Oxnard began to use these techniques to examine the general relationship between structure and function in living species. Functionally related measurements were used in multivariate analysis to derive morphological groupings. Ashton and Oxnard (1964) related these groupings to behavioural categories established on the basis of anecdotal observations of travellers. The paucity of behavioural information unfortunately lead to misleading identifications of *Propithecus* as suspensory and *Galago* as quadrupedal.

In 1967, an important field study was undertaken by Ripley who went to Sri Lanka to study *Presbytis entellus*. The study involved observations of substrate types, use and distribution of branches, and locomotion within and between populations. It was not a quantitative study, but was a major step forward in taking into account form and function, and also the biological role of locomotion in primates. As we have noted, in the same year, Napier and Napier's (1967) classification of primate locomotion divided primates into three broad categories: vertical clingers and leapers (VCL); quadrupedalists (with subcategories), and brachiators (also with subcategories). Each class was categorised on the basis of anatomical features, one of which was the 'intermembral index'. This is the ratio of

$$\frac{\text{Length of the humerus + length of the radius}}{\text{Length of the femur + length of the tibia}} \times 100$$

Intermembral indices of vertical clingers were found to lie between 53 and 64 (short arms and long legs) compared to 67 - 106 for quadrupeds and 104 - 145 in brachiators (long arms and short legs). Napier and Walker (1967) went on to describe VCL in more detail as a locomotor behaviour common to many prosimians such as tarsiers, galagos and mouse lemurs, as well as some of the larger lemurs and indriids. Cartmill (1972) however noted that some of the morphological characteristics used by Napier and Walker did not distinguish VCL from non-VCL animals. It was pointed out by Oxnard (1973) that there were two (now three, Oxnard *et al.* 1990) separate morphological groups within 'VCL'. He showed that several different mechanical modalities were being utilized for this behaviour. The three groups Oxnard *et al.* (1990) recognised are (to recap): an indriid group associated with *Lepilemur*, a galagine group (with the exception of *Galago senegalensis* and *G.alleni*) linked with *Varecia, Eulemur* and all species of Cheirogaleinae; and lastly a tarsier group linked with *G.senegalensis* and *G.alleni*. *Hapalemur* and *Lemur catta* are linked with both of the first two groups mentioned. The galagine group are essentially morphologically unspecialized leapers. Hind-limb proportions and myology suggest biomechanics differ between the 'indriid leapers' and the 'galago-tarsier' group. Both are morphologically specialized, but in different ways. The 'indriid group' have elongation of the femur (the 'extended femur system') while there is elongation of the foot (the 'extended calcaneum lever system') in the 'galago-tarsier' group (Lessertisseur 1970; Cartmill 1972; Oxnard 1973; 1983, Stern &

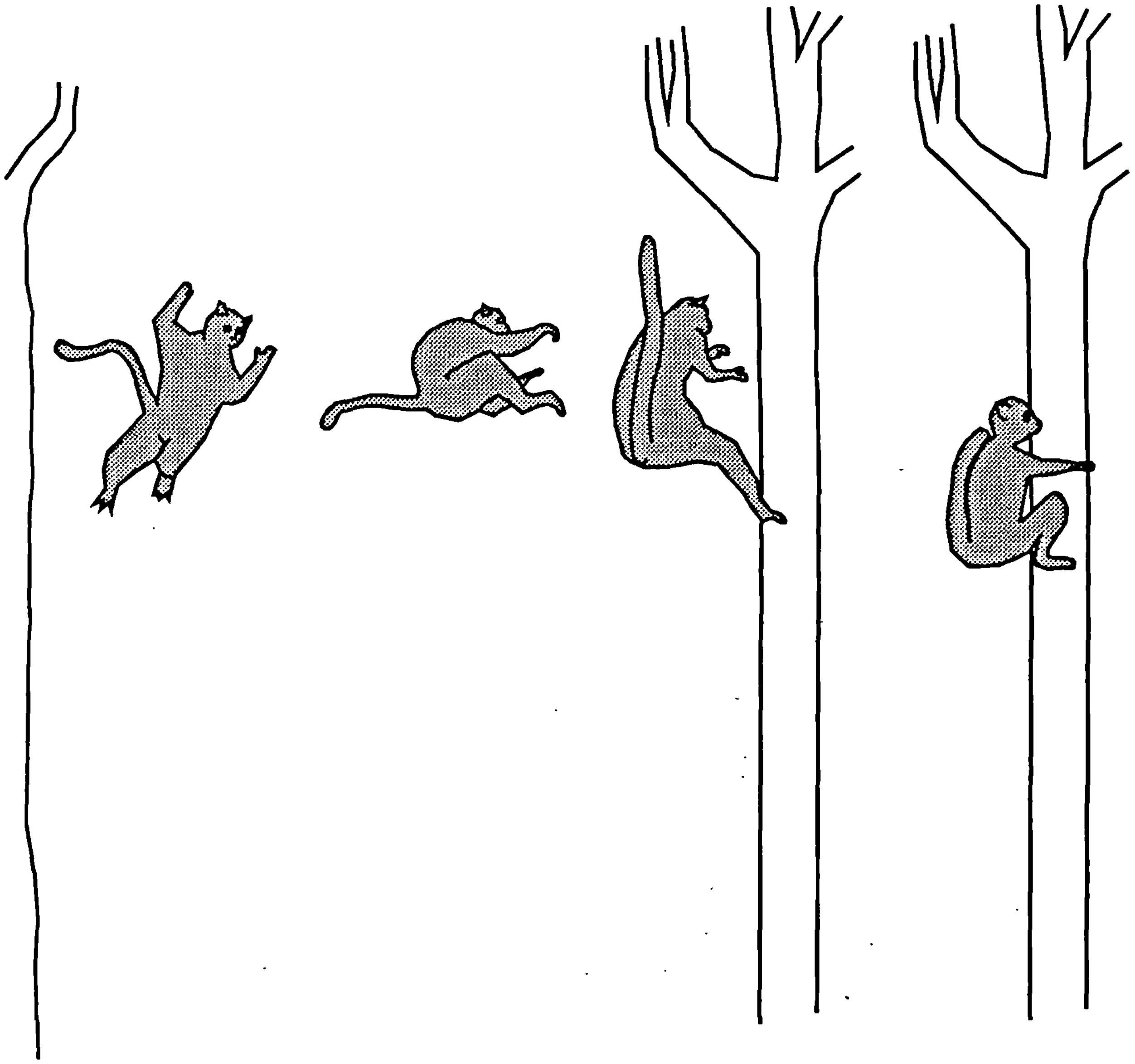
Oxnard 1973; Oxnard *et al.* 1981; Jouffroy *et al.* 1982). However there are some animals such as *Galago crassicaudatus* and *Cheirogaleus* which have elongated calcanea (Jouffroy & Lessertisseur 1979; Jouffroy & Günther 1985) but show less frequent leaping in the wild (Crompton 1984; Crompton *et al.* 1993) than would be expected from their morphology. It is a regrettable fact that multivariate statistics is still used primarily as a tool to aid what amounts to pigeon-holing of locomotor behaviour into certain morphological groups. In reality, most primates show a broad repertoire of locomotor patterns that have different frequencies of performance. But it is to be expected that a relatively infrequent behaviour may yet be of considerable evolutionary significance if it is ecologically adaptive. In this context, Grand (1984) has emphasized that locomotor categories should not be regarded as 'frozen' and will often require further analysis; and Day (1979) stated that multivariate analysis of the same data may lead to different results because a decision of the statistician which variables are important and which to drop is essentially a subjective one.

Classification aids human understanding of the natural world but it should never be forgotten that it is a human imposition. In this study *Lepilemur edwardsi* and *Avahi occidentalis* both fall into the VCL category and the 'elongated femur' group, so they are under similar mechanical constraints in terms of both body design and the most frequent locomotor behaviour. However, *Lepilemur* has also been described as a '*slow clinger and leaper*' (*sic*) (Richard & Dewar 1991), which utilizes predominantly vertical supports. Nevertheless, for ease of reading, both species will be referred to as 'vertical clingers and leapers' (VCL) in this text but it is important to bear in mind that the accompanying biomechanical adaptations are very distinct.

The arboreal biotope is a highly mixed environment in which to move. It presents a vast array of substrates (branches, twigs, trunks *etc.*) all at varying heights, diameters, and angles. Further, arboreal primates require precise coordination of limb movements as a consequence of the interrupted nature of the substrate (Peters & Preuschoft 1984). In this environment, jumping or leaping is a favoured mode of locomotion. The most specialized of the jumping primates are the prosimians, which are often thought to leap from predominantly vertical, or near vertical, supports. A 'typical' resting posture for a specialized 'vertical clinger and leaper' such as *Lepilemur* or *Avahi*, is to grip a vertical, or near vertical, substrate with the body upright, its legs bent at the hip and knee, and grasping the branch with its feet (Fig. 2.1a). When such an animal leaps it pushes off the branch with a powerful extension of the hind limbs not unlike that in the leaping movement of a frog, and the trajectory tends to be flat (Sellers 1992). The animal will then twist up to 180° in mid air to face the landing tree. Tarsiers and galagines use a highly accelerated flicking of the tail to brake the axial rotation of the body (Niemitz 1984b). The changing mass moments of inertia of the tail can stop or accelerate the axial rotation of the body. For example a tail-flick of 120 degrees can reduce or increase the body rotation by approximately 35 degrees (Peters and Preuschoft 1984). Prior to landing, the angular motion of the animal bends its trunk ventrally, lowering the tail, and flexes the hips forward extending the lower limbs out to meet the substrate. The tail is lifted during the final part of the leap to raise the body to an upright position for landing. On touch-down the legs are allowed to bend thereby losing kinetic energy (kinetic energy lost = force x distance), until eventually the hands make contact and motion ceases (see Fig.2.1a). Split second adjustment to the leap is often required, for example , when *Propithecus* lands on the spiny stems *of Alluadia* trees in the 'thorny forests' of Madagascar.

Leaping from vertical supports may give very high speeds with relatively flat trajectories. Two of the best studied VCL species are *Galago alleni* and *Tarsius bancanus* (Charles-Dominique 1971, 1974, 1977; Niemitz 1979a, b, c, 1984a,b and Crompton & Andau 1986). They can jump up to fifteen times their own body length without losing height. Powerful leaps, with high take-off speeds, are provided with energy by hind-limb muscle contractions but it is also possible that some of the kinetic energy in landing is stored as elastic energy in hind-limb tendons, and returned to the next take-off This has been observed in dogs, gazelles and kangaroos (Alexander 1977, 1984; Alexander & Vernon

Fig. 2.1a Diagram of *Lepilemur* leaping (after Oxnard *et al.* 1990)



1975) but has not yet been observed in small mammals. Bennet-Clark (1967,1975) showed that fleas and locusts store the energy necessary to attain the distance jumped as elastic strain energy, which is released during take-off (rather like a pogo stick). Bennet-Clark (1977) also suggested another mechanism, 'catapult action'. In the prosimian *Galago senegalensis* he proposed that elastic tendons in the legs of this species were stretched by limb flexion before the leap and the energy then released on take-off, but no such mechanism has yet been found. However, while both *G.senegalensis* and *Tarsius spectrum* show a considerable degree of morphological adaptation to leaping, it should be noted that behaviourally, they are less specialized (*i.e.* more eurytopic and *r*-selected), than the stenotopic, k-selected *Tarsius bancanus* which occupies a niche in more stable and diverse ecologically tropical rainforest (Crompton 1989).

The height and range of a jump are determined by its initial velocity. This is in turn determined by the kinetic energy imparted to the animal by its muscles. The forces these can make available for leaping are a function of cross-sectional area. On the other hand, the force necessary to give a particular acceleration is proportional to body mass (Alexander 1985). The above imply that with increased body size, animals will take longer to reach the same velocity. But for small leapers with absolutely smaller limb dimensions, accelerations take place over shorter distances. Therefore, larger accelerations are needed by small animals to reach the same take-off speed. But because forces are proportional to muscle cross-sectional area, they are bigger in proportion to body mass for smaller animals. As small animals, we would expect that both *Lepilemur edwardsi* and *Avahi occidentalis* should have increased hind limb length in order to reduce the forces necessary for take-off. This is indeed what we find.

A large amount of experimental data has been collected on prosimian leaping, but the overwhelming majority of studies have concentrated on the morphological function of the long-footed leapers (such as tarsiers and galagos). For instance, papers by Jouffroy *et al.* (1984) and Jouffroy and Günther (1985) emphasized the difference between five of the galagos and three of the tarsier species. They examined how the elongation of the calcaneum affected the load arm of the musculoskeletal levers of the foot and the biomechanics of the system. To leap with a short acceleration phase, there needs to be a strong propulsive force at take-off. This requires considerable muscle force from, in particular, the quadriceps femoris and the triceps surae. The quadriceps femoris constitutes one third of the muscle mass of the thigh in *Galago senegalensis* and *Galago crassicaudatus*, and the triceps surae one-third of the muscle mass of the calf (Grand 1977). The action of these muscles has been further analyzed by Jungers *et al.* (1983) using telemetered electromyography (EMG). Günther (1985) using high speed cinematography and a three-component forceplate, has shown that for *Galago senegalensis* the peak force for leaping is 35 N (which is about thirteen times the body weight) and work is 22 J/kg . Preuschoft *et al.* (1979) indicated roughly the same values for *Tarsius bancanus* (27J/kg), and, indeed, Alexander and Vernon (1975) give similar values for the hopping of kangaroos (19 J/kg). Further work by Preuschoft (1985) showed that for several species of primate taking off and landing on a horizontally-mounted force-plate, higher forces are transmitted, in a shorter interval, at landing than at take-off.

2.2 Aims

A full understanding of the ecological factors associated with locomotor behaviour is essential for comprehension of an animal's lifestyle and the evolution of primate locomotion. Without field data, the correlations between morphology and behaviour are at best incomplete. Further, we have seen that while our knowledge of the saltatory prosimians of mainland Africa and South-East Asia is quite well developed, very little is known of the locomotion of the specialized Malagasy leapers. This study is therefore intended to examine the function and, importantly, the biological role, of the locomotion of *Lepilemur edwardsi* and *Avahi occidentalis*. Both have the extended femur system (Oxnard 1973, Oxnard *et al.* 1981 and Oxnard *et al.*1990) rather than the extended calcaneum lever system found in the more extensively studied galagos and tarsiers.

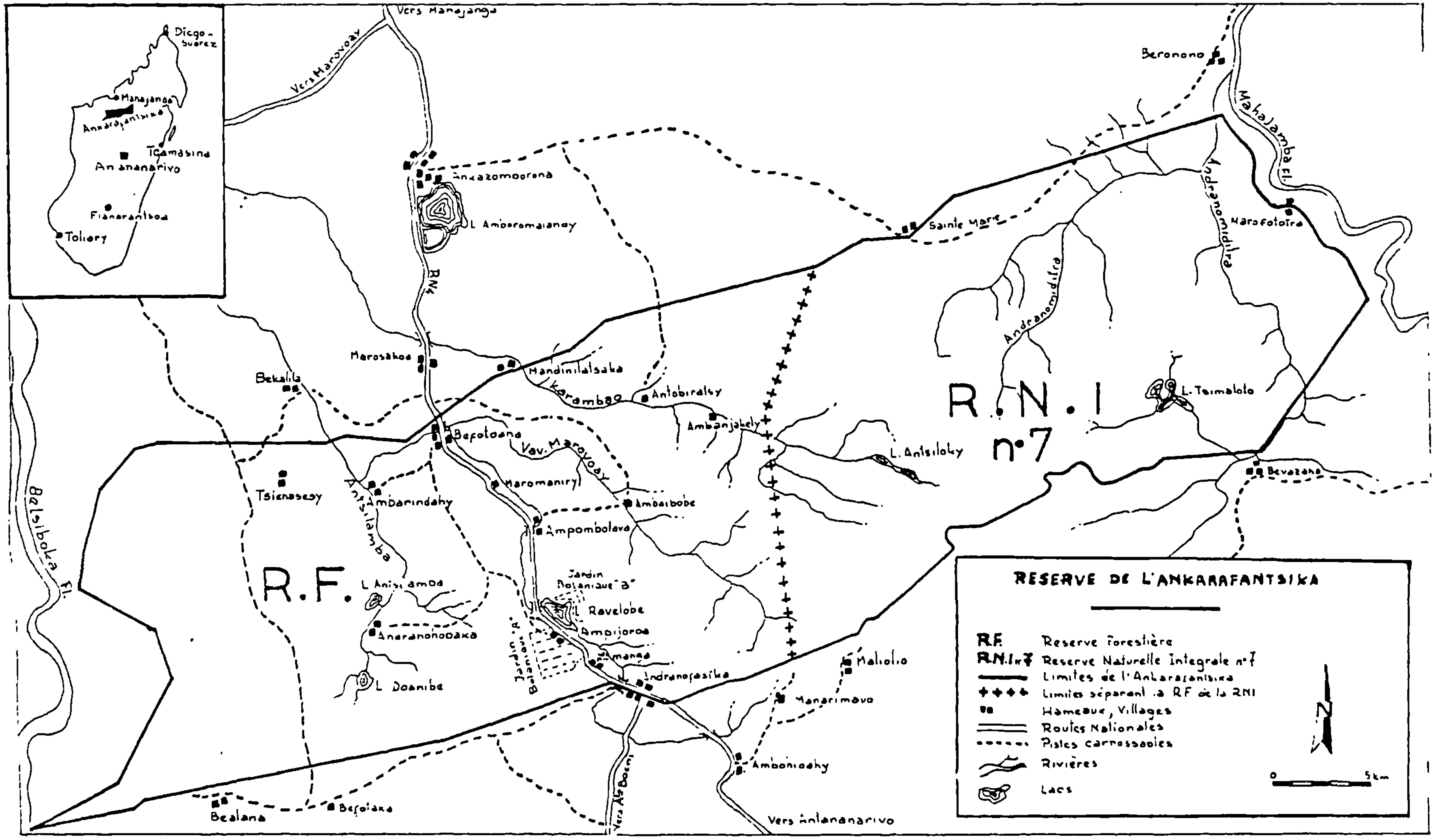
2.3 Methods

2.31 Study site

The forestry station of Ampijoroa is located in the Strict Nature Reserve of Ankarafantsika at 16°15'S, 46°48'E; 120 km south of the town of Mahajanga (Fig 2.3a). The forest is 250 m above sea level. It consists of a sandy plateau on which grows a very diverse forest; with predominantly *Dalbergia, Commiphora* and *Hildegardia* species (IUCN/UNEP/WWF 1987). Ninety seven percent of the rainfall occurs from November to April. Total rainfall is between 1000 and 1500 mm a year, and the maximum rainfall occurs in January. There is a marked dry season of around six months in which there is very little rainfall. The mean annual temperature is 26°C with a maximum of 39.3°C and minimum of 11.4°C during the months of October and June respectively (Ramangason, 1986). The relatively high temperatures throughout the year cause high rates of evaporation, and, combined with low rainfall for six months, this encourages leaf loss in a large proportion of the trees (Ramangason, 1988). As a consequence of the variation in soil quality, topography and edaphics, there is an extreme variability in size and density of individual trees within the forest, giving a mosaic effect not unlike that observed in rainforest (Whitmore 1984). Vertical stratification is different in each element of the mosaic, but the forest is typically dense with considerable undergrowth and lianas (Nicoll & Langrand 1989). The height of the canopy varies from 15-25 m in the valleys and in well watered areas, to 5-10 m on the sandy plateau.

The fauna at Ampijoroa is also rich, including seven sympatric species of lemur: *Propithecus verreauxi coquereli, Eulemur fulvus fulvus, Eulemur mongoz, Avahi occidentalis, Lepilemur edwardsi, Cheirogaleus medius* and *Microcebus murinus*. Of the seven species only *P.verreauxi coquereli* is diurnal; *E.fulvus fulvus* and *E. mongoz* are cathemeral (active day or night); whilst the remaining four are all nocturnal.

Fig. 2.3a: Map of the reserve of Ankarafantsika, showing the position of Ampijoroa and Jardin Botanique A (after Projet PNUD/UNESCO Ankarafantsika).



An area of forest called 'Jardin Botanique A' was selected as the study site on the basis of its accessibility and on account of the knowledge of the head forester that both *Avahi occidentalis* and *Lepilemur edwardsi* were living sympatrically there. Within Jardin Botanique A, there were paths previously cut into the forest, but these were no longer equidistant or perpendicular as a result of regrowth which had occurred in the sixties. These paths were therefore ignored in this study. A rectangular quadrat of 300 m by 350 m was set up without any trail cutting using nylon forestry tagging-tape. The quadrat was measured in relation to a concrete reserve boundary marker and to a large East-West main trail on which it lay. Walking on a compass bearing, with a measuring tape, a piece of flagging was left at ten metre intervals. A distance and compass bearing on each gave a grid reference in relation to the concrete marker (for example, flag N50W200 was 50 metres north and 200 metres west of the marker).

2.32 Field Methods

The field work took place between May 1992 and October 1993 (see list of dates in Appendix 3). Four *Lepilemur edwardsi* and four *Avahi occidentalis* were captured within the quadrat. The *L.edwardsi* studied were simply the individuals that it was possible to capture, but two *A.occidentalis* were selected and caught from each of the two families that lived in the quadrat, one of each sex from each family. The *L.edwardsi* were difficult to catch. Catching was done by noosing them with a piece of cord round the neck and then coaxing them from their sleeping holes. Due to their aggressive nature and to ease handling, an intra-muscular injection of 0.1 ml of the muscle relaxant ketamine hydrochloride was given in the thigh muscle. The *A.occidentalis* were caught using either a blow pipe or an air-gun (Telinject, France) to propel darts (Distinject, Switzerland) which injected a drug on hitting the target. The darts contained 0.2 ml of ketamine hydrochloride, double the dose used for a direct intra-muscular injection, because it was found that not all of the drug was injected by the darts, and this dose was therefore the minimum quantity required for an effective result. The animals were shot in the muscular part of the thigh or buttock. The animals were rehydrated regularly with a pipette of water given orally. Full recovery occurred within an hour. Each individual was weighed and morphometric data were taken on body size and limb length. A permanent ear notch was made for future identification. Each animal was fitted with an emitter (Biotrack, Wareham) with an unique frequency. The assembly had an average mass of about 3 % of the body mass, well under the maximum recommended (15% of the animals body mass (Kenward 1987)) and the transmitters had a range of approximately 120m. They were soldered to an antenna and battery at the field-station and encased in dental acrylic to prevent the animal from damaging the assembly. This whole unit was then sewn onto a piece of silk backed leather to prevent chaffing of the animals' skin and clipped into place using metal fasteners. Originally, the emitter was fitted round the waist as a belt, to be as close to the animal's centre of gravity as possible. However, after several attempts this arrangement was found to be unsatisfactory, since the animals were able to rub off the assembly. The emitter was then fitted in 'rucksack' fashion on the back of the animal, with soft nylon webbing holding it in place (Fig. 2.3b). This proved to be satisfactory position as it did not interfere with feeding and grooming (as it would if placed round the neck) and, as it was also closer to the animal's centre of gravity, this helped to prevent extra locomotor stresses (Zimmerman *et al.* 1975; Kenward 1987). The animals were released on recovery and left undisturbed for the next two nights.

An animal selected was located in late afternoon (Fig. 2.3c). Using a directional Yagi antenna attached to a portable receiver (Mariner Radar) which gave its strongest signal when the animal was directly in front of the observer, with a second peak directly behind. The subject was then tracked all night using this equipment and a halogen caving head lamp, until it reached its sleeping site for the next day. The animals showed considerable indifference to the observer,

Fig. 2.3b *Lepilemur edwardsi* with the transmitter fitted rucksack style

Fig. 2.3c Radio-tracking late afternoon to locate the study animal at Ampijoroa

to the extent that it was possible to approach as close as 5 m from the animals without disturbing them. A red filter was originally used on the lamps, but the light was then found to be too weak to pick up the animal's eye-shine at long distances. The lamps were however, used with dipped beam when close to the subject.

Using a cassette recorder, an observation was recorded each time there was a change in the locomotion or behaviour, (that is an observation or activity bout started and ended with a change in behaviour) (Doran 1992). Records were made of the time; the activity which had occurred; estimated heights; diameter and angle of the initial and terminal supports and bout length (*i.e.* distance travelled horizontally if any) along with any anecdotal observations (Table 2.3a). The locomotion was classified into different classes based on preliminary observations of typical behaviour (Table 2.3b). Three resting postures were also classified. A bout was recorded only when there was a change in behaviour so the basic descriptive data describe frequencies of bouts recorded and not the time during which the animal was engaged in this activity, thus, a resting bout that continued for three hours would be classed as one bout. Considerable self-training in estimating heights, diameters and distances between trees was performed during daylight hours. In this, heights of specific trees were estimated and the estimates compared to the actual heights of these trees as measured using a sextant and a tape. Similarly, horizontal distances were estimated, and then measured using a tape measure; and branch diameters estimated using the known size of the limbs and hands of the target species as size referents.

The animals were followed for a complete night, from the time they left their sleeping sites to the time that they returned. The data were then transcribed the following day into note books. No particular order was observed in those individuals followed but at least four all night 'follows' were made on each individual, with a total of over 560 hours of observations over an eighteen month period.

Table 2.3a: Brief definitions of the locomotor categories

Locomotor mode	Definition
Sitting	The animal is stationary and supported under the rump by a branch.
Standing	The animal is stationary and upright on its hind limbs.
Clinging	The animal is stationary and upright, holding onto a vertical or angled support with both fore and hind limbs.
Leaping	Locomotion in which the animal jumps across discontinuities using an extension of the hind limbs.
Climbing	Quadrupedal locomotion where height is gained or lost by moving up or down a single support which is vertical or angled.
Walking	Quadrupedal locomotion where at least three limbs are in contact with a substrate which has an oblique or horizontal orientation.
Foliage Crossing	Quadrupedal locomotion where the animal reaches across a gap to grasp foliage with one hand and then slowly moves the other limbs across one at a time.
Cantilevering	Holding on to the substrate with a pair of limbs only, and leaning across a gap to grasp another support.
Frog Hopping	Jumping along the same support with the fore limbs as well as the hind limbs in contact with the support at the beginning and end of the leap.
Kangaroo Hopping	Jumping along the same support with only the hind limbs in contact with the support at the beginning and end of the leap.
Running	Fast quadrupedal locomotion where only two limbs are in contact with a support, which is oblique or horizontal.
Ladder Climbing	Climbing up or down a number of supports of any orientation using the supports like rungs of a ladder.
Other	Any locomotion category not specifically described above.

Table 2.3b: Schedule of Locomotor Observations

1	Date
2	Animal species and identification number
3	Time
4	Locomotor/postural mode
5	Initial support diameter: foliage (0<0.5 cm); small (0.5-5 cm); medium (5.1-10 cm); large (10.1-15 cm); enormous (15+ cm)
6	Initial support orientation:vertical (81-90°); angle (46-80°); oblique (11-45°); horizontal (0-10°)
7	Terminal support diameter (cm)
8	Terminal support orientation (see 6)
9	Initial height (m)
10	Terminal height (m)
11	Horizontal distance travelled (m)
12	Activity: rest; travel; feed;auto-groom; allo-groom; other
13	Continuous from previous observation (yes or no)
14	Number, direction and distance of calls of the same species
15	Position of feed tree

2.33 Data Analysis

Data were entered and checked using dBASE III (Ashton Tate 1985) where unreasonable values for variables could be easily identified and corrected. The data were then imported into two computer packages,SPSSPC+ (Norusis/SPSS Inc. 1990) and SAS for Microsoft Windows (SAS Institute Inc. 1993), for analysis.

Comparisons of locomotion and species have been carried out using the 'Proc GLM' statement in SAS for an unbalanced analysis of variance (anova) (Milliken & Johnson 1992). This compensates for the unequal numbers of observations for the different combinations of 'class' variables in the model statement. That is, in these data, there are different numbers of observations for each species and different numbers of observations for each locomotor mode. Typical class variables in this analysis are species and locomotor mode. Proc GLM calculates F ratios with degrees of freedom, sums of squares and the probability of obtaining that particular F ratio. Least mean squares (LSM) were calculated within the GLM procedure along with the corresponding standard errors (SE). The type III hypothesis was used to calculated sums of squares (SS). The latter is the most useful hypothesis to adjust all the terms in the model so that each observation is treated equally (i.e.'treatments' with more observations are more influential (Milliken & Johnson 1992)).

Significant differences were obtained between classes when the value of the probability (P) was less than 0.05. For example, a model would be a comparison between the mean horizontal distance of each locomotor mode and between species. If the model in the Proc GLM statement was significant, one would then look to see if there was any 'interaction' between the parts of the model (*i.e.* is there an overall significant difference between species only, between locomotor modes only, or is there a significant interaction where one species may have a significantly longer leaping bout, and the other species a significantly longer climbing bout). If F ratios were significant at the 0.05 level, the data were further analyzed using oneway analysis of variance, within the Proc GLM command of SAS or SPSS/PC+, (for example, comparing locomotor modes in only one species).

Unplanned comparisons between classes, *(i.e.* comparisons where the results were not previously predicted), were tested using Scheffé's test (Milliken & Johnson 1992). Least mean squares are estimations of the class marginal means that would be expected had the data been balanced. Standard errors are estimates of the true standard deviations of a population mean necessary when one is referring only to a sample mean. The coefficient of variation is given, and this is used to allow comparison of the relative amounts of variation in populations having different means. Analysis of covariance was used in some cases to test a dependant variable for homogeneity among group means after the means had been adjusted for an independent variable (Sokal & Rohlf 1981). An example of this would be to see if there was still a significant result in a comparison of change in height of leaping when the effect of horizontal distance of the leap is removed. If there was no significance, in this case, it would imply that any significance in height change was due to the horizontal distance of the leap.

2.4 Results

2.41 Statistical Tables

The results of the statistical tests are summarised in this section. The detailed tables of statistical results are found in Appendix 1.

Table 2.4a: Descriptive statistics for *Lepilemur edwardsi* for each locomotor mode

Locomotor mode	N	Horizontal distance LSMean	Standard Error LSMean	P
leap	876	1.36	0.0	0.00
climb	593	0.71	0.0	0.00
walk	147	0.73	0.1.	0.00
foliage cross	81	0.29	0.1	0.00
cantilever	3	0.88	0.5	0.07
frog hop	37	0.70	0.1	0.00
kangaroo hop	5	0.48	0.4	0.20
other	54	0.38	0.4	0.37
run	14	1.13	0.2	0.00
ladder climb	2	0.15	0.6	0.80

Table 2.4a: This table shows: the least mean square (LSMean) of the horizontal distance travelled for a bout of each locomotor mode; the standard error of the least mean square and the probability (P) of this mean occurring in comparison to the LSMean of other locomotor bouts.

Table 2.4b: Descriptive statistics for *Avahi occidentalis* for each locomotor mode

Locomotor mode	N	Horizontal distance LSMean	Standard Error LSMean	P
leap	1050	1.51	0.0	0.00
climb	365	0.51	0.0	0.00
walk	130	0.77	0.1	0.00
foliage cross	39	0.39	0.1	0.00
cantilever	18	0.51	0.2	0.01
frog hop	35	0.70	0.1	0.00
kangaroo hop	15	0.66	0.2	0.00
other	13	0.53	0.2	0.02
run	39	0.90	0.1	0.00
ladder climb	50	0.11	0.1	0.36

Table 2.4b: This table shows: the least mean square (LSMean) of the horizontal distance travelled for a bout of each locomotor mode; the standard error of the least mean square and the probability (P) of this mean occurring in comparison to the LSMean of other locomotor bouts.

Table 2.4c: Descriptive statistics for oneway analysis of variance comparing height gained in each locomotor mode for *Lepilemur edwardsi*

Locomotor mode	N	Height gained LSMean	Standard Error LSMean	P
leap	193	0.66	0.0	0.00
climb	263	0.71	0.0	0.00
walk	44	0.38	0.1	0.00
foliage cross	8	0.30	0.2	0.10
cantilever	2	1.00	0.4	0.00
frog hop	30	0.51	0.1	0.00
kangaroo hop	3	0.60	0.3	0.04
other	1	0.30	0.5	0.56
run	5	0.75	0.2	0.00
ladder climb	1	0.75	0.5	0.14

Table 2.4c: This table shows: the number of bouts of each locomotor mode (N); the least mean square (LSMean) of the height gained for a bout of each locomotor mode; the standard error of the least mean square and the probability (P) of this mean occurring in comparison to the LSMean of other locomotor bouts.

Table 2.4d: Descriptive statistics for oneway analysis of variance comparing height lost in each locomotor mode for *Lepilemur edwardsi*

Locomotor mode	N	Height lost LSMean	Standard Error LSMean	P
leap	681	0.04	0.0	0.00
climb	353	0.73	0.0	0.00
walk	101	0.17	0.1	0.02
foliage cross	74	0.10	0.1	0.23
cantilever	1	0.30	0.7	0.67
frog hop	5	0.04	0.3	0.90
kangaroo hop	2	0.05	0.5	0.92
other	2	0.15	0.5	0.76
run	9	0.53	0.2	0.02
ladder climb	1	0.50	0.7	0.48

Table 2.4d: This table shows: the number of bouts for each locomotor mode (N); the least mean square (LSMean) of the height lost for a bout of each locomotor mode; the standard error of the least mean square and the probability (P) of this mean occurring in comparison to the LSMean of other locomotor bouts.

Table 2.4e: Descriptive statistics for oneway analysis of variance comparing height gained in each locomotor mode for *Avahi occidentalis*

Locomotor mode	N	Height gained LSMean	Standard Error LSMean	P
leap	142	0.64	0.1	0.00
climb	139	0.79	0.1	0.00
walk	37	0.27	0.1	0.00
foliage cross	2	0.65	0.4	0.11
cantilever	3	0.30	0.3	0.36
frog hop	2	0.45	0.1	0.00
kangaroo hop	11	0.87	0.2	0.00
other	3	0.27	0.3	0.42
run	17	0.41	0.1	0.00
ladder climb	26	0.59	0.1	0.00

Table 2.4e: This table shows: the number of bouts for each locomotor mode (N); the least mean square (LSMean) of the height gained for a bout of each locomotor mode; the standard error of the least mean square and the probability (P) of this mean occurring in comparison to the LSMean of other locomotor bouts.

Table 2.4f: Descriptive statistics for oneway analysis of variance comparing height lost in each locomotor mode for *Avahi occidentalis*

Locomotor mode	N	Height lost LSMean	Standard Error LSMean	P
leap	897	0.48	0.0	0.00
climb	244	0.84	0.0	0.00
walk	93	0.13	0.1	0.07
foliage cross	36	0.10	0.1	0.07
cantilever	14	0.01	0.2	0.94
frog hop	10	0.00	0.2	1.00
kangaroo hop	4	0.58	0.3	0.09
other	12	0.15	0.2	0.44
run	22	0.29	0.1	0.05
ladder climb	24	0.73	0.1	0.00

Table 2.4f: This table shows: the number of bouts for each locomotor mode (N); the least mean square (LSMean) of the height lost for a bout of each locomotor mode; the standard error of the least mean square and the probability (P) of this mean occurring in comparison to the LSMean of other locomotor bouts.

Table 2.4g: Descriptive statistics for the locomotor modes of *Lepilemur edwardsi*

Locomotor mode	Diameter of first support (N, mean ± std.error)	Diameter of second support (N, mean ± std.error)	Height of first support (N, mean ± std.error)	Height of second support (N, mean ± std.error)	Horizontal distance (N, mean ± std.error)
leap	1177, 3.733± 0.08	979, 3.373± 0.89	1188, 5.018± 0.05	984, 4.398± 0.7	970, 1.229± 0.03
climb	644, 3.642± 0.13	615, 3.635± 0.14	653, 5.376± 0.08	629, 5.15± 0.09	511, 0.818± 0.04
walk	157, 2.707± 0.19	148, 2.324± 0.17	162, 5.817± 0.16	151, 5.591± 0.19	151, 0.709± 0.06
foliage cross	82, 3.290± 0.28	82, 2.729± 0.40	82, 5.263± 0.20	82, 5.590± 0.19	81, 0.293± 0.02
cantilever	3, 3.000± 0.1.00	3, 2.667± 0.88	3, 5.467± 0.88	3, 6.033± 1.30	3, 0.883± 0.32
frog hop	39, 5.231± 0.72	38, 4.500± 0.69	39, 5.283± 0.28	38, 5.382± 0.35	34, 0.765± 0.23
kangaroo hop	5, 3.800± 0.72	5, 2.300± 0.46	5, 5.620± 0.71	5, 5.960± 0.63	5, 0.480± 0.16
other	10, 2.750± 1.14	3, 2.00± 0.00	10, 6.858± 0.82	5, 4.670± 1.22	3, 0.500± 0.25
run	14, 4.000± 1.37	14, 3.500± 0.79	14, 6.364± 0.63	14, 6.291± 0.55	14, 1.129± 0.18
ladder climb	2, 4.500± 1.50	2, 2.500± 0.50	2, 5.250± 0.25	2, 5.375± 0.88	1, 0.300

Table 2.4h: Descriptive statistics for the locomotor modes of *Avahi occidentalis*

Locomotor mode	Diameter of first support (N, mean ± std.error)	Diameter of second support (N, mean ± std.error)	Height of first support (N, mean ± std.error)	Height of second support (N, mean ± std.error)	Horizontal distance (N, mean ± std.error)
leap	1514, 3.308± 0.05	1186, 2.994± 0.06	1527, 6.103 ± 0.50	1193, 5.222± 0.07	1164, 1.361± 0.03
climb	400, 3.080± 0.12	398, 3.062± 0.11	405, 6.596± 0.10	401, 6.160± 0.11	278, 0.664± 0.05
walk	141, 2.436± 0.13	137, 2.453± 0.14	145, 7.026± 0.16	137, 6.693± 0.21	135, 0.742± 0.05
foliage cross	39, 2.539± 0.25	36, 1.958± 0.25	40, 7.600± 0.36	39, 7.362± 0.41	39, 0.385± 0.05
cantilever	18, 2.033± 0.29	18, 1.889± 0.23	18, 6.611± 0.56	18, 6.983± 0.41	18, 0.508± 0.06
frog hop	25, 3.171± 0.31	35, 2.871± 0.25	35, 6.537± 0.27	35, 6.857± 0.27	33, 0.747± 0.08
kangaroo hop	15, 3.267± 0.59	15, 2.833± 0.47	15, 6.013± 0.31	15, 6.500± 0.32	15, 0.660± 0.14
other	19, 1.032± 0.12	16, 1.656± 0.33	19, 7.326± 0.47	17, 6.471± 0.78	12, 0.571± 0.11
run	47, 2.596± 0.19	38, 2.737± 0.21	47, 6.447± 0.27	39, 6.733± 0.27	38, 0,925± 0.08
ladder climb	52, 2.750± 0.44	50, 2.430± 0.23	55, 6.500± 0.21	50, 6.367± 0.22	10, 0.535± 0.12

Table 2.4i: General Linear Model (GLM) test of significance between species for each variable (** = 0.05, *** = 0.01 level)

Locomotor mode	Diameter of first support	Diameter of second support	Height of first support	Height of second support	Equal height and height lost	Height gained	Horizontal distance
leap	***	***	***	***	***		***
climb	***	***	***	***	***		***
walk			***	***			
foliage cross			***	***			**
cantilever							
frog hop	***	***	***	***			
kangaroo hop							
other	***						
run							
ladder climb							

Table 2.4i: NB: equal height and height lost refers to the vertical distance maintained or lost in a locomotor bout. This was separated from height gained to aid locomotion energy cost calculations because gaining height (and hence doing work against gravity) is more expensive than sustaining or losing height. Height gained is the vertical distance gained in a locomotor bout. Horizontal distance is the horizontal distance covered in a locomotor bout.

Table 2.4j: Frequency (%) of use of the first support orientation for each locomotor mode in *Lepilemur edwardsi*

Locomotor mode	N	vertical (%)	angled (%)	oblique (%)	horizontal (%)	fork (%)	foliage (%)
leap	1191	52.4	28.6	6.8	3.7	6.6	1.9
climb	654	47.5	31	7.1	2.9	9.1	2.5
walk	162	13.6	32.7	29	11.1	5.6	8
foliage cross	82	29.6	39.5	14.8	1.2	12.3	2.5
canti-lever	3	33.3	66.7	0	0	0	0
frog hop	40	41	38.5	7.7	0	12.8	0
kangaroo hop	5	0	40	0	0	60	0
other	11	27.3	36.4	0	18.2	9.1	9.1
run	14	0	50	28.6	14.3	0	7.1
ladder climb	2	0	0	0	100	0	0

Table 2.4k: Frequency (%) of use of the second support orientation for each locomotor mode in *Lepilemur edwardsi*

Loco-motor mode	N	vertical (%)	angled (%)	oblique (%)	horizontal (%)	fork (%)	foliage (%)
leap	1191	56.4	29.2	6.4	3.4	2.4	2.2
climb	654	49.4	29.5	5.2	1.8	11.1	3
walk	162	8.1	32.9	32.2	15.4	5.4	6
foliage cross	82	37.8	34.1	12.2	6.1	1.2	7.4
canti-lever	3	100	0	0	0	0	0
frog hop	40	37.5	33.3	11.1	2.8	11.1	0
kanga-roo hop	5	20	40	20	0	0	20
other	11	0	66.7	33.3	0	0	0
run	14	7.1	42.9	28.6	14.3	7.1	0
ladder climb	2	0	100	0	0	0	0

Table 2.4l: Frequency (%) of use of the first support orientation for each locomotor mode in *Avahi occidentalis*

Loco-motor mode	N	vertical (%)	angled (%)	oblique (%)	horizontal (%)	fork (%)	foliage (%)
leap	1537	48.1	26.2	14.1	6.3	4.4	1
climb	408	42.5	25.9	11.4	5.7	10.2	4.2
walk	145	10.4	12.5	45.1	20.1	7.6	4.2
foliage cross	40	32.5	30	17.5	10	2.5	7.5
canti-lever	37	8.6	37.1	31.4	17.1	5.7	0
frog hop	15	6.7	73.3	13.3	0	6.7	0
kanga-roo hop	15	6.7	73.3	13.3	0	6.7	0
other	19	0	5.3	47.4	36.8	5.3	5.3
run	47	14.9	27.7	51.1	4.3	2.1	0
ladder climb	55	12.7	9.1	43.6	25.5	3.6	5.5

Table 2.4m: Frequency (%) of use of the second support orientation for each locomotor mode in *Avahi occidentalis*

Locomotor mode	N	vertical (%)	angled (%)	oblique (%)	horizontal (%)	fork (%)	foliage (%)
leap	1537	51.9	29.1	13.1	3.3	1.7	0.8
climb	408	55.9	24.1	5	4.2	7.3	3.4
walk	145	2.3	9.2	51.5	33.1	3.8	0
foliage cross	40	30.8	20.5	15.4	23.1	2.6	7.7
cantilever	18	27.8	16.7	38.9	16.7	0	0
frog hop	37	22.9	17.1	28.6	25.7	5.7	0
kangaroo hop	15	33.3	33.3	33.3	0	0	0
other	19	26.7	0	46.7	26.7	0	0
run	47	2.6	23.1	66.7	7.7	0	0
ladder climb	55	12	24	36	24	4	0

2.42 Description of the locomotion of *Lepilemur edwardsi*

Leaping

Leaping made up 55.1% of the locomotion bouts that were recorded (Fig. 2.4e,g). For these animals, it was typical to jump from a resting posture. The animal gripped the vertical, or near vertical, substrate with the body upright. The legs were bent at the knee and hip, and the branch was grasped with the feet. When the animal leapt, it pushed off the branch with a powerful extension of the hind limbs not unlike the leaping movement of a frog. The animal did not take-off facing the direction of the landing tree, but typically had to twist up to 180° in mid flight, before extending the lower limbs out to meet the substrate. On 'touch down', the legs were rapidly and acutely flexed until subsequently the fore limbs touched down. The hands were typically used only as props and played no part in propelling the leap. The tail was stretched out horizontally whilst in flight, but was brought up to an upright position on landing, to orientate the body into an upright posture. Leaps could also be 'ricochetal', where the animal immediately leapt off again to another substrate, apparently using its legs as springs (although it is unclear whether there is any possibility for elastic storage in the tendons of the hind limbs). While mean leap length of *Lepilemur edwardsi* was 1.36 m, the maximum leap distance recorded for this species was 7 m. (A very impressive leaper!). The animal leapt from a branch of an average 3.7 cm in diameter, to one 3.4 cm in diameter, and from a mean height of 5 m to 4.4 m, losing height as it leapt. The preferred orientation of the branches from which it jumped was vertical. Indeed, 52.4% of the supports it leapt from were vertical (81-90^0) and a further 28.6% were angled (46-80^0), (Table 2.4j). 56.4% of the landing branches were also vertical and 29.2% angled (Table 2.4k).

Fig. 2.4a Frequency histogram of the first support orientation for each species

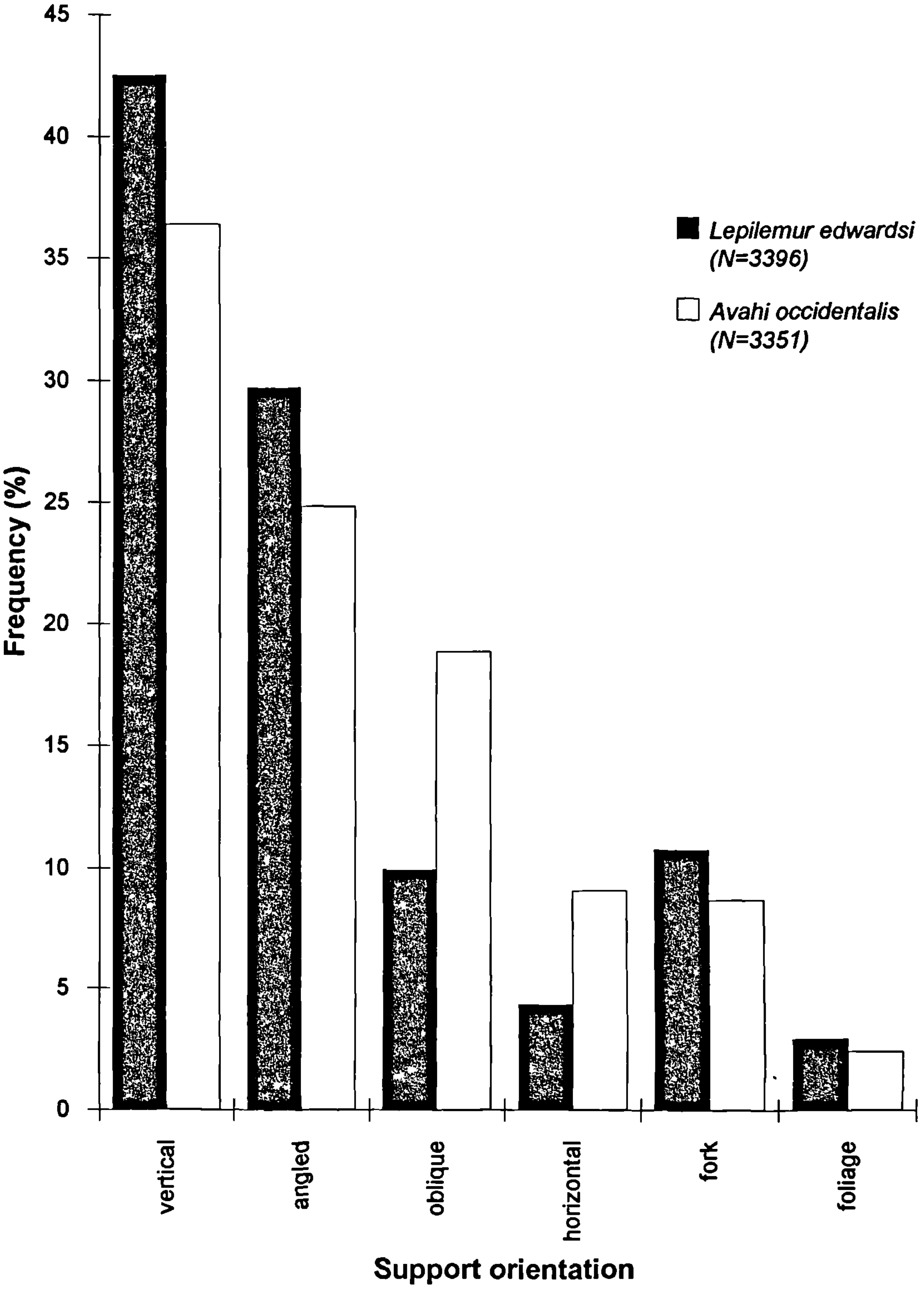


Fig. 2.4b Frequency histogram of the second support orientation for each species

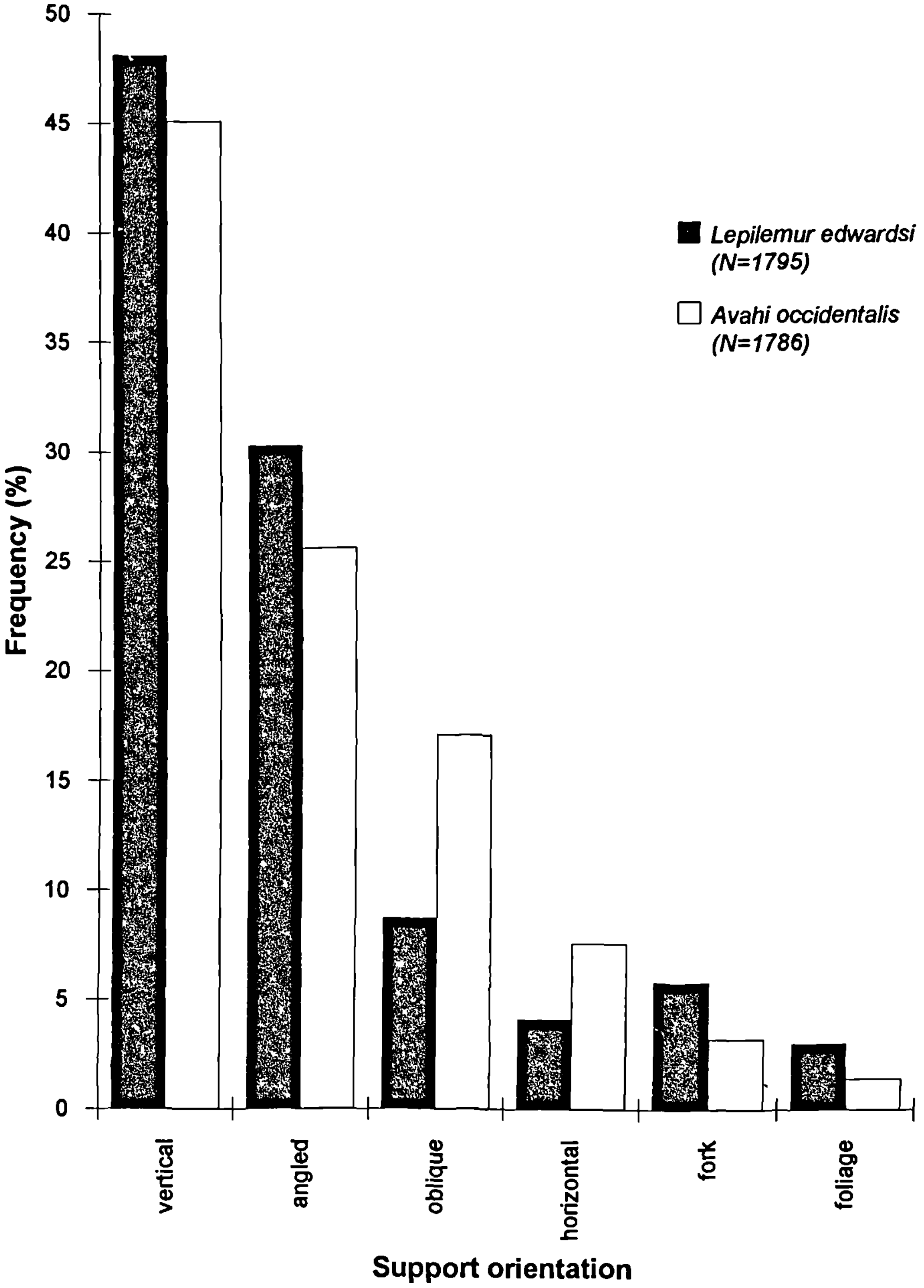


Fig. 2.4c Mean height of each locomotor mode on the first support for each species

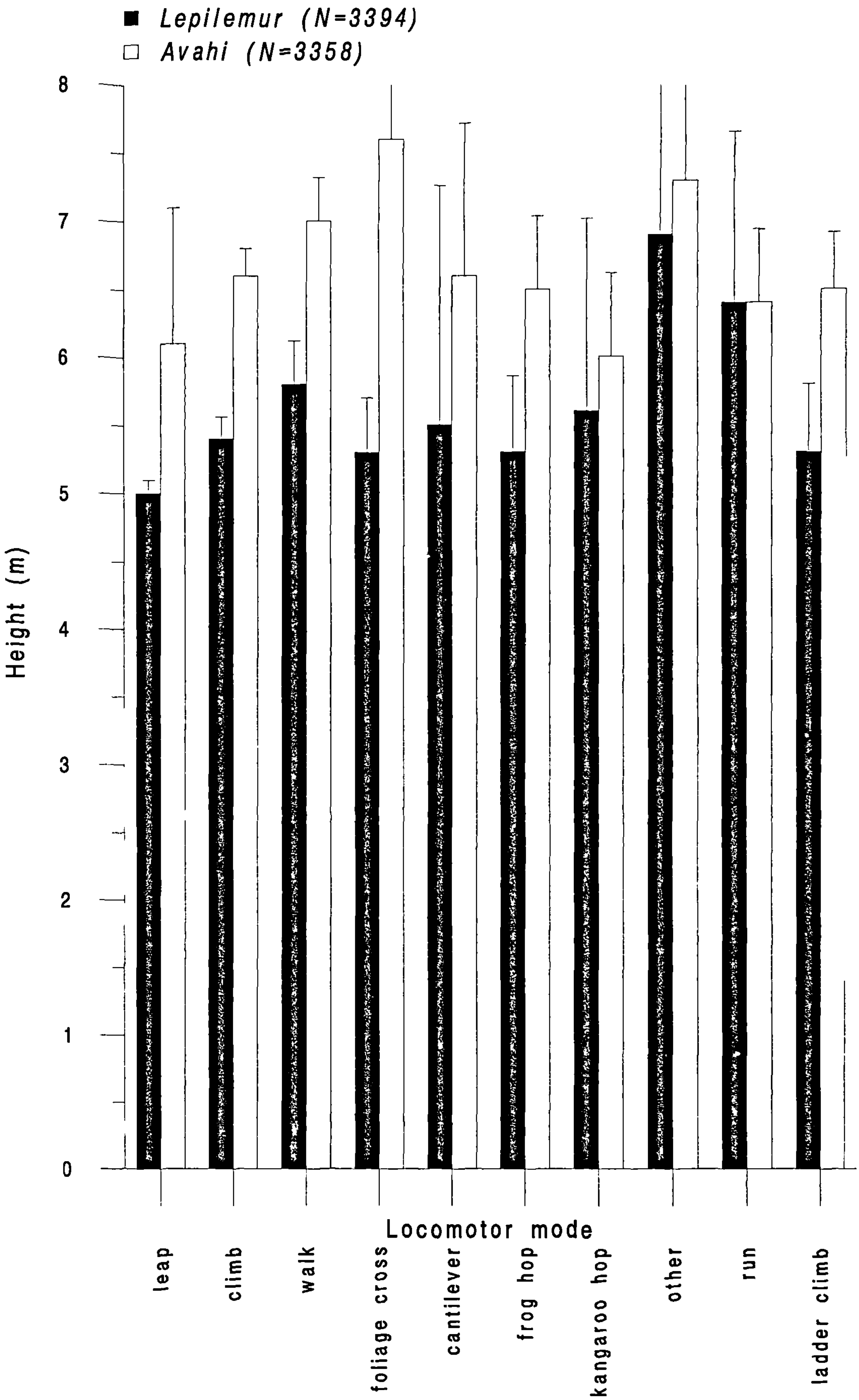


Fig. 2.4d Mean height of each locomotor mode on the second support for each species

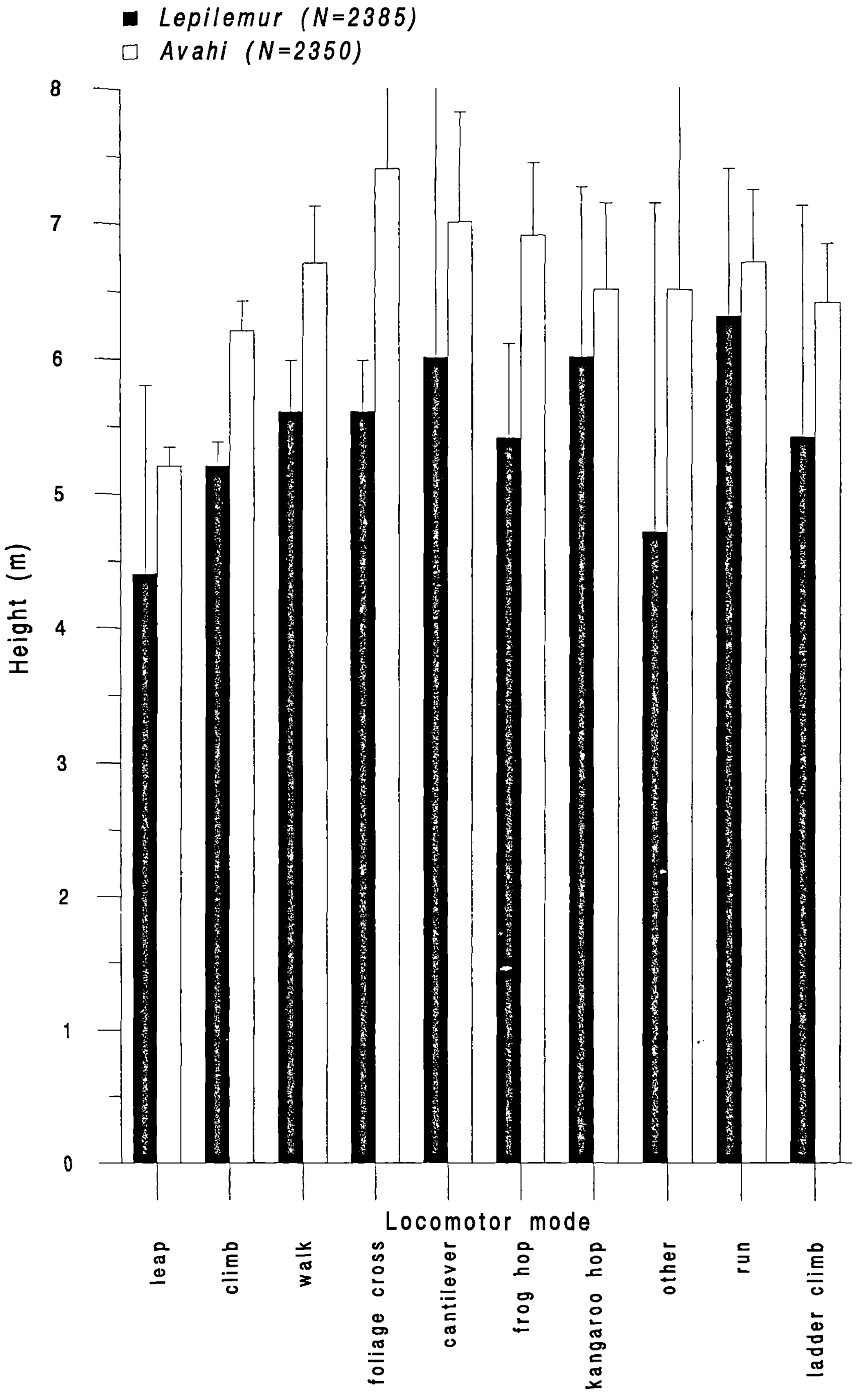


Fig. 2.4e Frequency histogram of the bouts of each locomotor mode for each species

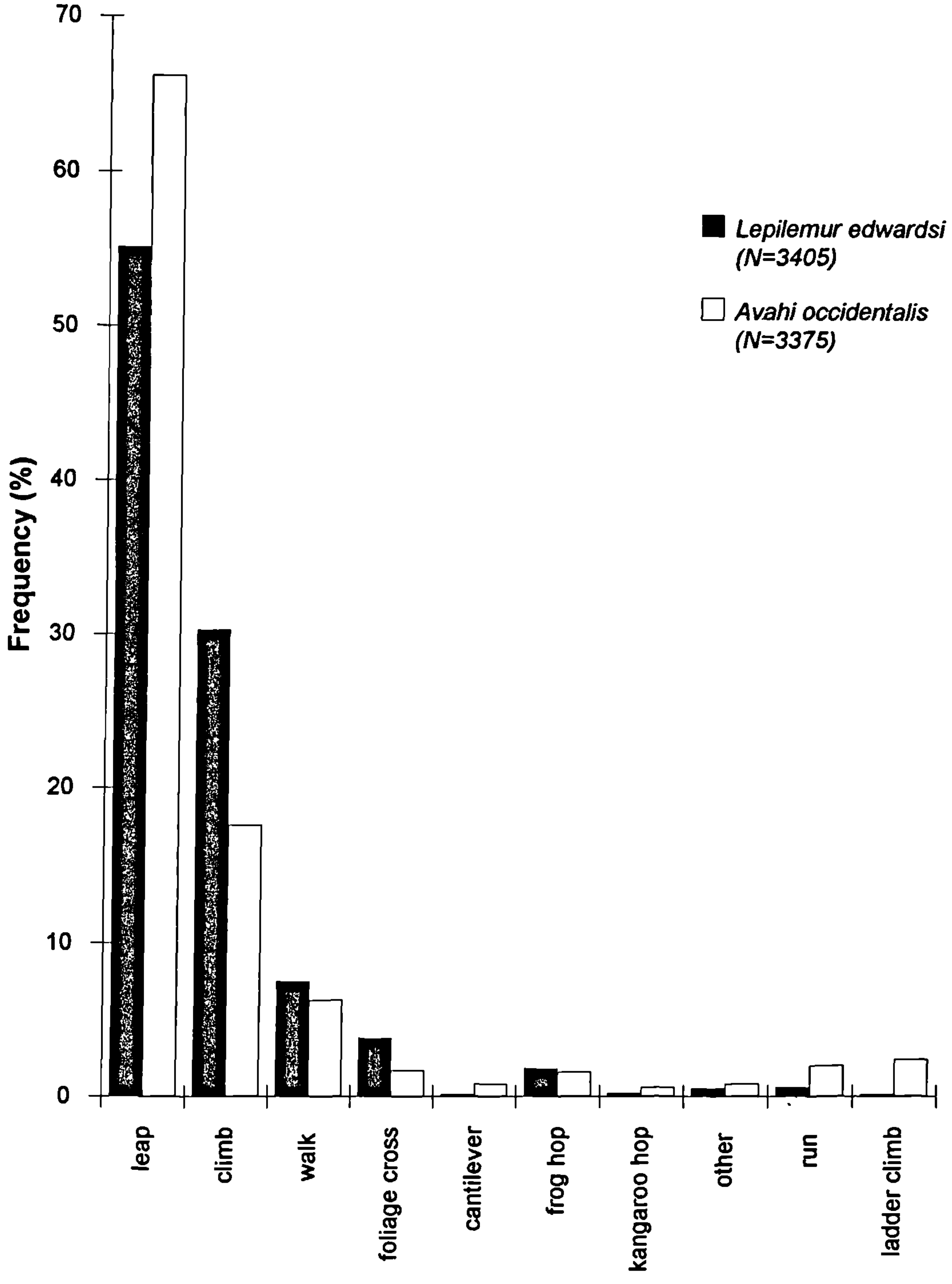


Fig. 2.4f Frequency histogram of the metres per kilometre of each locomotor mode for each species

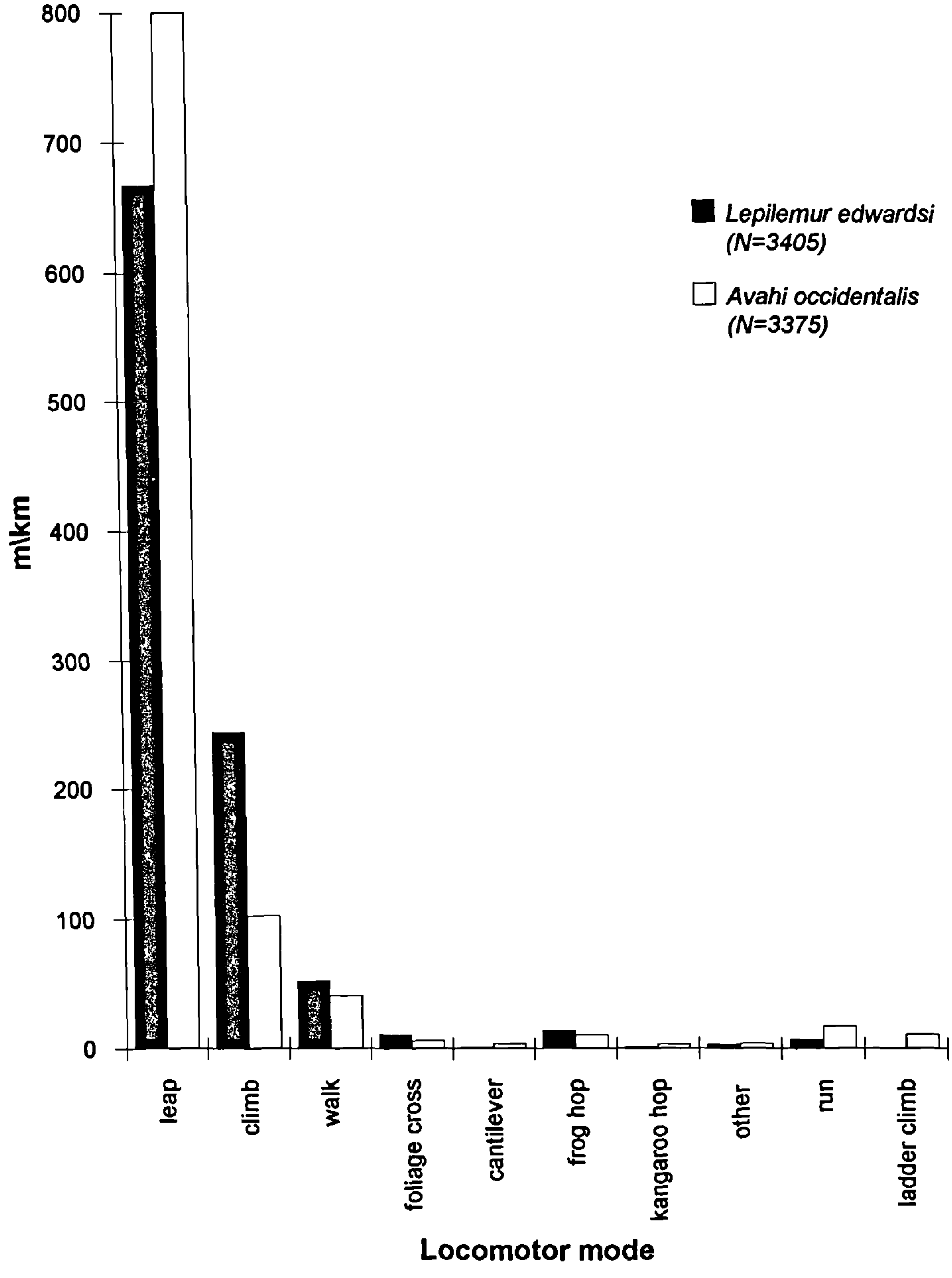
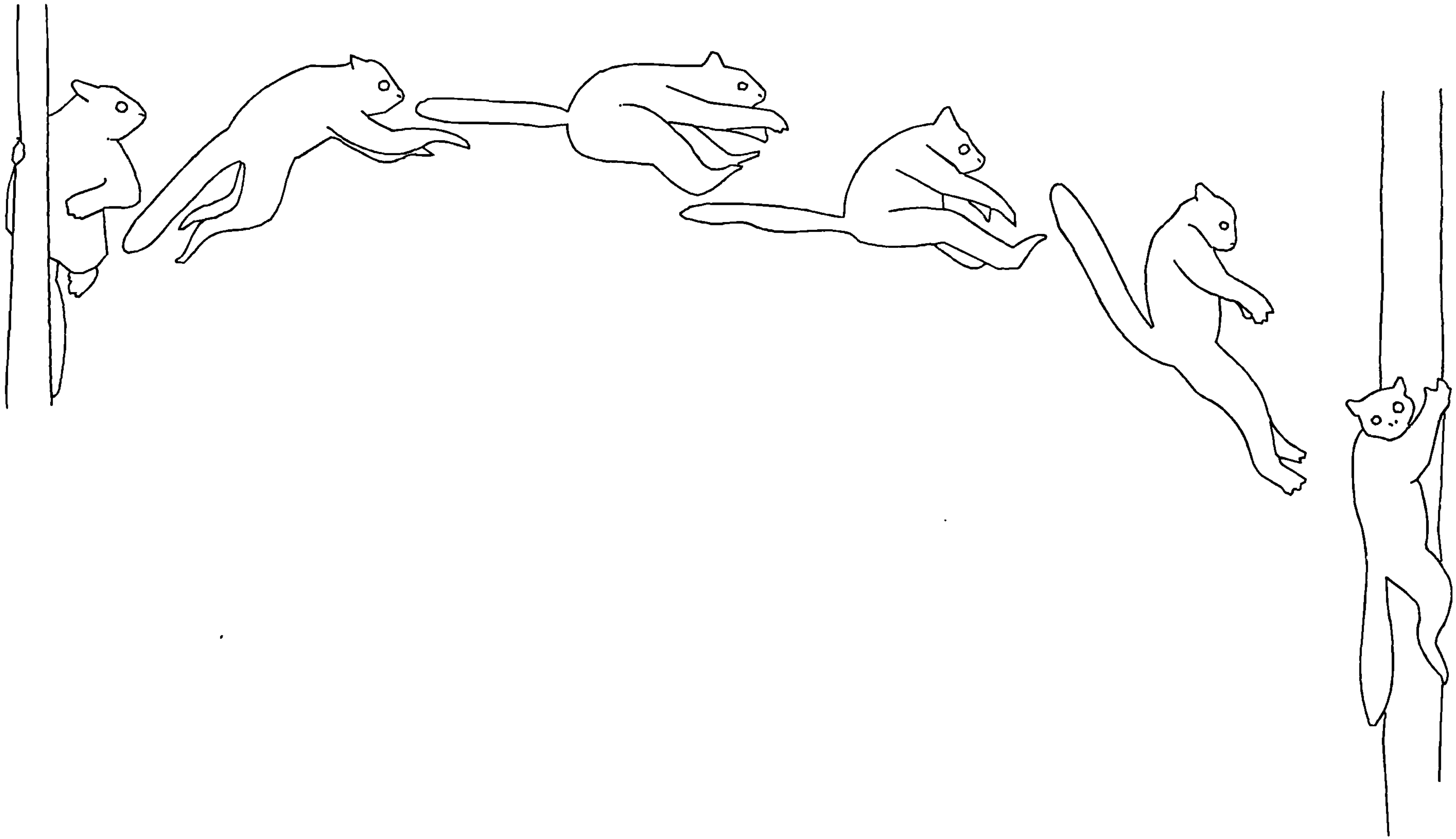


Fig. 2.4g *Lepilemur edwardsi* leaping
(drawn from still frames of a video sequence)



Climbing

Climbing was a common form of locomotion, seen in 30.2% of the bouts (Fig.2.4e). Two different types of climbing were distinguished. The first occurred when an animal gained or lost height on a single support (Fig. 2.4h). The second, ladder climbing, involved a change in height, using numerous supports, as if using the rungs of a ladder, rather than a single pole. In both modes of climbing, the animal's body was upright. It was never observed to descend head first. When climbing a single vertical support, such as a trunk of a tree, the body was flat against the bark and the limbs straddled wide for grip. Climbing was achieved by bringing the legs up towards the arms and then grasping the trunk with the feet while the hands were slid up the tree (reminiscent of a coconut collector). The mean bout length was 0.71 m (Table 2.4a) and mean height was 5.4 m, similar to the take-off height for leaping, as was the mean diameter of the first support which was 3.6 cm (Table 2.4g). *Lepilemur edwardsi* appeared to choose to jump from trunks of trees. To achieve this, before the leap there was often a bout of climbing to position the animal in a suitable position for take-off. Ladder climbing was very rare in *L.edwardsi*. As this species moved predominantly by leaping, any height lost in a leap has to be regained to maintain arboreality. This height gain was usually from climbing rather than leaping (Table 2.4c).

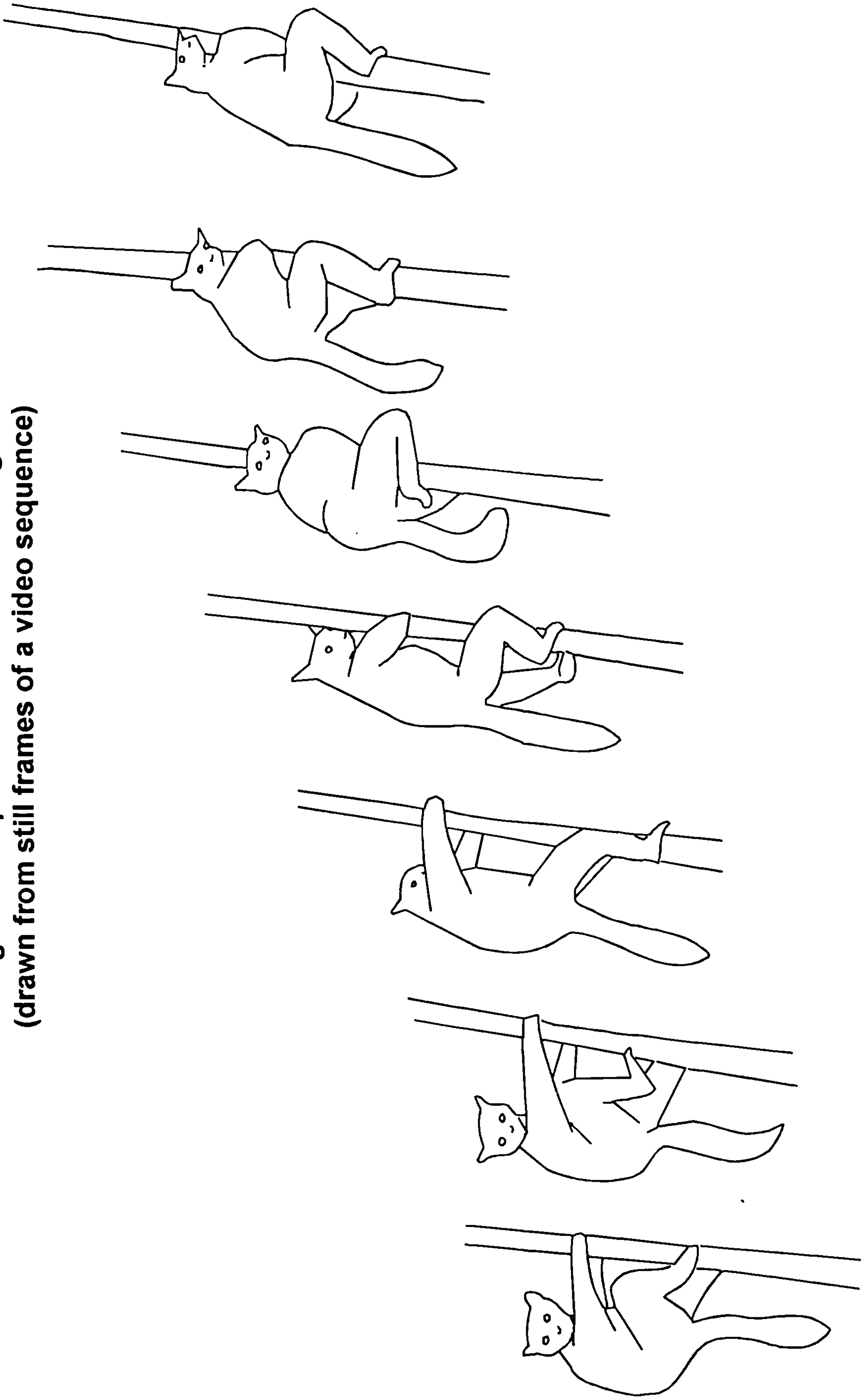


Fig. 2.4h *Lepilemur edwardsi* climbing
(drawn from still frames of a video sequence)

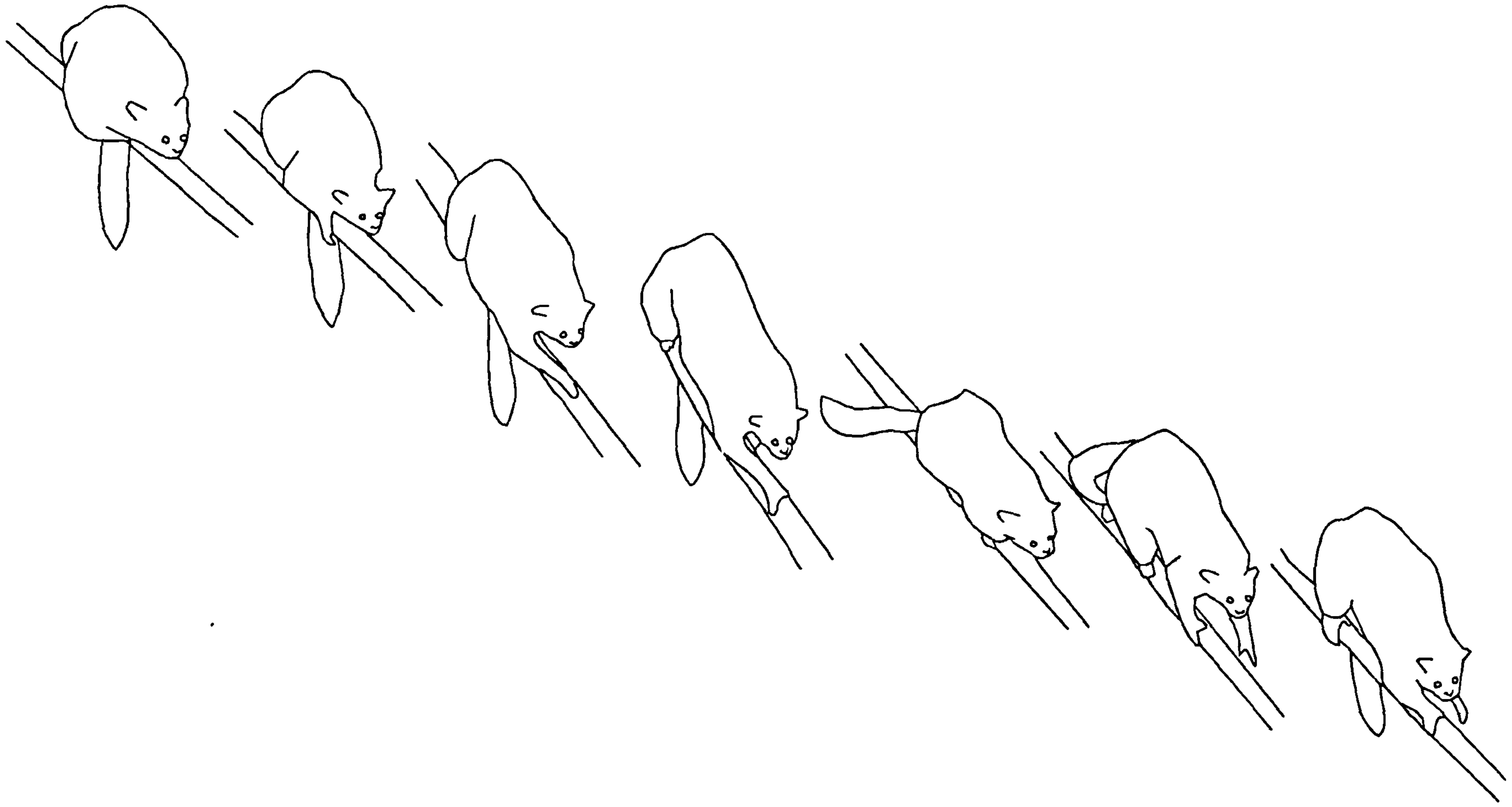
Walking and Running

Walking and running were two other locomotor classes recognised (Fig 2.4i). 7.5% of the locomotor bouts recorded were walking and 0.6% running (Fig. 2.4e). The nature of the vertical forest stratification meant that often there were fewer opportunities for quadrupedal locomotion. It was only the large trees that had boughs of an oblique or horizontal orientation that made walking or running possible. Most frequently, *L.edwardsi* used angled (32.7%) or oblique (29%) branches on which to walk. The use of horizontal branches was rarer (Table 2.4g). Running was a rare activity. If a speedy means of moving was required, (for instance, when fleeing from predators or aggressors), the animal tended to jump rather than run. The mean height of walking on the first support was 5.8 m (Table 2.4g), on a 2.7 cm branch with an average bout length of 0.71 m.

Frog Hopping and Kangaroo Hopping

L.edwardsi also showed two types of leaping behaviour described as frog hopping and kangaroo hopping. The first involves springing with all limbs touching the substrate at take-off and landing, and the second is a hop with the hind limbs only in contact with the support. Take-off and landing always occurred on the same support. Neither was particularly common. Frog hopping occurred at a frequency of 1.8%, compared to 0.2% for kangaroo hopping, and it was most frequently seen on vertical or angled supports at a height of around 5 m (Table 2.4g,j,k).

Fig. 2.4i *Lepilemur edwardsi* walking
(drawn from still frames of a video sequence)



Foliage Crossing

Foliage crossing involved moving across discontinuities via thin branches and foliage, usually reaching out with one forearm to grip a branch and then walking across the gap. The mean bout length was low at 29 cm (Table 2.4a), and the preferred mean diameters used were 3.2 cm for the initial support and 2.7 cm for the second support, both at a mean height of 5.2 m (Table 2.4g,j,k).

Cantilevering

Cantilevering occurred when the lemur stretched out with both its fore limbs to a second support whilst gripping the original substrate with its feet. This mode of locomotion had the lowest frequency of observed bouts at 0.1%.

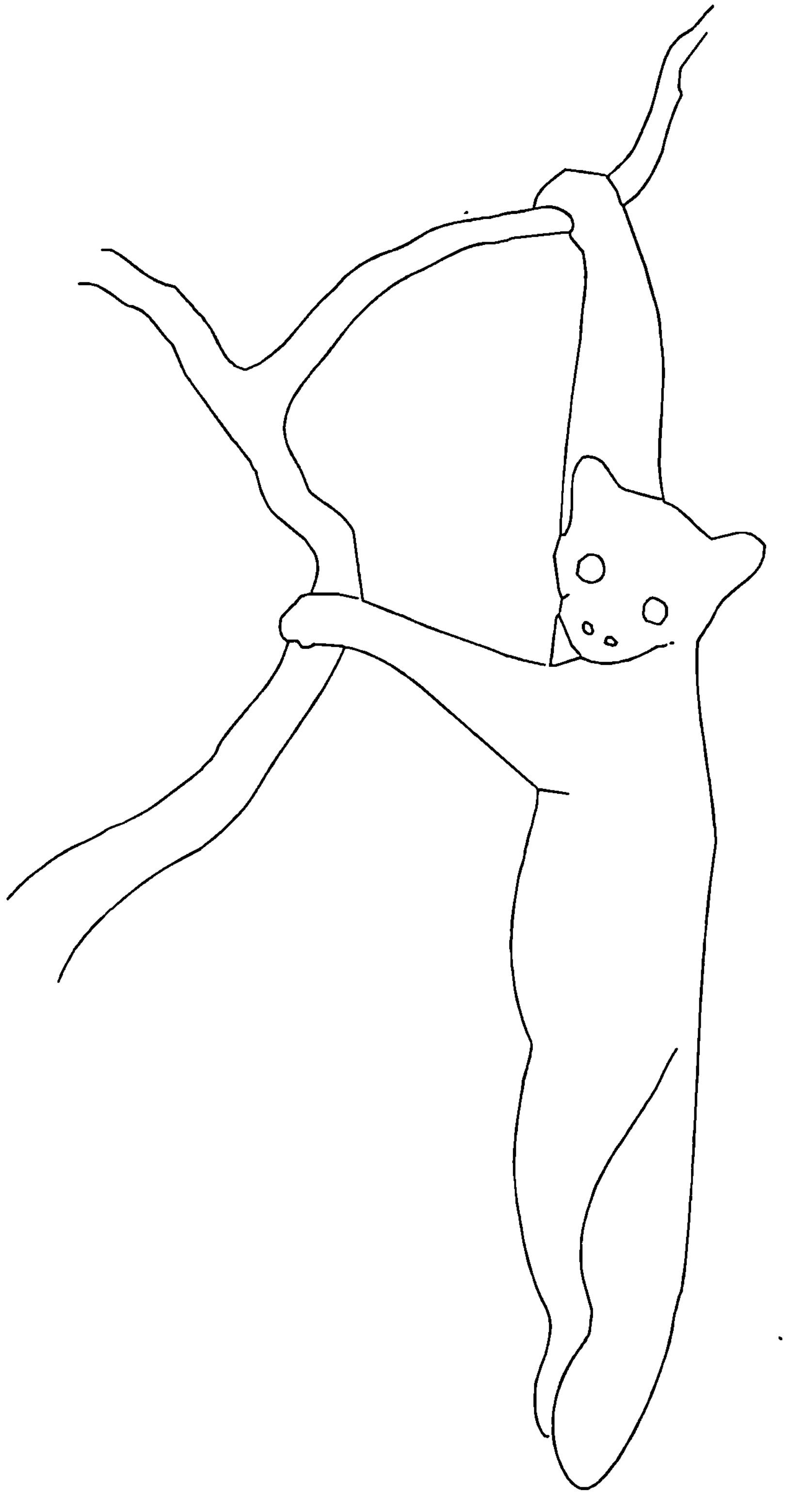
Other modes

0.3% of the bouts recorded were a miscellany of other modes of movement. The majority of these were instances of arm swinging (Fig. 2.4d). Arm-swinging was not categorised as brachiation because it was not used for travelling long distances as much as in foraging. Typically, it occurred when the animal was feeding or moving through a dense tangle of branches; but bouts of around a metre were recorded with two or three 'strides' involved. *Lepilemur edwardsi* was also seen to hang under a branch and move in a sloth like manner.

Contribution of each locomotor mode to a kilometre of travel

The contribution to a kilometre of travel (m/km) of each locomotor mode was calculated. Over 650 m of the kilometre were covered by leaping, along with 250 m by climbing and 50 m by walking. All the other categories formed only a very small proportion of the distance travelled horizontally (Fig.2.4 n, **N.B**: This does not reflect the *time* spent doing each activity).

Fig. 2.4j *Lepilemur edwardsi* arm-swinging (drawn from still frames of a video sequence)



2.43 Description of the locomotion of *Avahi occidentalis*

Leaping

Leaping was the most frequently observed locomotor mode, making up nearly two-thirds of all of the observed locomotor bouts of *Avahi occidentalis* (Fig.2.4e). *Avahi* took off from a crouched position with the hind limbs flexed sharply at the hip and knee (Fig 2.4k). The fore limbs acted as stabilisers while their head was bobbed from side to side to select a suitable support. Head bobbing also occurs in *L.edwardsi*, and may aid with 3-D imaging of the forest at night, both by refreshing the retina, and by enhancing parallax cues (Pariente 1977; Allman 1977; Julesz 1981; Allman & McGuiness 1988). On take-off the legs were powerfully extended propelling the animal into the air. There was usually some degree of twisting necessary whilst air borne to reorientate the animal towards the landing substrate. The greatest necessary angle of spin was 180^0, but it was often less than this. When approaching the landing site, the hind limbs were brought forward and were extended out to meet the branch before flexing acutely on contact. The hands were then brought into contact with the substrate and the animal came to rest. The mean bout length for leaping in *A.occidentalis* is 1.5 m (Table 2.4b). The overall contribution to a kilometre of travel was 800 m (Fig. 2.4f). *Avahi* are therefore very committed leapers. The mean heights of leaping were from an initial support of 6.1 m to a terminal support of 5.2 m; on average losing 1 m in height (Table 2.4h). The preferred diameters were 3.3 cm and 3 cm (Table 2.4h). Nearly 50% of the leaps were from vertical supports and another 26% were from angled supports (Table 2.4l). Fifty two percent of the landing branches were vertical and another 29 % angled, so the description of these animals as 'vertical clingers and leapers' seems very appropriate.

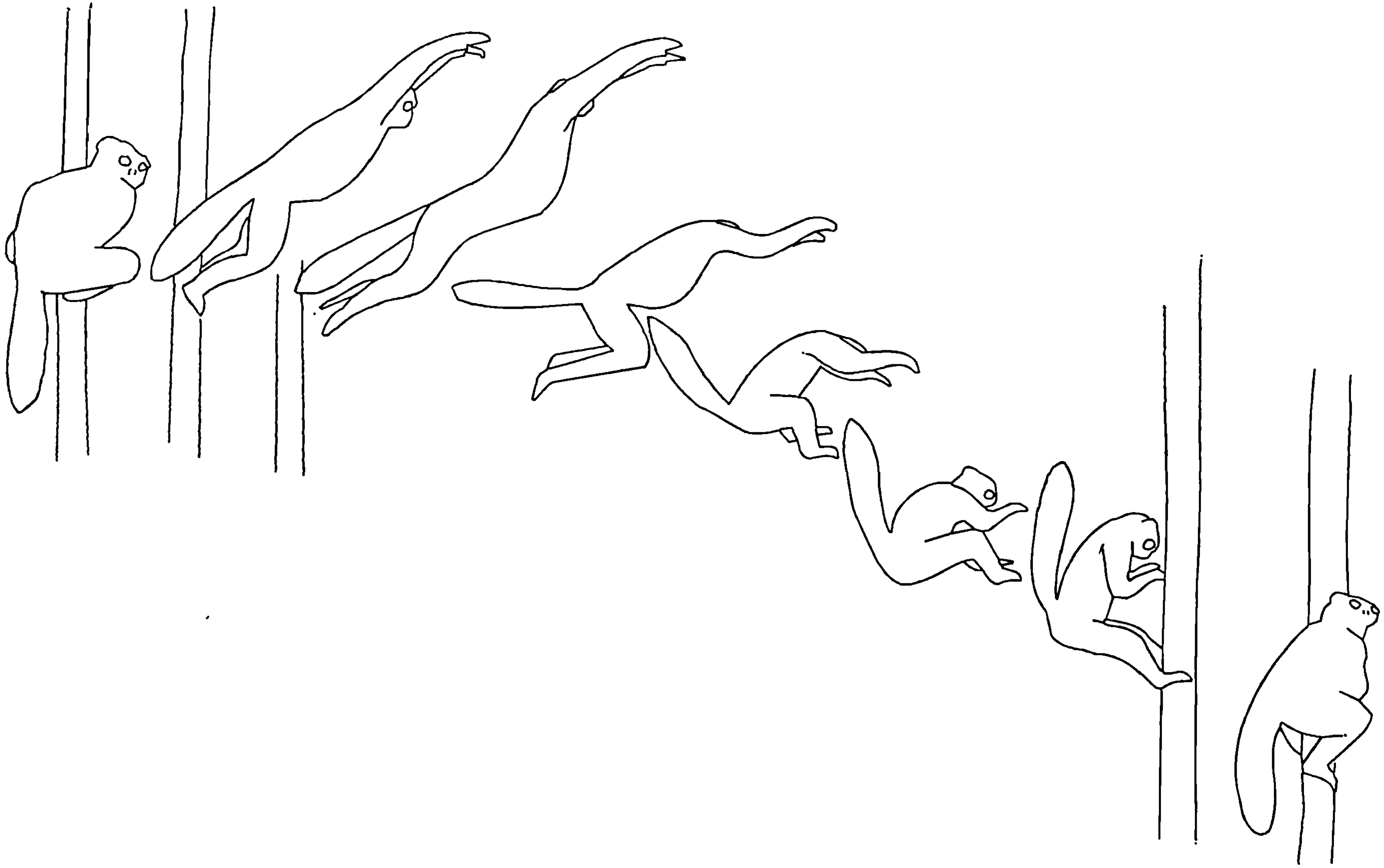


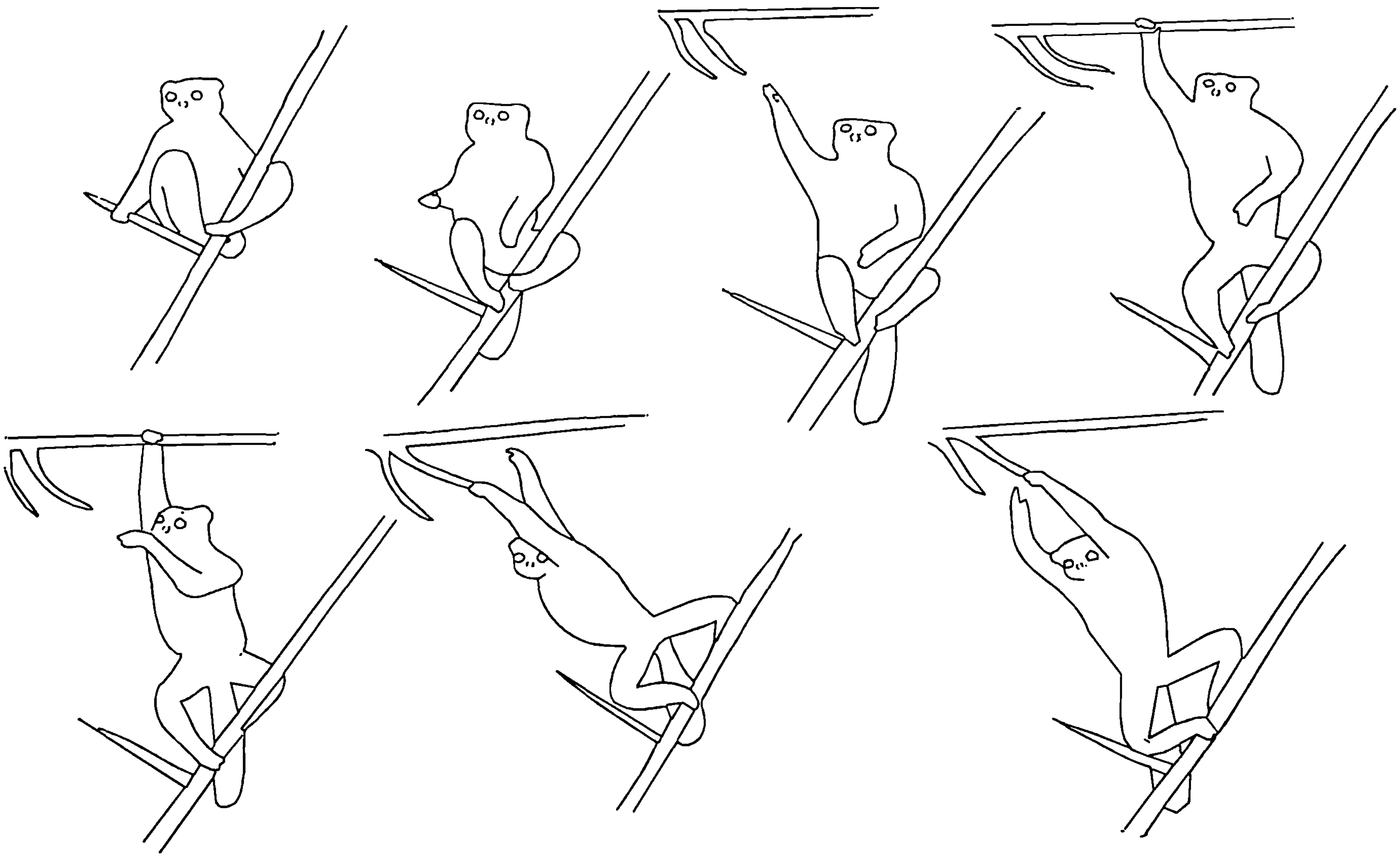
Fig. 2.4k *Avahi occidentalis* **leaping**
(drawn from still frames of a video sequence)

Climbing

Observation of climbing in *A.occidentalis* showed that two distinct types existed. The first is 'normal' climbing in which the subject climbed up a single support; two thirds of such supports were vertical or angled (Fig.2.4l, Table 2.4l). *A.occidentalis* climbs hand over hand, slowly and precisely. Such deliberation was typical of all the locomotor behaviour of *A.occidentalis* with the exception of leaping and running. Each bout of locomotion appeared to be a precisely considered piece of behaviour, accurately executed. The impression given was, however, one of unhurriedness not of sluggishness. The mean bout length was 0.67 of a metre on branches with a mean diameter of 3 cm and mean height of 6.5 m (Table 2.4h). The contribution of 'normal' climbing to a kilometre of travel was 103 m, the second greatest amount after leaping (Fig 2.4f).

The other form of climbing noted, was 'ladder climbing' in which the animal climbed over a network of branches using the twigs as if they were the rungs of a ladder, with three limbs usually in contact with the substrate. Ladder climbing thus seemed a quadrumanous mode of losing and gaining height. Ladder climbing occurred in 2.5% of the bouts observed, but as this locomotion tended to take place in the canopy, (where meshworks of branches usually occurred), there may have been a bias against its observation as it might have been more difficult to see. The most commonly used orientations of branches in this mode of locomotion were horizontal and oblique most often at a height of 6.5 m (Table 2.4h). In fact, it was when climbing that *A.occidentalis* made the commonest use of horizontal branches. The mean bout length was 0.5 m, and the mean diameter of branches used was low, at around 2.5 cm (Table 2.4h). Eleven metres out of each kilometre of travel were covered by this form of climbing (Fig 2.4f).

Fig. 2.4l *Avahi occidentalis* climbing
(drawn from still frames of a video sequence)



Walking and Running

Walking and running made up 6.3 % and 2% respectively of bouts observed. Running only occurred when the animal was in flight and usually preceded a leap. Running took place mostly on angled and oblique branches, at a mean height of 6.3 m, and with a mean bout length of 92 cm, and mean diameter of 2.5 cm (Table 2.4b,h). Walking was usually observed at a height of 7 m with a slightly longer mean bout length than running, of 74 cm and a diameter of 2.4 cm. The speed of walking was very slow and it was again a very controlled form of motion (Fig.2.4m).

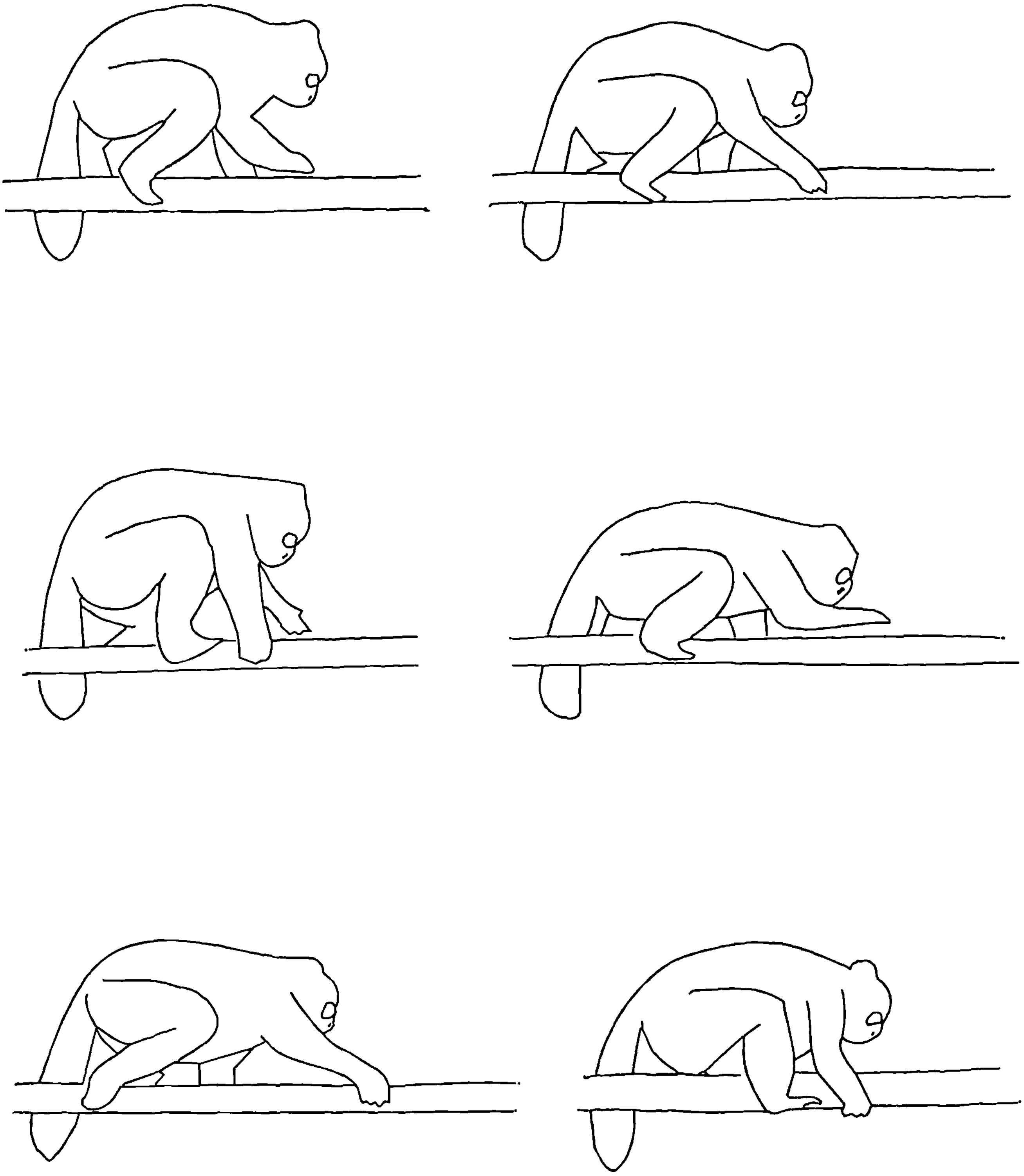
Foliage crossing

Foliage crossing by *Avahi occidentalis* occurred in 1.7 % of observations, at a mean height of 7.6 m with a small mean bout length of 38 cm and diameter of 2.5 cm for *A.occidentalis* (Fig 2.4e and Table 2.4b,h). This is, like ladder climbing, a very quadrumanous form of locomotion, as *A.occidentalis* crossed discontinuities by grasping thin twigs and traversing the gap with three limbs always grasping the substrate. The slowness of this form of locomotion was reminiscent of a slow loris's movements.

Cantilevering

This was a rare form of locomotion in *A.occidentalis*, and when observed was normally a mix of climbing, walking, and foliage crossing high up, in the crown of the trees. The animals gripped a branch with their feet and reached out with their fore arms to the target substrate. As usual, the impression given was that *A.occidentalis* prefer to have at least three limbs in contact with the tree; hence other modes of locomotion were preferred even when crossing gaps where cantilevering could occur.

Fig 2.4m ***Avahi occidentalis*** **walking**
(drawn from still frames of a video sequence)



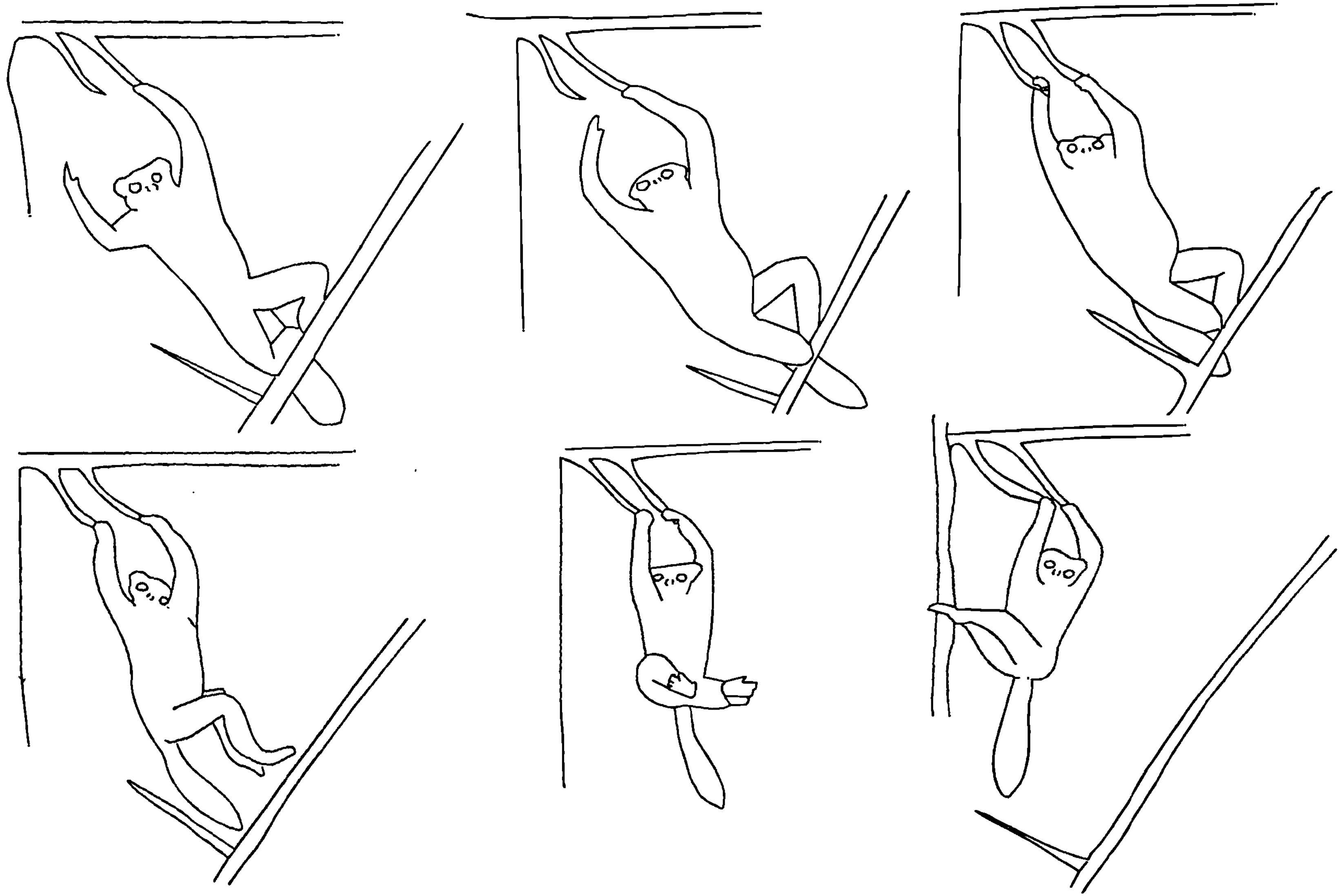
Frog hop and Kangaroo hop

A 'frog hop' was a hop that occurred with all four limbs making contact with the branch during take-off and landing. It occurred at a mean height of 6.5 m, on branches of a mean 3.1 cm diameter and with a mean bout length of 75 cm (Table 2.4h). The preferred orientations of branches were angled, oblique and horizontal. Indeed, 17 % of the bouts observed of this form of locomotion were observed on horizontal supports, the second highest occurrence of this orientation of branch in *A.occidentalis* locomotion, the first being ladder climbing. Kangaroo hopping, in which the animal 'bounces' without using the fore-limbs at all, was very rare, only seen in 0.6 % of the bouts observed (Fig 2.4e). The mean bout length for this was 66 cm (Table 2.4h) and the proportion of a kilometre that could be expected to be covered by this form of locomotion was only 3.4 m (Fig 2.4f).

Other modes

'Brachiation' and 'suspensory' locomotion made up the bulk of other locomotor observations. These were seen most frequently in the tree crowns, among smaller branches. When foraging, the animals were seen to hang by their arms and travel a short distance by brachiation (Fig.2.4n). Swinging also occurred during ladder climbing, in which cases *A.occidentalis* would reach down below its legs and grasp the branch. Then it would release the grip of its feet and swing the legs round underneath itself before moving off using another locomotor mode. These latter forms of suspensory locomotion, unlike brachiation, were only ever seen one at a time. Brachiation however, could cover several metres if needed. Suspensory postures, in which the animal hung by two or three limbs, were often seen when *A.occidentalis* was selecting food.

Fig. 2.4n *Avahi occidentalis* arm-swinging
(drawn from still frames of a video sequence)



2.5 Discussion

Table 2.5a below summarizes some of the findings reported above on the frequency of individual locomotor modes. The locomotor patterns of *L.edwardsi* are probably more analogous to that of *A.occidentalis* than to any of the other prosimians in terms of the relative pattern of preference of each mode, but in detail, and for absolute values, comparisons are closer elsewhere. For instance, leaping is the most frequently observed locomotor mode in both species, followed by climbing. However the absolute frequency of leaping seen in *A.occidentalis* is closer to that of *T.bancanus* (66.1%, Crompton and Andau 1986) and *T.spectrum* (63%, MacKinnon and MacKinnon 1980), while the frequency of leaping observed in *L.edwardsi* is similar to that of *G.senegalensis* (53%, Crompton 1984).

Table 2.5a: The frequency of locomotor modes of *L.edwardsi* and *A.occidentalis*

Locomotor mode	*Lepilemur edwardsi* (%)	*Avahi occidentalis* (%)
leaping	55.1	66.2
climbing	30.3	17.6
walking	7.5	6.3
foliage crossing	3.8	1.7
cantilevering	0.1	0.8
frog hopping	1.8	1.6
kangaroo hopping	0.2	0.6
other	0.5	0.8
running	0.6	2
ladder climbing	0.1	2.4

It is immediately apparent from the above that *A.occidentalis* is a more committed leaper than *L.edwardsi.* This is borne out by considering the contribution of leaping to a kilometre of travel. *A.occidentalis* not only leaps more often, but covers considerably more of each kilometre of travel by leaping:

800 m/km versus 667 m/km. The mean length of *A. occidentalis*' leaps is also greater at 1.51 m, versus 1.36 m in *L.edwardsi.* The m/km value for leaping in *A.occidentalis* is very similar to that (882 m/km) found in *T.bancanus*, perhaps the most specialized prosimian leaper (Crompton & Andau 1986) whereas the figure for *L.edwardsi* is closely similar to that for *G.senegalensis* (670 m/km, Crompton 1984), which is one of the two most specialized leapers amongst the galagos. However, the frequency of climbing for *L.edwardsi*, (far higher than in *A.occidentalis),* is similar to that seen for *T.bancanus*, while *A.occidentalis* in this respect is comparable to *G.senegalensis*, conversely to the case for leaping frequencies.

Ricochetal leaping by *Avahi* took place on many occasions, but the distance covered and duration of such bouts was difficult to observe. Richochetal leaping may be important in contributing to energy saving. These could be derived from use of the landing substrate as a spring board for the next leap (Günther 1985). However, Alexander (1991) suggested that storage of energy within the animal in tendons is more likely. Ricochetal leaping was also observed on several occasions for *L.edwardsi*, but the same restrictions of visibility apply.

Other species in the family Indriidae such as *Indri indri* and *Propithecus verreauxi*, the sifaka, are also specialized leapers, although few quantitative data are available. While ricochetal leaping is common in *Propithecus verreauxi,* sifakas do however show a greater frequency of climbing and quadrupedalism than do *Indri* (Richard 1974, 1977). Pollock (1975,1977) reported that *Indri* moves by ricochetal leaping, with brief bouts of climbing and quadrupedal locomotion. *Indri* leaps generally lose height and are parabolic in trajectory, the latter indicating they are energy-optimized, as in *G. senegalensis* and *Tarsius bancanus* rather than speed-optimized like the majority of prosimian leapers (Crompton *et al.,* 1993). Only 13.6% of the leaps observed for *A.occidentalis* actually gained height, compared to 22.1% for *L.edwardsi.* It therefore seems probable that like *Indri*, *A.occidentalis* predominantly lose height in leaping. One hypothesis which might be thought to explain this finding could be that when traversing the canopy, as *Avahi* was often seen doing, it might be preferable to jump to larger, more stable supports; and these are more frequently found lower down in the forest. However diameter of terminal supports in leaping was in fact less than that for take-off, so the data do not support this argument (the data also suggest that energy loss to the substrate is avoided in take-off and sought in landing). Qualitative observations indicated that the *Avahi* tended to jump from the top of the canopy to the periphery of the canopy lower down, and then to run or walk upwards along the landing support to sturdier resting places within the crown, where ladder climbing was often employed to regain height lost. This observation is consistent with Norberg's (1981) findings in studies of foraging in birds. He suggested that it is energetically cheaper to climb vertically up a tree when searching for food and then fly down from the top of one tree to the bottom of the canopy of the next tree. However, if this principle is applied to leaping animals, any energetic advantage would be diminished by the cost of leaping, and it would probably be just as efficient to climb up and leap down, as to leap up and climb down (Alexander pers. comm.).

It has been shown that brachiation is an element of the locomotor repertoire of *Avahi* when moving just below the canopy, and suspensory postures also occur in feeding. Suspension is not, however, as common as it is in the indriid *Propithecus verreauxi,* the sifaka, where suspension from the fore-limb is an important element of foraging behaviour (Richard 1974, 1977). Given these characteristics of *Propithecus verreauxi*, it does not seem surprising that the smallest member of the family, *Avahi occidentalis*, combines a predominance of leaping with suspensory postures, the latter particularly observed when accessing the small branch niche. The presence of suspension in *A. occidentalis* is not surprising, in view of its occurrence in other members of the genus, but this study is the first time that it has been recorded in *Lepilemur*. As with cantilevering (below) tensile forces and forelimb tension during suspension may be adaptively critical factors, but suspension may yet be favoured because it permits exploitation of the small branch niche (particularly in *A.occidentalis.*)

The mean height of the first support in *Lepilemur edwardsi* (5.28 m) was substantially less than that for *Avahi occidentalis* (6.4 m). *A.occidentalis* clearly occupied a higher stratum than *Lepilemur edwardsi* and in nearly every type of locomotion, the mean height of observation was a metre above that for *L.edwardsi.* (5 out of the 10 modes showed statistically significant mean heights). In this respect, however, absolute heights for the two species resembled each other closer than they do the other VCL species for which we have quantitative data: *Galago alleni* Charles-Dominique (1977), *G.zanzibaricus* (Harcourt & Nash 1986b), *Tarsius spectrum* (MacKinnon & MacKinnon 1980) and *Tarsius bancanus* (Crompton & Andau 1986) all have mean heights of observation below 5 m and they are very often found below 2 m. Only *G. crassicaudatus* (Crompton 1984) occupies a similar stratum in the forest to the study species and only *G. crassicaudatus* shows the general aversion to the ground seen in this study, where at no time throughout the eighteen month study, were *L.edwardsi* or *A.occidentalis* observed moving on the ground . This result is of course exactly what would be expected if two folivores are compared with gumnivore-insectivores and animalivores like the bushbabies and tarsiers.

Comparing the diameter of the first support used by the two species (Table 2.4i), it is evident that both first and second support diameters are larger (p<0.01) *for L. edwardsi*, whose preferred support diameter is virtually the same as *T.bancanus*'. *L.edwardsi* also used vertical and angled supports more often than did *A.occidentalis.* This combination of use a low stratum with larger and more vertical supports recalls the behaviour reported for *G. senegalensis* (in contrast to *G. crassicaudatus*, which moved higher, in the low canopy) and also the locomotor niche of *Tarsius bancanus* in Crompton's studies (Crompton 1984; Crompton and Andau 1986). It is this kind of locomotor niche that I would like to propose for *L.edwardsi.* In the dry deciduous forest of Ampijoroa, this species tends to travel on the trunks rather than in the crowns of the trees, while for *A.occidentalis* the opposite applies, so that the two species are separated spatially within the forest. This hypothesis is supported by the preferred heights of locomotion of the two species and the corresponding diameters and orientations of the supports. Anecdotally, on several occasions *A.occidentalis* was seen to move in the crown of a tree above *L.edwardsi*, which was seen lower down in the primary fork of the tree or clinging to the tree trunk.

However, an analogy with tarsiers and bushbabies is not to be taken too far, as *T.bancanus* uses verticals in 72.4% of cases (Crompton and Andau, 1986), while *G.alleni* was observed by Charles-Dominique (1980) on vertical supports in 73% of observations (although Charles-Dominique recognised only 3 orientation categories: vertical, oblique and horizontal). Both species of lemur in this study therefore use vertical supports less than these two species, which are both usually observed on young saplings within a rainforest environment, where one would expect vertical supports to be most available.

Cantilevering, or the 'flag posture' is a seen in most bushbabies, lorises and cheirogaleines (Martin 1972. Walker 1979, Crompton 1983) as well as in *T.bancanus*. Despite always being a rare form of locomotion, it may be adaptively critical as the posture is likely to produce very high bending moments on the leg and foot. In these species, it is usually associated with insect feeding (Crompton 1983). Both *L.edwardsi* and *A.occidentalis* display cantilevering at a low frequency, (lower in the former species than the latter) but in this study it appeared to be used to cross discontinuities rather than to feed.

Thus, to summarise, *Avahi occidentalis* and *Lepilemur edwardsi*, whilst showing a generally similar locomotor repertoire, differ in emphasis, especially with respect to stratum: *Avahi* is the more dedicated leaper, but it is *Lepilemur,* moving lower down which both uses and encounters a greater number of vertical, large-diametered supports.

3 Habitat Structure

3.1 Introduction

It has been shown that while both species are predominantly vertical clingers and leapers, substrate use differs, especially with respect to stratum (see Chapter Two). However, this raises several further questions: Do the animals use the most available supports in the forest? Do the animals have preference for certain angles, sizes and heights of supports? Do these preferences vary between the two species despite their morphological similarity?

Forest is inherently a demanding habitat in which to move. To begin with, arboreal animals are faced with problems of substrate discontinuity. The base of the forest can be considered to consist primarily of the tree trunks, usually vertical in orientation and of larger diameter than the supports higher in the canopy. However, discontinuities are fewer but large. Further up, the first spreading branches are encountered, which then radiate smaller branches which orientate the leaves towards the sun. In the peripheral canopy, substrates appear to be randomly placed with different angles, sizes and flexibility. Gaps here tend to be small but numerous.

Branches are asymmetrical in structure (McMahon 1975). Their stiffness is greatest at their widest part and decreases towards the periphery, where the branch is more slender. For an arboreal vertebrate, this presents a problem of substrate deformation. The branches bend under the weight of the animals and are left vibrating when they jump from them. Arboreal animals thus run a higher risk of injury, by falls from substrates which are unstable, compared to animals on solid ground. The flexibility of branches, also makes arboreal locomotion more expensive in terms of energy than running on rigid ground. It seems probable that branches on which the animals travel are more compliant than is optimal for locomotion, making the arboreal habitat an energetically expensive place in which to travel.

The diversity of supports, their discontinuities and flexibilities are all 'hurdles' obstructing the most direct path. Animals have constant choices to make concerning the optimal route from one tree crown to the next, minimizing departures from the ultimate goal (Temerin & Cant 1983), and the morphology and behaviour of the animals will constrain the choice of paths through the canopy. For the observer, it is therefore tempting to attribute all aspects of functional morphology as an adaptation to the habitat structure. However, it must be borne in mind that features may be proximal adaptations to previous environmental conditions.

Quantitative studies have related frequencies of locomotor behaviour to the types of substrates used, often focusing on sympatric species (Morbeck 1977; Mittermeier 1978; Fleagle 1978; Fleagle & Mittermeier 1980; MacKinnon & MacKinnon 1980; Gittins 1983; Crompton 1984; Harcourt & Nash 1986). Forest structure has been described by quantifying the density of different tree sizes and diameters of tree crowns (Gautier-Hion *et al.* 1981, Whitten 1982, Crompton 1984, Ganzhorn 1989), but these researchers have not related these variables to choice of supports by primates. Only very few researchers have studied substrate use in conjunction with substrate availability. These include in particular Cannon & Leighton (1994). In Cannon and Leighton's study, the canopy elements used by Bornean agile gibbons and long-tailed macaques were contrasted and related to the species' characteristic locomotion. They postulated that locomotor behaviour and selection of canopy strata for travel are constrained particularly by wide gaps between trees and choices are ultimately made for 'efficient direct line travel between distant points'.

Despite a considerable number of studies on VCL, none to date has related 'vertical clinging and leaping' to substrate availability. This study is a first step in filling this gap in our knowledge of prosimian locomotor behaviour.

3.2 Aims

As sympatric species, *Lepilemur edwardsi* and *Avahi occidentalis* have the same forest environment available to them. Having similar body mass, morphology and diet, they presumably have analogous ecological relationships with food resources and predators. However, we have seen that their locomotion differs (see Chapter Two). *A.occidentalis* used a higher part of the forest and seemed to be a more committed leaper than *L.edwardsi,* which mostly remained lower down and showed more climbing behaviour. In this chapter, these basic differences in the locomotor behaviour are related to the availability of supports at Ampijoroa. This Chapter examines the structure of their habitat; and asks how the animals organize their locomotion in response to the available supports. It addresses the question: is the pattern of the use of a support a simple reflection of its availability within the environment or is the support selected because of properties which make it preferable for locomotion?

3.3 Methods

3.31 Field Methods

The study site was selected and a quadrat marked out as described in Chapter Two, section 2.31. An analysis of support availability was then performed using a botanical technique normally used to assess canopy spread and vertical stratification (Ramangason 1986). Two long pieces of rattan were marked with bands at 1 m intervals. A horizontal transect line 200 m long was marked out running through the centre of the quadrat. Marker poles were then placed at two metre intervals along the transect and the forest was observed in respect to cuboids of space along this line (Fig.3.3a). Each cuboid observed was two metres in length, one metre high and one metre deep. Observations consisted of estimating the volume taken up within a cuboid by various classes of supports (*e.g.* 'vertical medium branch'). These volumes were recorded as a fraction of eight (*e.*g.1/8 represents 12.5% of the volume of the box). After all the supports in this box had been described, the observer then analysed the next cuboid, one metre higher up (and so on until there was no further canopy). The poles were then moved onto the next two metre section and this process was repeated. If a given class of support did not make up 1/8 of the volume it was ignored. This transect survey took place in the dry season for ease of observation, and was repeated so that any discrepancies in figures could be checked due to problems in estimation with increased height above the ground.

Further, a 1 km long transect was set out within the study area along the quadrat lines. Distances between trees at the tree base, the diameter at breast height (DBH, breast height, taken to be 1.3 m), and the maximum crown width of all trees with their trunks directly on the transect line were measured. Further, a forest profile was drawn for a 20 m length along the centre portion of the transect and the major trees within it were identified (for method, Mueller-Dombois & Ellenberg 1977).

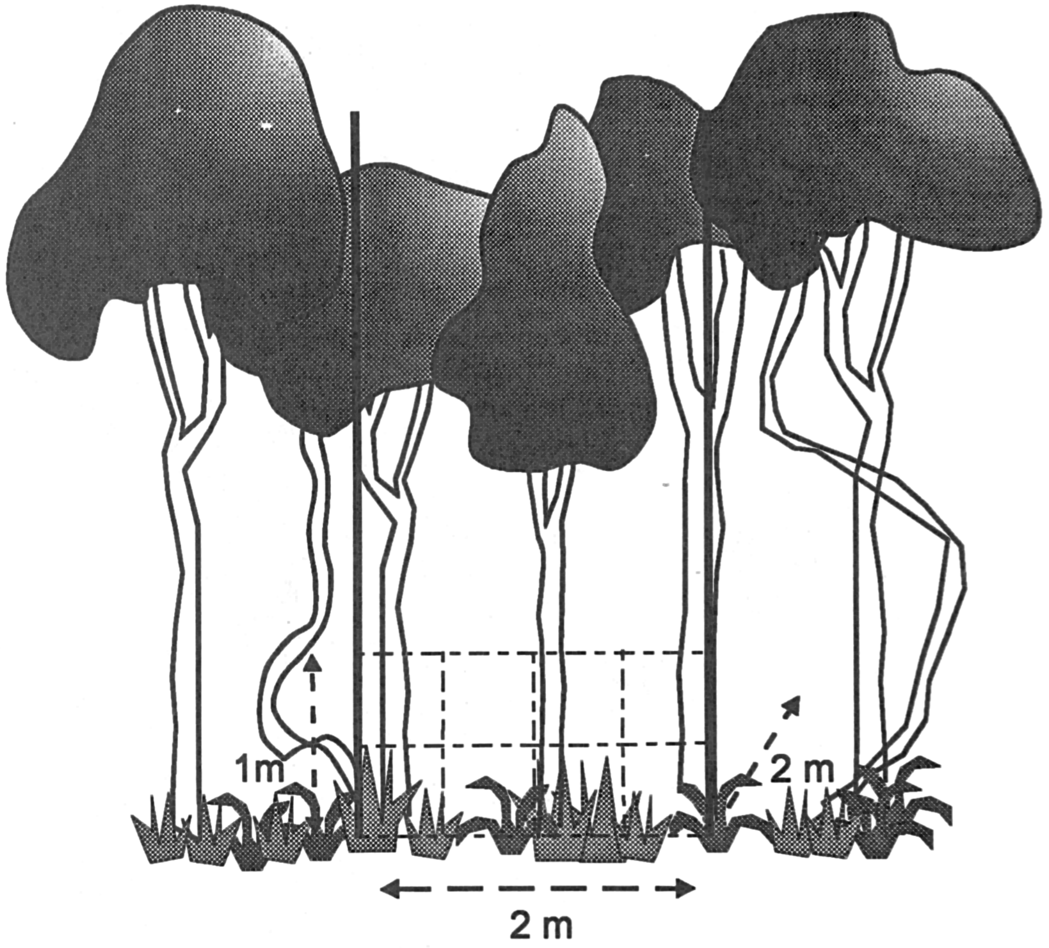


Fig. 3.3a Method to assess vertical stratification

The locomotion data used in this chapter were collected as described in Chapter Two using the identical support categories.

Table 3.3a: Support details collected using the pole method.

Support variable	Support class	Class details
Orientation	vertical	81-90^0
	angled	46-80^0
	oblique	11-45^0
	horizontal	0-10^0
Size	foliage	0≤0.5 cm
	small	0.5-5 cm
	medium	5.1-10 cm
	large	10.1-15 cm
	enormous	15.1+ cm
Height	metre gradients (*e.g.* 1m, 2m, 3m *etc.*)	m

3.32 Data Analysis

Data were entered and checked using dBASE III (Ashton Tate 1985). The data were then imported into SPSSPC+ (Norusis/SPSS Inc. 1990), for analysis. Contingency table analysis was performed on the frequency of observations of bouts of locomotion on different supports by both species of lemur studied. If significance was obtained at the P<0.05 level the data were collapsed to a simple 2x2 chi-squared table (Cannon & Leighton 1994). Frequency of usage of the support class in question was thus compared to all other classes of that variable (the support availability data were, of course, used as expected values). In the contingency table analysis, classes were constructed to satisfy the rules set out in Conover (1980) to ensure robustness of results. Fisher's exact test (Norusis/SPSS Inc. 1990) was calculated to compensate for any expected values less than five.

Jacob's D value was used as an index to assess preference for different supports (Jacobs 1974):

$$D=(r - p)/(r + p - 2rp)$$

where r is the relative use of the support and p is the relative availability of the support within the forest. The value of the index ranges from -1 for avoidance, to +1 for preference, and is symmetrical around 0, which value indicates neutrality of choice. The value relies directly on the availability of the variable, in this case the support (Cock, 1978). Note that since Jacob's D is a dimensionless number, standard errors and Student's t-test are not appropriate.

3.4 Results

3.41 Support Availability in the Habitat

Table 3.4a: The statistical results of forest variables

Forest variable	mean	standard error	F value	N	P<
inter-tree distance	2.551	±0.09	25.81	613	0.001
diameter at breast height	4.507	±0.25	204.23	616	0.001
maximum crown diameter	2.803	±0.11	17.67	569	0.001

Figures 3.4a,b,c show some of the characteristics of support availability. Figure 3.4d shows the percentage of supports of each orientation class at Ampijoroa when the heights are amalgamated into three metre clumps to show the change in availability of different support orientations at different heights. Figure 3.4e shows the proportion of branches of different sizes and orientations. Figure 3.4f is a forest profile of a 20 m strip on a transect at Ampijoroa.

3.42 Support Preference of *Lepilemur edwardsi*

Lepilemur edwardsi did not use supports of varying orientation in the forest simply as a function of their availability for either the initial support (χ^2=292.64, 3 d.f., p<0.000) or the subsequent support (χ^2=96.84, 3 d.f, p<0.000). When a contingency table analysis was performed on the frequencies of observations of the animal on a support of a particular orientation, and compared to the other observations clumped together, significant results were obtained in each of the comparisons, except that comparing vertical supports for the second branch orientation (see Table 3.4b). The Jacob's D preference values can be seen in Figures 3.4g and 3.4h.

Neither did *Lepilemur edwardsi* use support sizes according to their availability (χ^2=4412.44, 4 d.f, p<0.000 for the first support, and χ^2=2510.75, 4 d.f., p< 0.000 for the second support). Each size category was preferred or avoided at significant levels apart from medium branches of 5.1 to 10 cm in diameter which were used according to their availability (Table 3.4c and Figures 3.4i and 3.4j).

Further, *Lepilemur edwardsi* did not use supports according to their frequency of occurrence at different heights (χ^2=1237.90, 14 d.f, p<0.000 for the first support and χ^2=721.46, 14 d.f., p<0.000 for the second support). Except at seven metres and twelve metres above the forest floor, supports were used selectively (Table 3.4d and Figure 3.4k and 3.4l).

Table 3.4b: Use of supports of various orientations by *Lepilemur edwardsi* compared to their availability, (N.S. not significant)

Support variable	Support class	χ^2	d.f.	Significance p <
Orientation of first support	vertical	14.72	1	0.000
	angled	25.22	1	0.000
	oblique	538.60	1	0.000
	horizontal	166.04	1	0.000
Orientation of second support	vertical	0.04	1	N.S.
	angled	22.14	1	0:000
	oblique	20.04	1	0.000
	horizontal	63.94	1	0.000

Table 3.4c: Use of supports of various sizes by *Lepilemur edwardsi* compared to their availability, (N.S. not significant)

Support variable	Support class	χ^2	d.f.	Significance p <
Size of first support	foliage	3937.26	1	0.000
	small	25.27	1	0.000
	medium	0.29	1	N.S.
	large	15.59	1	0.000
	enormous	3560.42	1	0.000
Size of second support	foliage	2260.66	1	0.000
	small	10.41	1	0.001
	medium	0.00	1	N.S.
	large	13.99	1	0.000
	enormous	1976.95	1	0.000

Table 3.4d: Use of supports of various heights by *Lepilemur edwardsi* compared to their availability, (N.S. not significant)

First support height	χ^2	d.f.	p <	Second support height	χ^2	d.f.	p <
1	211.54	1	0.000	1	111.62	1	0.000
2	135.71	1	0.000	2	76.56	1	0.000
3	38.94	1	0.000	3	8.89	1	0.001
4	438.81	1	0.000	4	272.76	1	0.000
5	239.63	1	0.000	5	133.80	1	0.000
6	113.59	1	0.000	6	57.91	1	0.000
7	0.19	1	N.S.	7	0.49	1	N.S.
8	18.42	1	0.000	8	18.14	1	0.000
9	70.52	1	0.000	9	46.18	1	0.000
10	70.67	1	0.000	10	56.83	1	0.000
11	14.51	1	0.000	11	7.15	1	0.001
12	0.21	1	N.S.	12	0.08	1	N.S.
13	8.41	1	0.001	13	3.39	1	0.05
14	9.30	1	0.001	14	5.81	1	0.05
15	9.10	1	0.001	15	5.58	1	0.05

3.43 Support Preference of *Avahi occidentalis*

Avahi occidentalis select supports with respect to orientation, size and height (χ^2 = 2255.93, 3 d.f., p<0.000 for the first support and χ^2 = 744.89, 3 d.f, p<0.000 for the second support). Selection is apparent for all orientations, whether positive or negative(Figure 3.4g, 3.4h and Table 3.4e).

Similarly, regular use of supports by *Avahi occidentalis* was not related to their availability (χ^2=5204.34, 4 d.f, p<0.000 for the first support and χ^2=2934.59, 4 d.f., p< 0.000 for the second support). Each size category was actively preferred or avoided apart from branches of 5.1 to 10 cm in diameter which were used according to their availability (Table 3.4f and Figures 3.4i and 3.4j).

Avahi occidentalis also selected with respect to height (χ^2=1182.72, 14 d.f, p<0.000 for the first support, and χ^2=636.53, 14 d.f., p<0.000 for the second support). Statistical tests showed that most supports at given heights were used at a frequency different from that expected from their availability (Table 3.4g and Figure 3.4k and 3.4l).

Table 3.4e: Use of supports of various orientations by *Avahi occidentalis* compared to their availability

Support variable	Support class	χ^2	d.f.	Significance p <
Orientation of first support	vertical	166.03	1	0.000
	angled	151.37	1	0.000
	oblique	1008.70	1	0.000
	horizontal	1157.46	1	0.000
Orientation of second support	vertical	18.75	1	0.000
	angled	103.27	1	0.000
	oblique	339.45	1	0.000
	horizontal	357.47	1	0.000

Table 3.4f: Significance of the use of supports of various sizes by *Avahi occidentalis* compared to their availability, (N.S. not significant)

Support variable	Support class	χ^2	d.f.	Significance $p <$
Size of first support	foliage	3618.63	1	0.000
	small	4927.12	1	0.000
	medium	0.01	1	N.S.
	large	47.15	1	0.000
	enormous	45.05	1	0.000
Size of second support	foliage	2071.97	1	0.000
	small	2756.00	1	0.001
	medium	0.61	1	N.S.
	large	24.14	1	0.000
	enormous	30.05	1	0.000

Table 3.4g: Use of supports of various heights by *Avahi occidentalis* compared to their availability, (N.S. not significant)

First support height	χ^2	d.f.	p <	Second support height	χ^2	d.f.	p <
1	264.01	1	0.000	1	142.91	1	0.000
2	237.90	1	0.000	2	140.11	1	0.000
3	202.32	1	0.000	3	89.30	1	0.001
4	8.25	1	0.001	4	0.15	1	N.S.
5	52.87	1	0.000	5	31.28	1	0.000
6	209.46	1	0.000	6	162.83	1	0.000
7	217.70	1	0.000	7	91.06	1	0.000
8	89.57	1	0.000	8	31.06	1	0.000
9	1.86	1	N.S.	9	5.94	1	0.01
10	5.47	1	0.01	10	4.14	1	0.01
11	3.19	1	0.05	11	1.30	1	N.S.
12	7.50	1	0.001	12	0.07	1	N.S.
13	0.99	1	N.S.	13	1.66	1	N.S.
14	5.05	1	0.01	14	4.43	1	0.01
15	7.31	1	0.01	15	3.79	1	0.05

Fig. 3.4a The frequency of supports at different heights above the forest floor at Ampijoroa

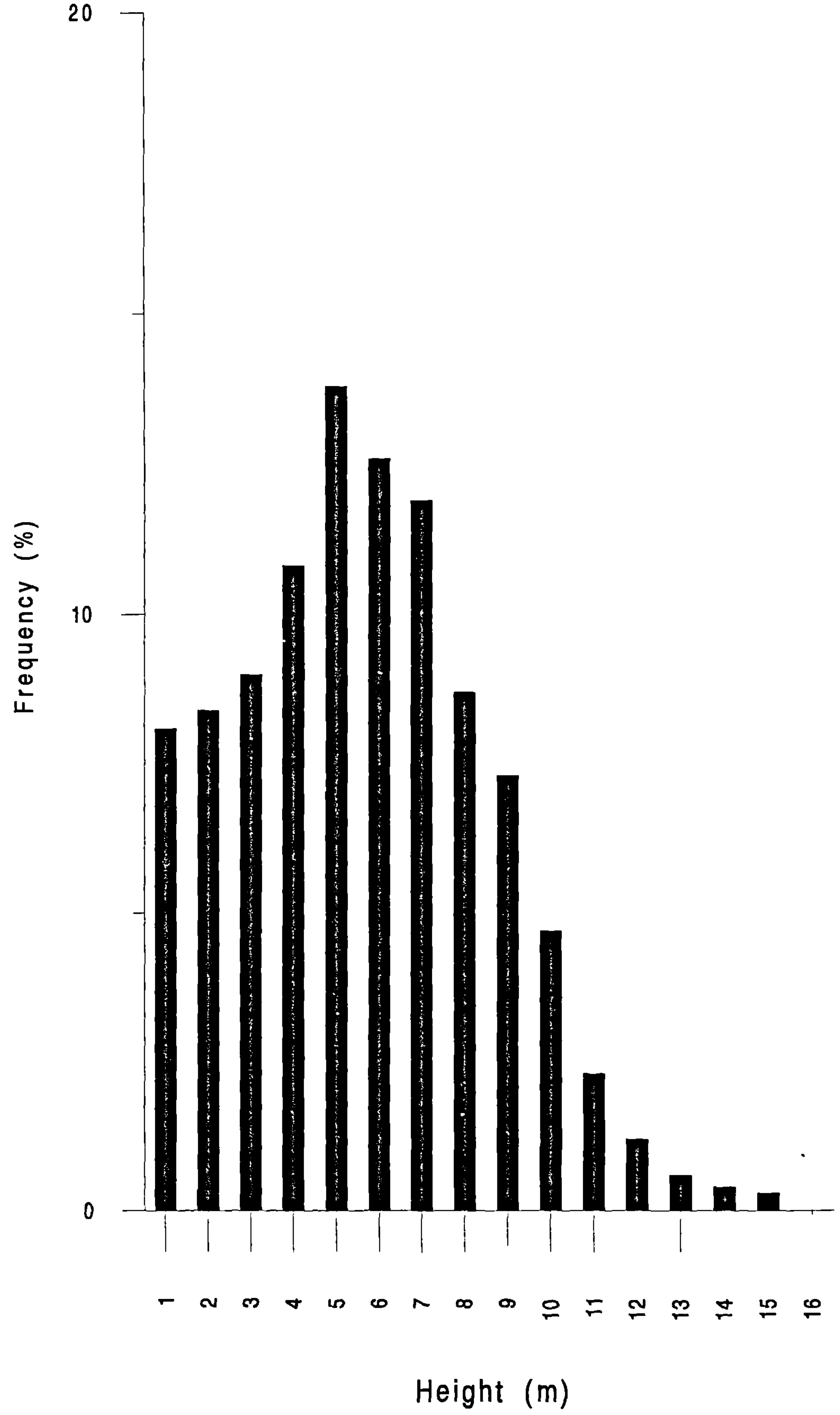


Fig. 3.4b The frequency of supports of different sizes at Ampijoroa

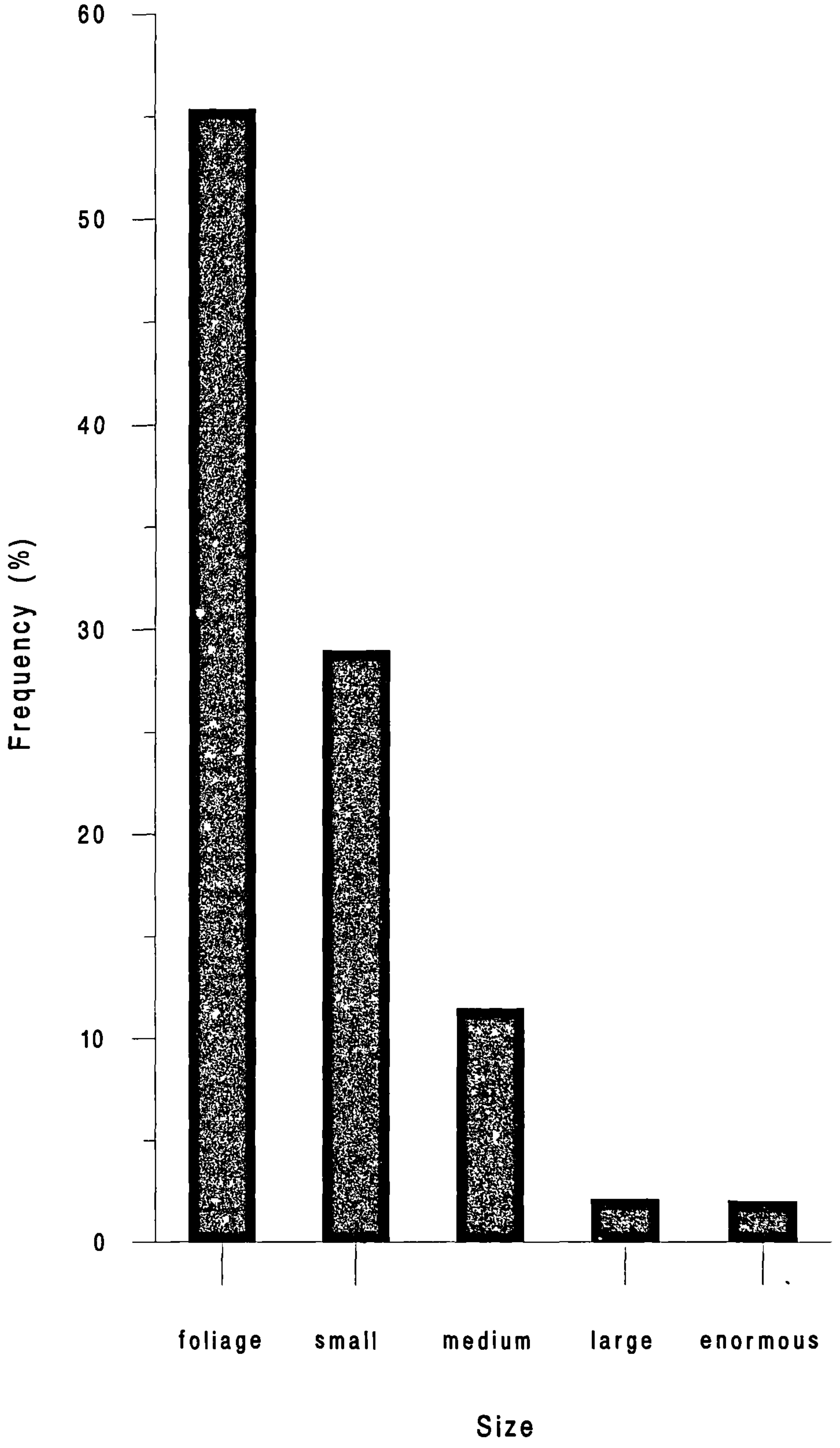


Fig. 3.4c The frequency of supports with different orientations at Ampijoroa

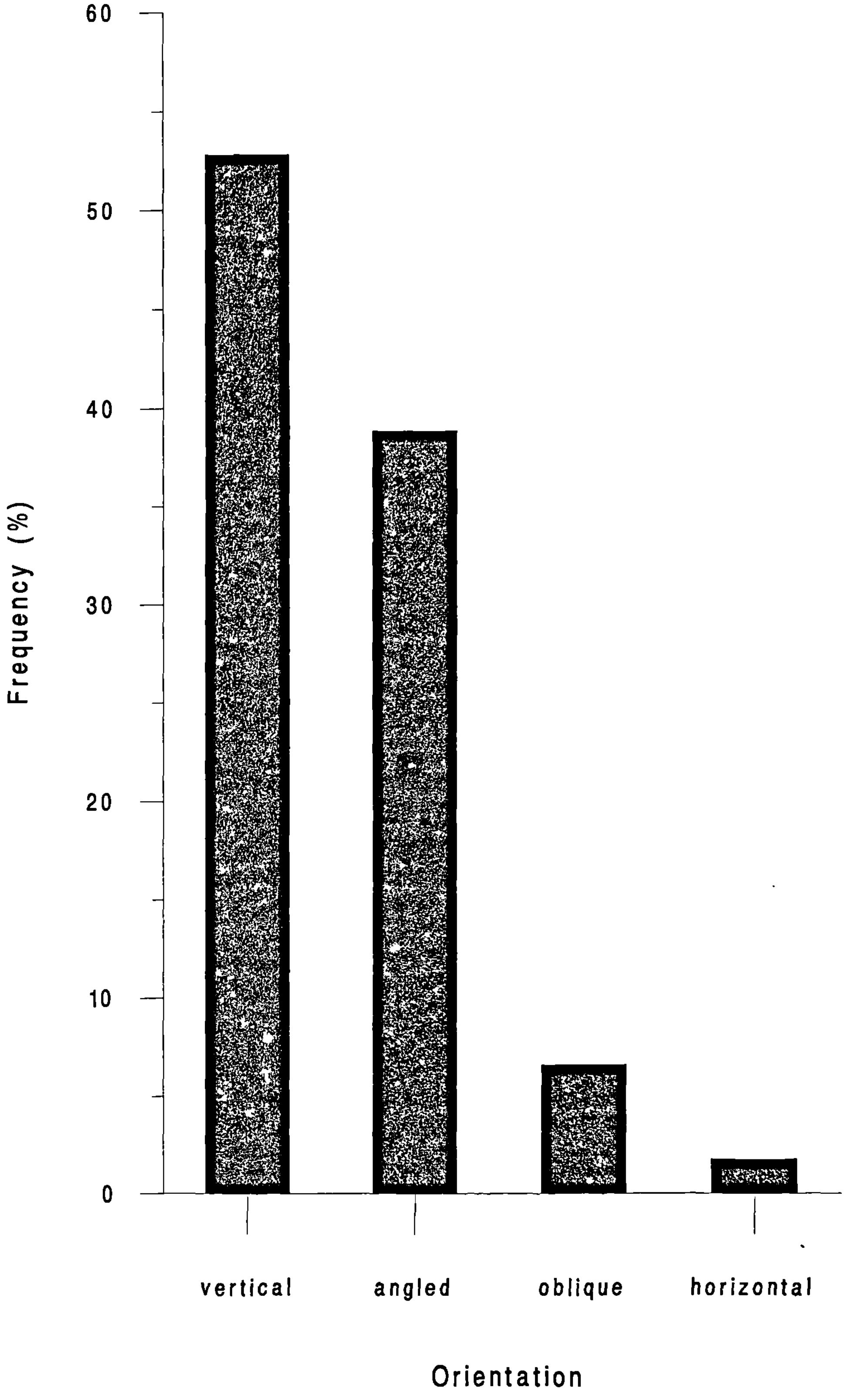


Fig. 3.4d Frequency of support orientations at various heights at Ampijoroa

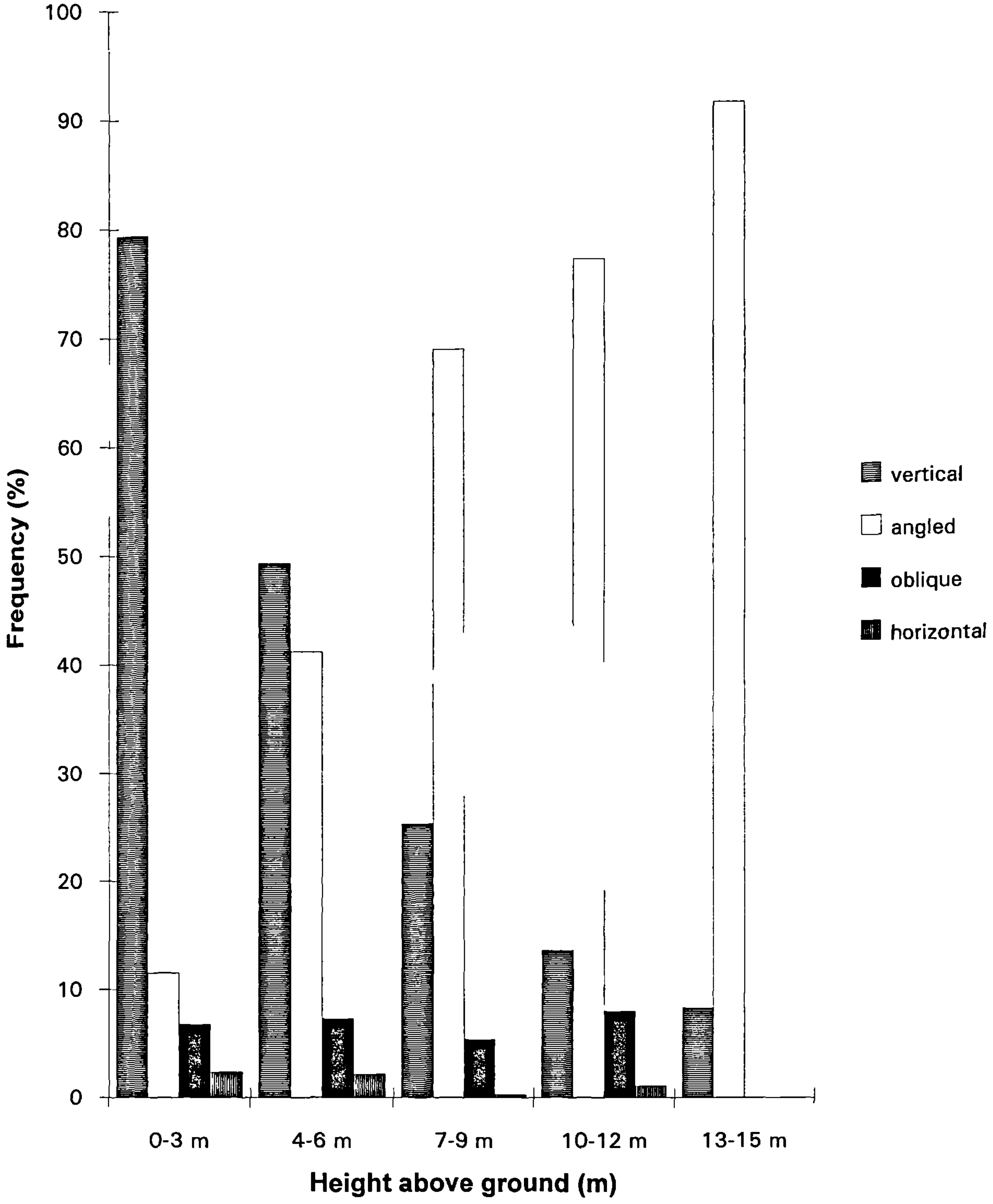


Fig. 3.4e Frequency of size by orientation of supports at Ampijoroa

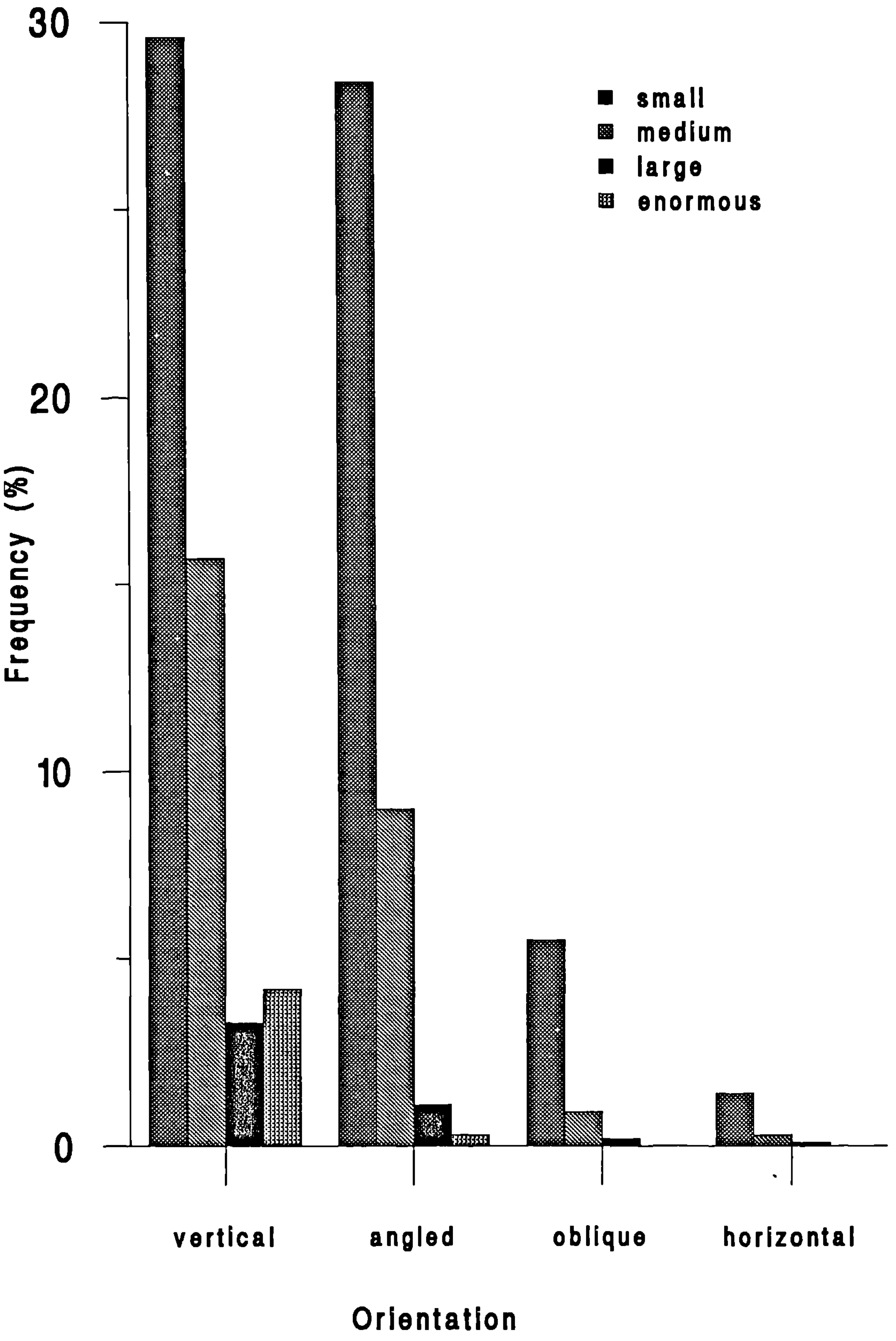


Fig. 3.4f Forest profile of the vegetation within the study quadrat at Ampijoroa

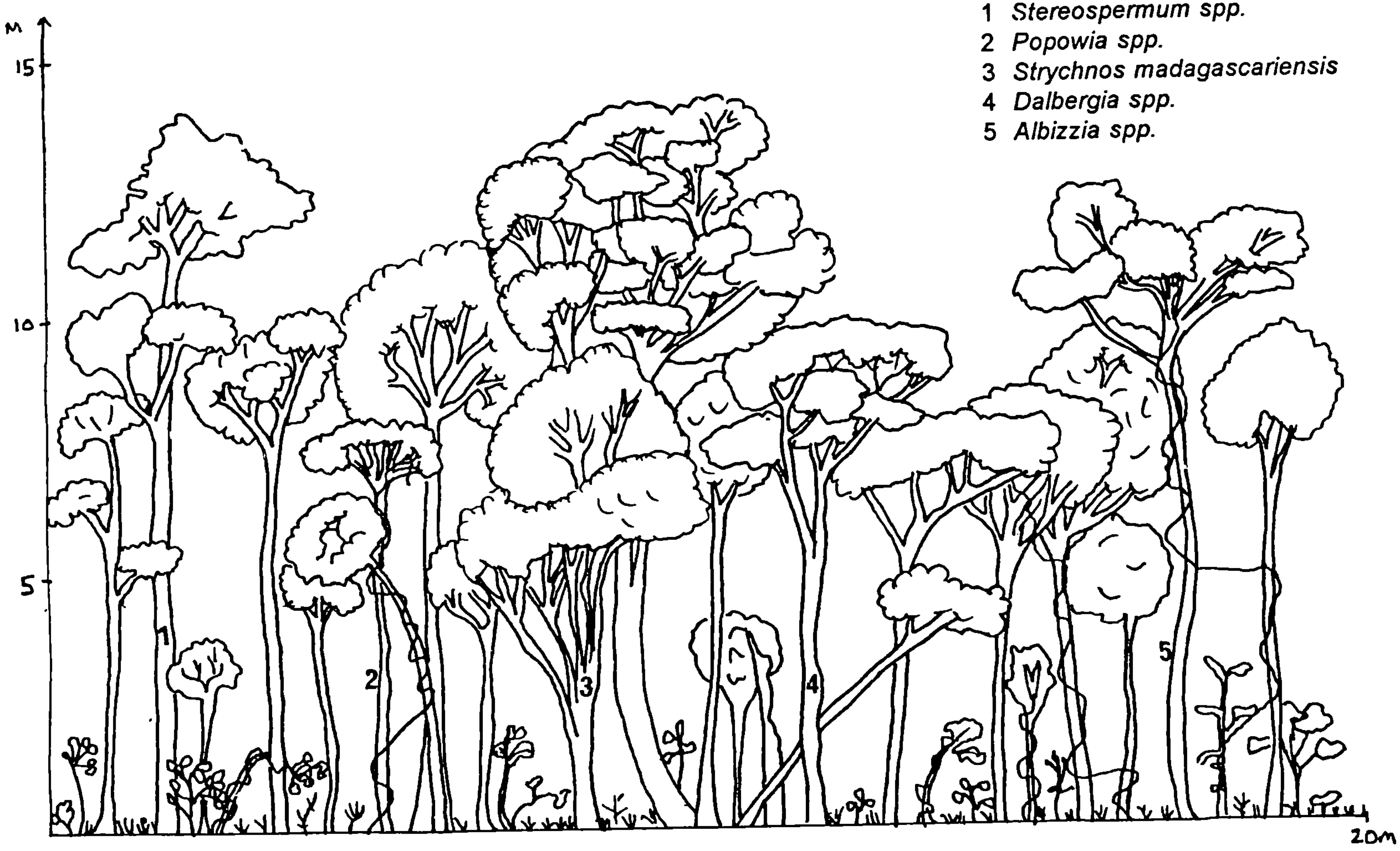


Fig. 3.4g The Jacob's D preference value for first support orientation

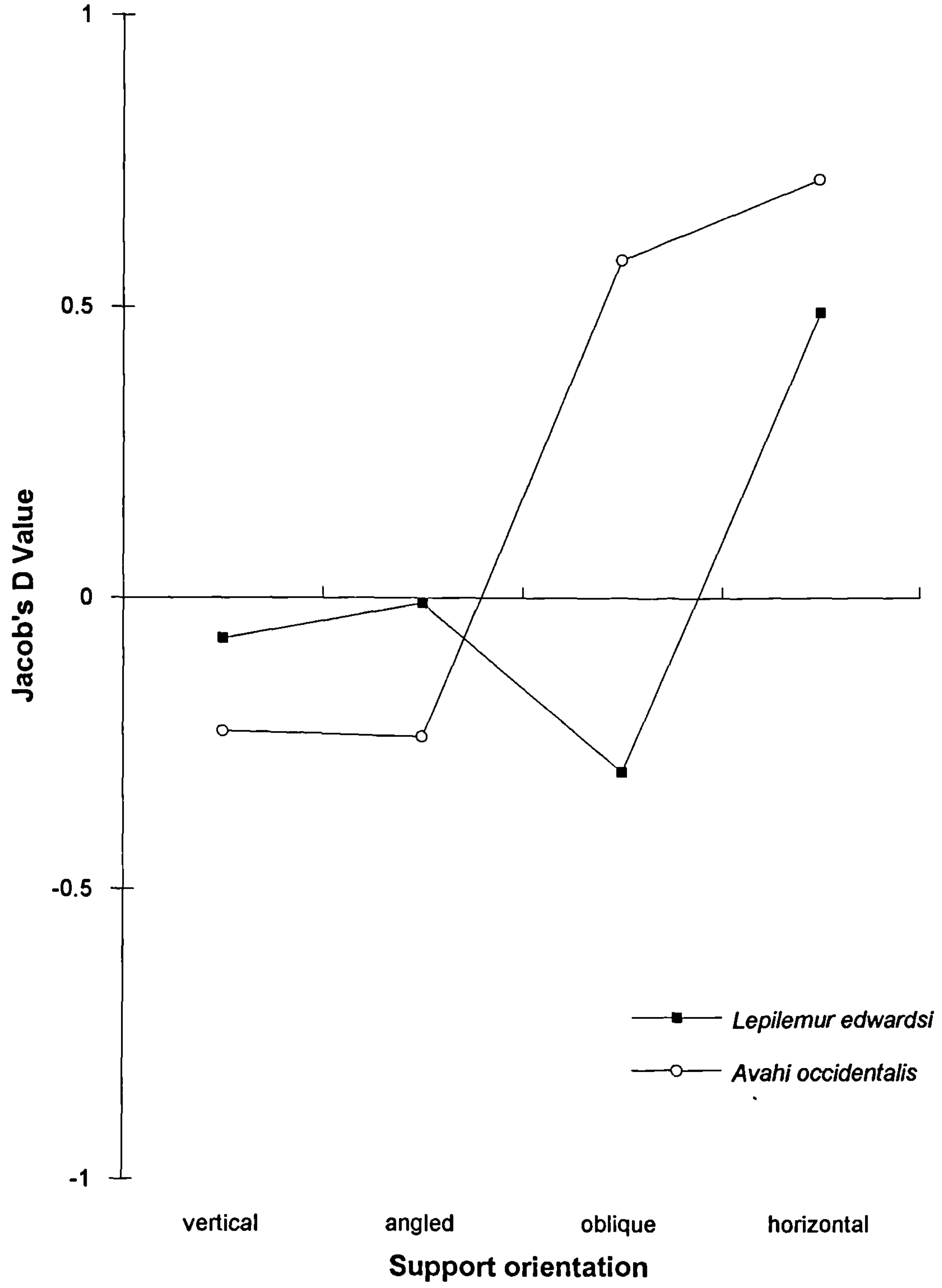


Fig. 3.4h Jacob's D preference value for the orientation of the second support

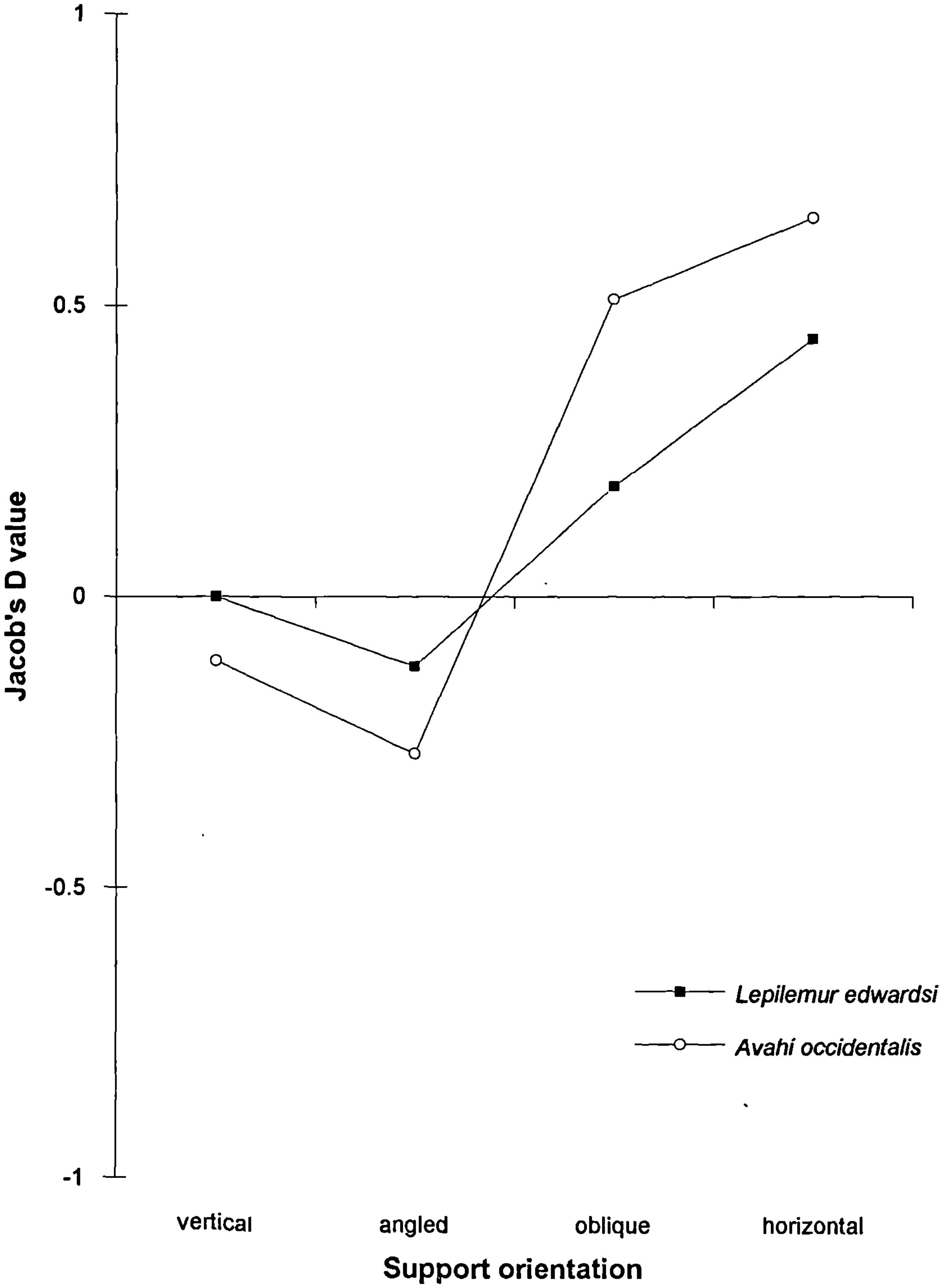


Fig. 3.4i Jacob's D preference value of the diameter of the first support

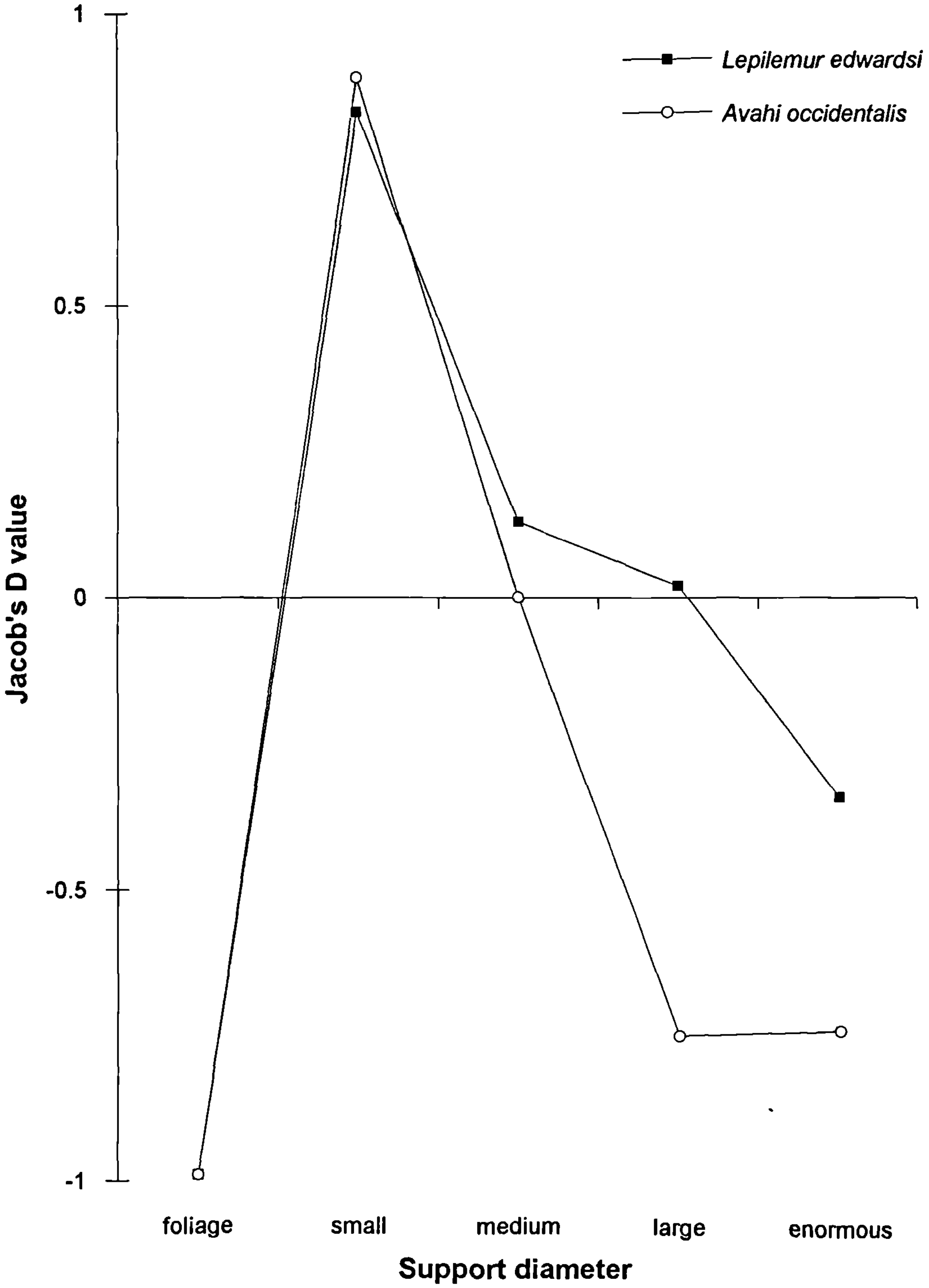


Fig. 3.4j Jacob's D preference value of the diameter of the second support

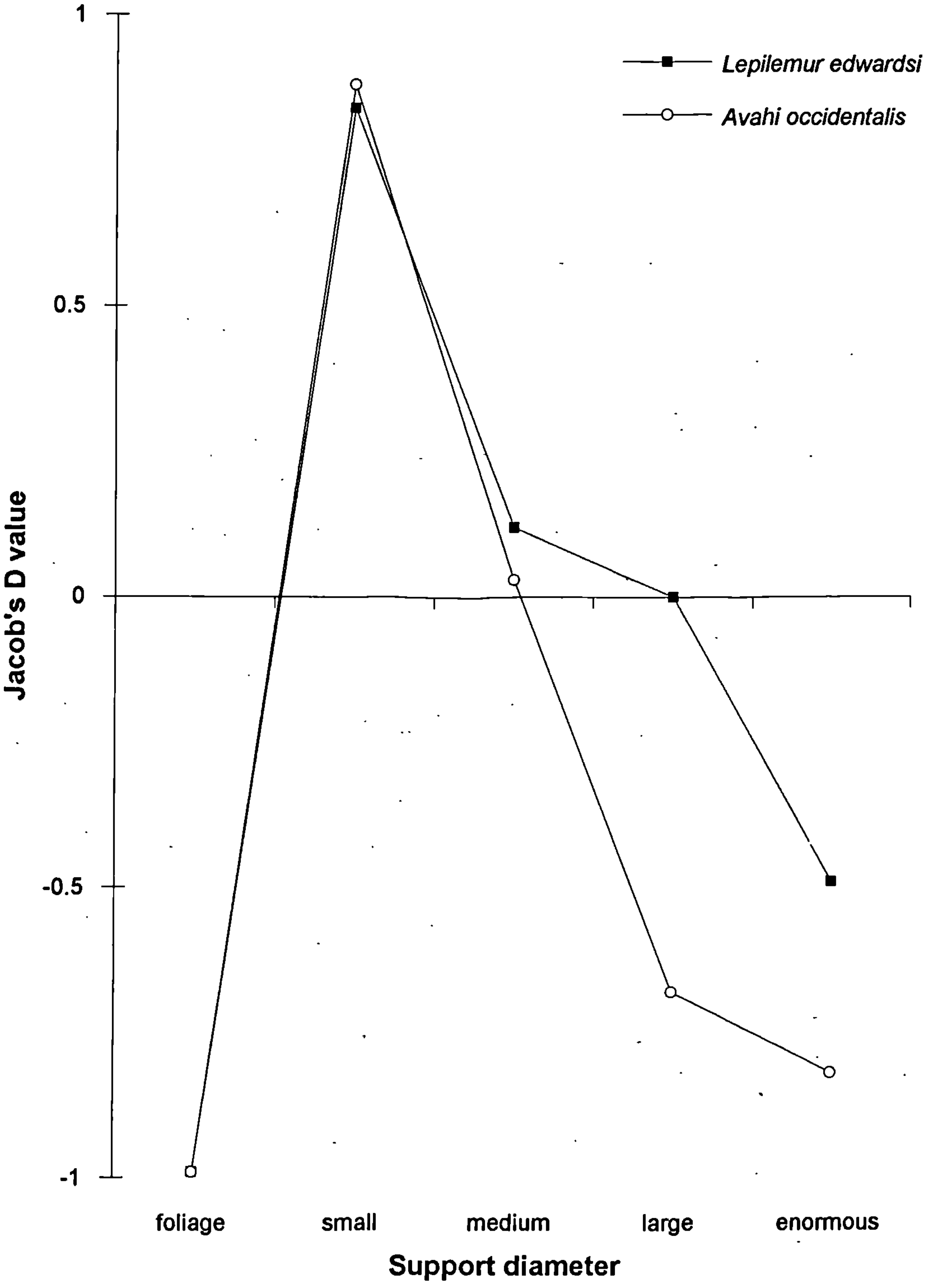


Fig. 3.4k Jacob's D preference value for the height above ground of the first support

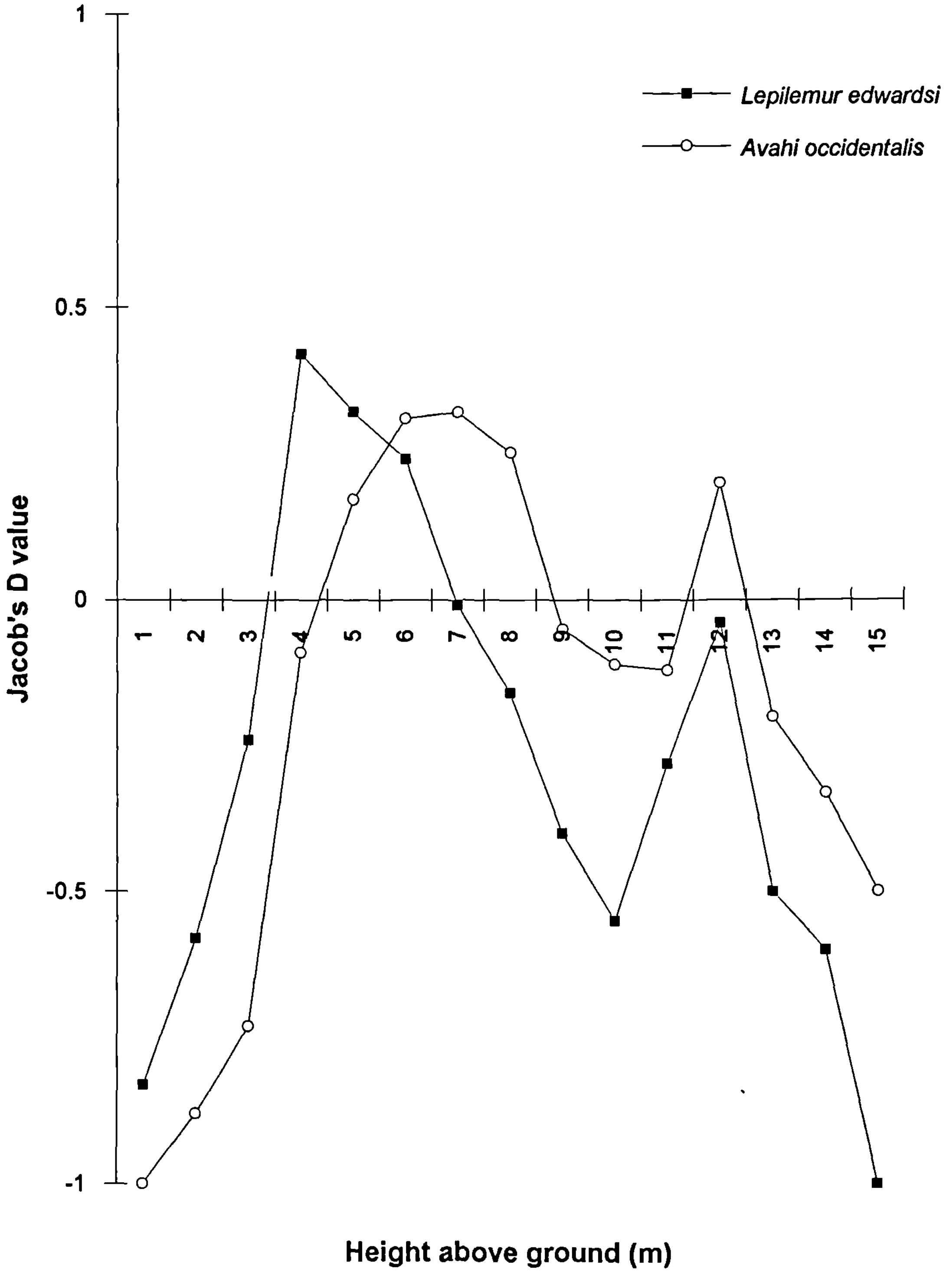


Fig. 3.4l Jacob's D preference value for the height above ground of the second support

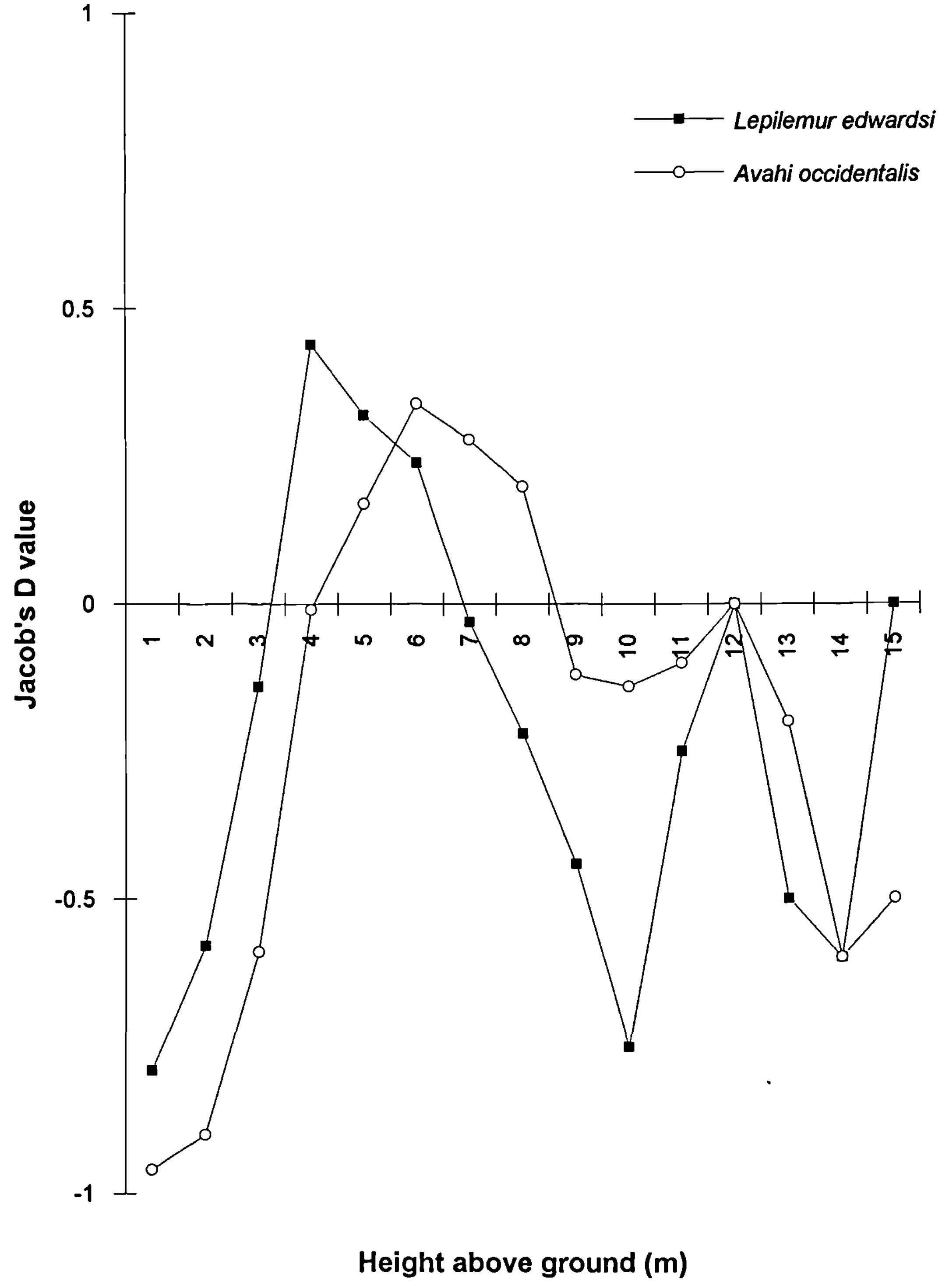


Fig. 3.4m The Jacob's D preference value for the take-off support orientation for leaping

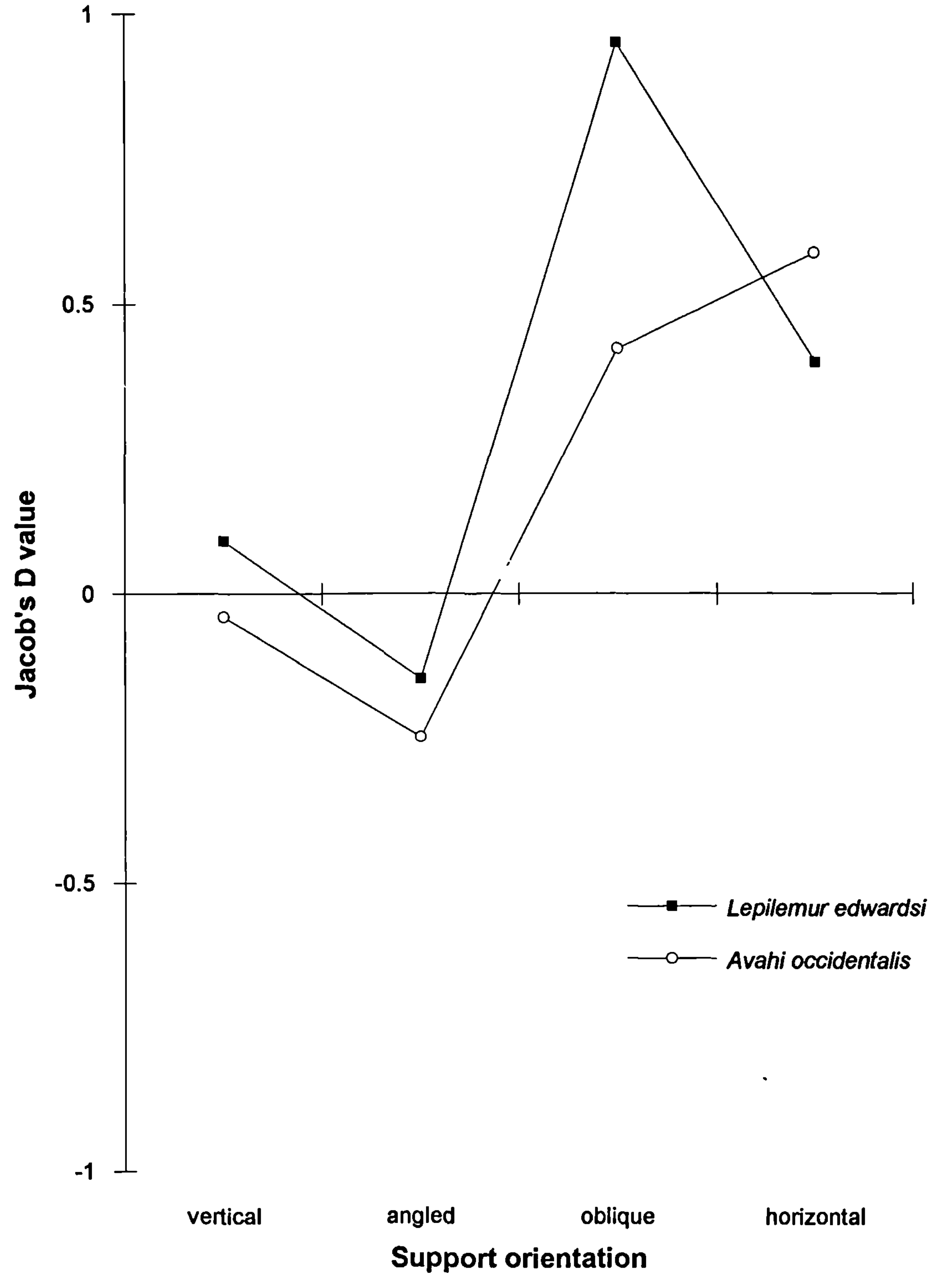


Fig. 3.4n The Jacob's D preference value for the landing support orientation for leaping

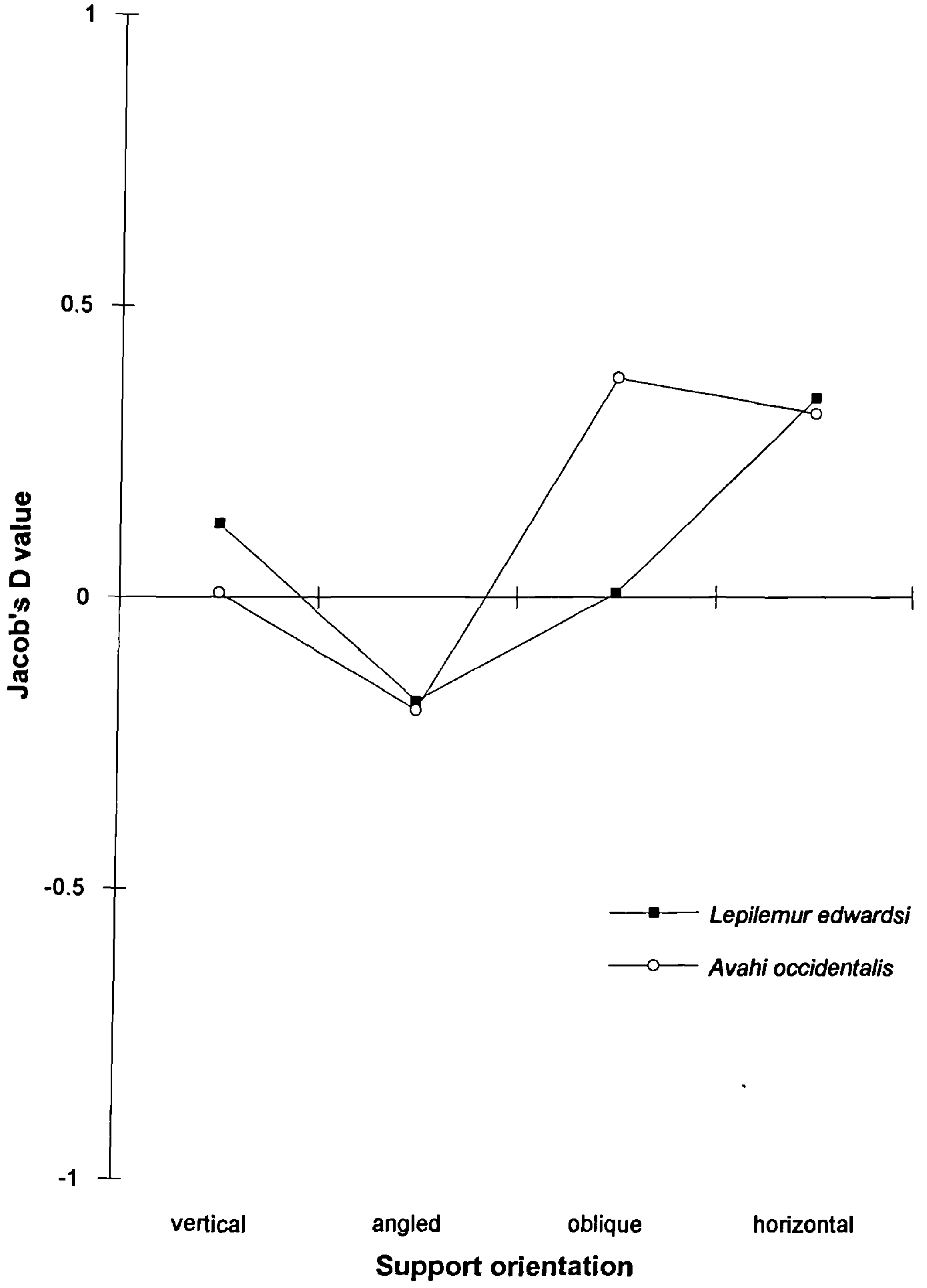


Fig. 3.4o The Jacob's D preference value for the take-off support diameter for leaping

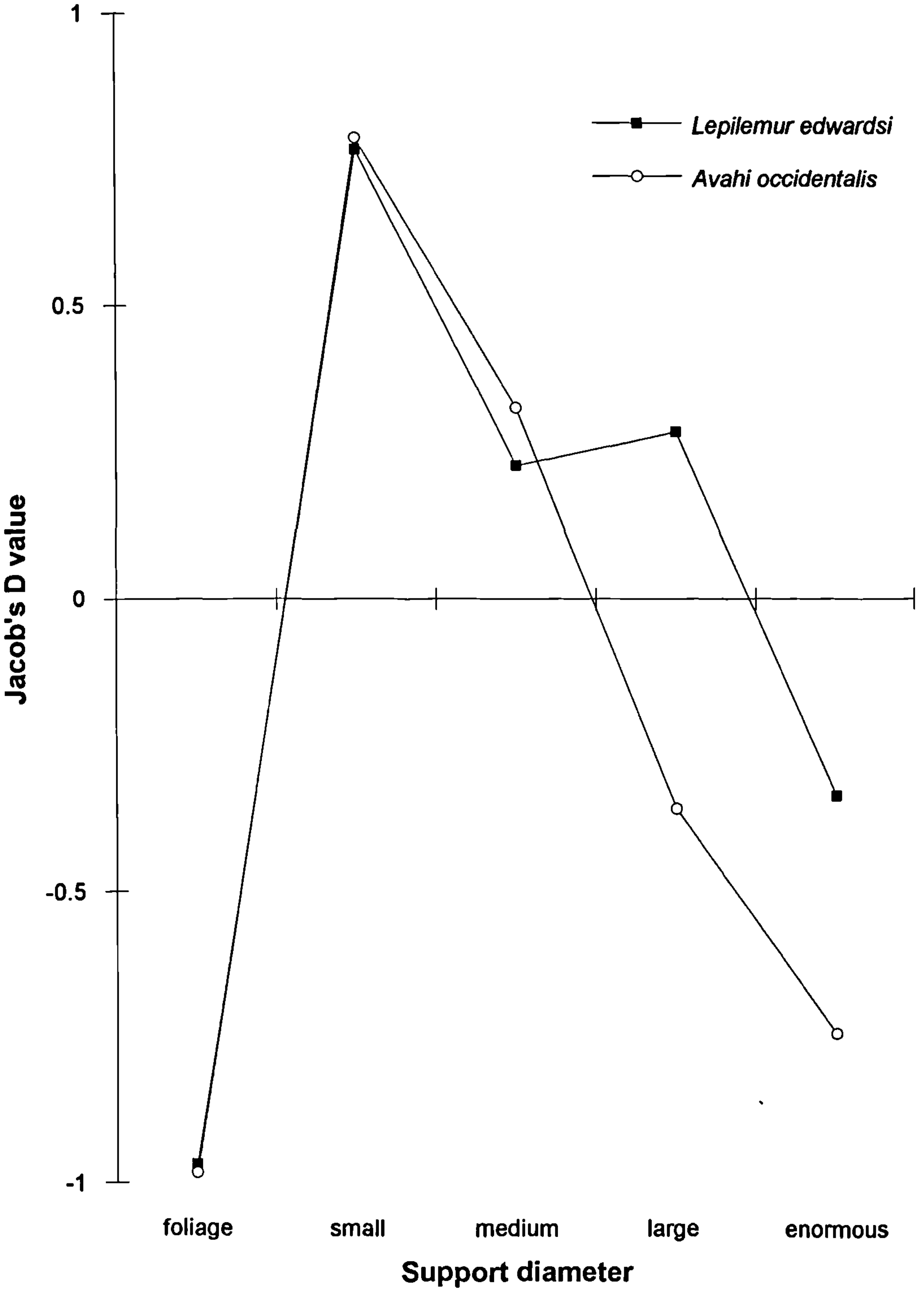


Fig. 3.4p The Jacob's D preference value for the landing support diameter for leaping

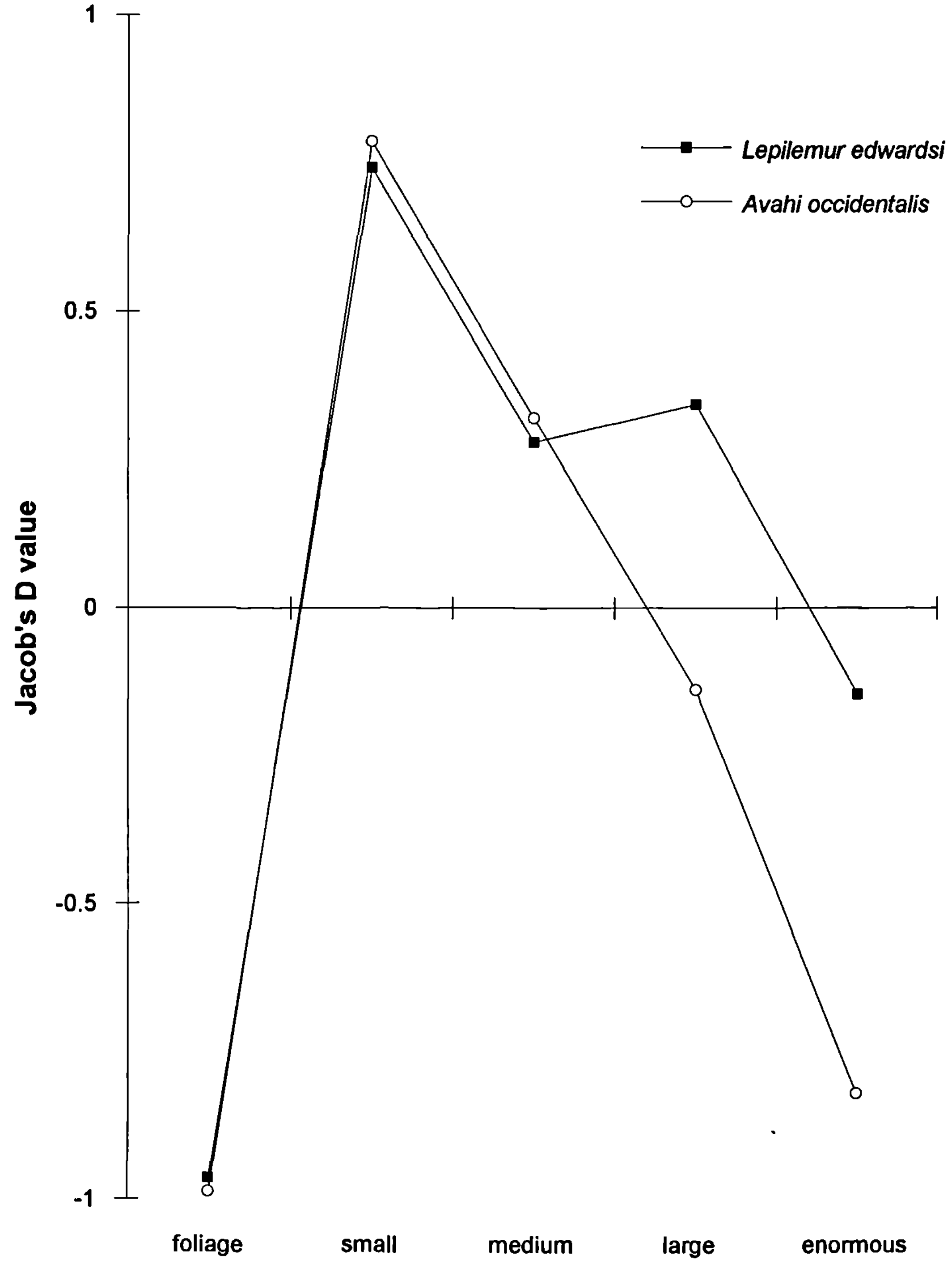


Fig. 3.4 q The Jacob's D preference value for the take-off support height for leaping

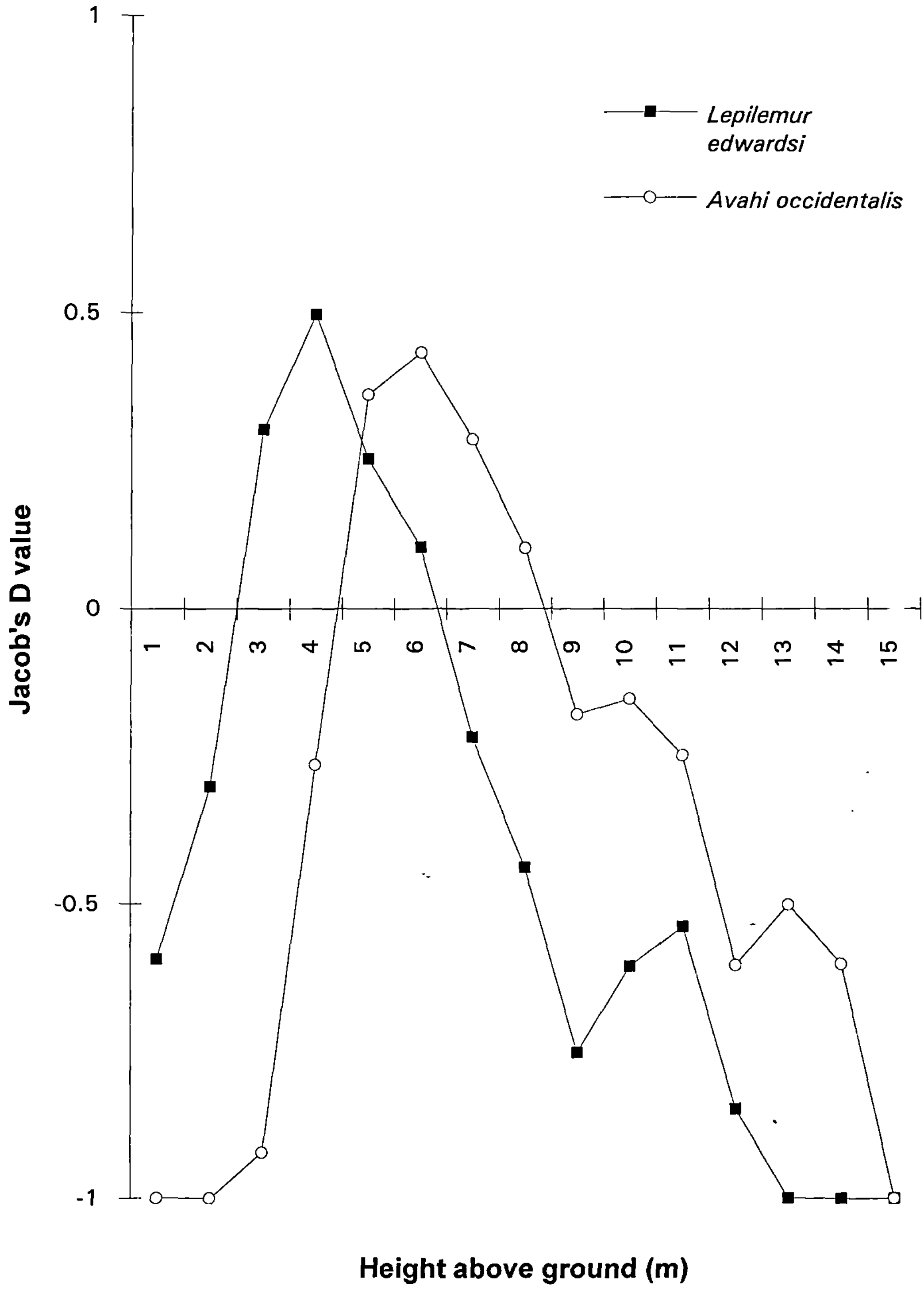
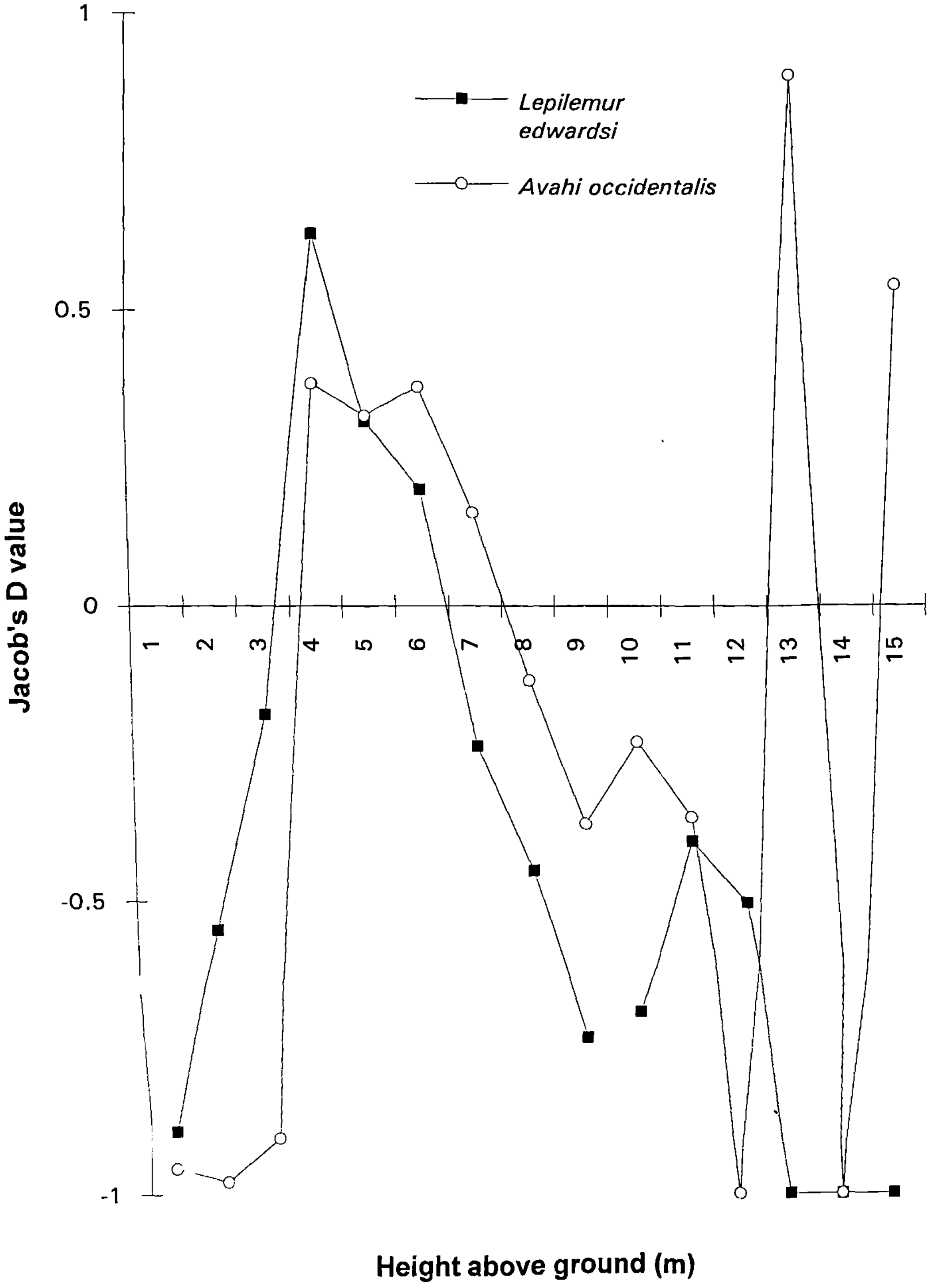


Fig. 3.4r The Jacob's D preference value for the landing support height for leaping



3.5 Discussion

Ampijoroa is a forest comprised predominantly of vertical and angled supports of a relatively small size. For exploitation of such a forest, an arboreal animal also needs to be of a relatively small size, so that the available substrates can support its weight. Further, since supports perpendicular to the forest floor predominate, a habitual quadruped may 'perceive' the forest as consisting more of discontinuities than might an animal which could utilize discontinuous supports for locomotion (*e.g.* a vertical clinger and leaper). It appears therefore that both *Lepilemur edwardsi* and *Avahi occidentalis*, which I have demonstrated as showing a predominance of *use* of such small vertical supports (see Chapter Two), would be ideal animals to exist within this environment. It is not possible to infer, however, that the vertical clinging and leaping behaviour in these species is a result of evolutionary adaptation to precisely this type of forest.

The Jacob's D preference values are of particular interest because they show the observed frequencies of use of substrates compared to their *availability* in the forest. It is therefore possible to assess whether or not the animals choose supports with particular qualities. Considering the orientations of supports in the forest, while vertical and angled branches are the most frequently used, both species in fact show a slight tendency for avoidance of angled and vertical supports. *A.occidentalis*, in particular, chose to use oblique and horizontal branches. The high preference for these types of support is possibly due to *Avahi*'s typical feeding behaviour. This species feeds higher up in the forest canopy than *Lepilemur edwardsi*, choosing the younger leaves and flowers (see Chapter Five). It seems likely therefore that the animals will choose oblique and horizontal supports within the tree crowns as stable bases whilst feeding. *L.edwardsi* tends to inhabit lower parts of the forest and feed on the more ubiquitous older leaves, which can be accessed lower down, from vertical trunks. It showed a marked avoidance for oblique first supports (Fig.3.4g). Interestingly, from Figure 3.4h, it appears that *L.edwardsi* shows a preference for oblique second supports, suggesting that it prefers to end locomotor bouts on a support which is sloping rather than angled in orientation. However, there is little difference in preference for the first and second support in *A.occidentalis* (Fig. 3.4g,h).

Both *Lepilemur edwardsi* and *Avahi occidentalis* show marked avoidance for 'foliage' (*i.e.* supports less than 0.5 cm in diameter) presumably because of their flexibility (Fig.3.4i,j). The patterns for the Jacob's D value are very similar for the first and second support suggesting no discrimination in choice of supports for the start and end of locomotor bouts. The animals are able to use foliage, but usually employ it as a 'mattress' for the landing after a jump, or when arm-swinging, (both of which were rare events, see Chapter Two). Cannon and Leighton (1994) showed that macaques used more flexible branches when crossing between tree crowns. This they linked to a limit in the size of gap the macaque could cross, concluding that the macaques were forced to use the extreme periphery of the crowns. Although compliance was not measured in the present study, the low frequency of use of branches and foliage of less than 0.5 cm in diameter, suggests that *L.edwardsi* and *A.occidentalis* are able to locate adequate numbers of branches large enough to support them, and are not forced to use the extreme periphery of a branch where the supports are possibly more densely packed.

Small supports of 0.5 to 5 cm in diameter are strongly preferred by both species. *A.occidentalis* strongly avoids branches over 10 cm in diameter. However, *L.edwardsi*, in this study, seem to use large supports of between 10.1 cm to 15 cm in diameter at their frequency of occurrence, although above this diameter, strong avoidance is displayed. Could the above suggest better morphological adaption to larger branches in *L.edwardsi*, or is this finding purely a consequence of difference in niche? Figure 3.4e shows that the largest percentage of bigger branches within the forest were vertical. This corresponds with a greater frequency of use of vertical supports, lower in the forest by *Lepilemur edwardsi* compared with *Avahi occidentalis*. The mean diameter at breast height (DBH) is within the preferred size of support for both species.

The patterns of Jacob's D value for the heights of supports are again similar for the first and second support (Fig. 3.4k,l). *L.edwardsi* preferred supports at a height of around four to five metres, with considerable avoidance of supports at around ten metres in height. At twelve metres *L.edwardsi* used the supports according to their availability. Higher categories were avoided. *A.occidentalis* preferred branches slightly higher than those chosen by *L.edwardsi*, at around six to seven metres above the forest floor. From Figure 3.4f it can be seen that the heights preferred by *A.occidentalis* coincide with the location of the greater part of the canopy. The lower heights preferred by *L.edwardsi* coincide with the location of most of the tree trunks. Why both species should show an increase in preference for supports twelve metres high is unclear. However, in Jardin Botanique A, twelve metres is the height of the top of the canopy. Supports higher than this were rare and were generally emergents (Fig. 3.4f). The top of the canopy was commonly used for calling, particularly by *Avahi occidentalis* (see Chapter Four).

For both species, the Jacob's D preference values for support use while leaping (Figures 3.4m - r), show a distinct difference in support preference for take-off and landing. *L.edwardsi* preferred oblique supports for take-off. In all cases angled supports were avoided by both species for landing and take-off. One possible reason for this may be related to the angle of contact that the feet have with the substrate at take-off and landing. When the animals are leaping, the feet need to have good contact when pushing off. It may be that if the support is vertical or sloping, the animal could push off from the side or the top of the branch. However, if the branch is angled, the top of the branch may be too slanted to push off from, and take off from the side of the branch may be precarious, as the body has to compensate for the downward slant of the support. Similarly, branch angle may present a problem for touch-down. The Jacob's D values show that despite the high frequency of vertical supports within the forest, *L.edwardsi* showed a yet higher frequency of preference for vertical supports for take-off and landing. This corroborates evidence suggesting a higher degree of specialization for vertical supports in *L.edwardsi* than *A.occidentalis.*

While small branches (0.5-5 cm) were the most frequent in the forest, it remains true that when leaping, both species showed a marked preference for small branches. The patterns of the Jacob's D value for the first and second support are very similar (Fig. 3.4o,p). In accordance with general support preferences during locomotion, *A.occidentalis* avoided branches of over 10 cm in diameter. *L.edwardsi* preferred small, medium and large branches, and avoided branches of over 15 cm in diameter. Both species strongly avoided using foliage for take-off and landing, and neither species had a strong tendency to use foliage as a 'mattress' for landing, as has been observed in leaf monkeys (Fleagle 1978).

The mean leap length for *L.edwardsi* and *A.occidentalis* is much less than the mean inter-tree distance observed. If *L.edwardsi* was indeed inhabiting the lower part of the forest where there is a predominance of tree trunks, one would expect its mean leap distance to be bigger than that of *A.occidentalis.* Presumably, in the canopy, the gaps between trees are smaller due to branch spreading. However, the locomotion data suggested that *A.occidentalis* is a more committed leaper than is *L.edwardsi* (see Chapter Two). It may be, therefore, that *L.edwardsi* picks its route through this part of the forest carefully, and chooses routes with small gaps. Cannon and Leighton (1994) showed that the majority of gaps present between tree crowns in Borneo were much wider than the gaps that were usually crossed by macaques; and for gibbons, one third of the existing gaps were too wide to cross. In this study, gap size was not measured, but the mean crown diameter was found to be 2.8 m This diameter is wider than the inter-tree distances so it is probable that there is some degree of canopy overlap between the trees. In travel, the animals usually do not need to take canopy gaps into consideration.

From qualitative observations it was soon apparent that the animals were regularly using particular arboreal pathways. The nature of the forest architecture appeared to limit the choices that the animals could make in, (for example) accessing favourite feeding trees. Support size, angle, and height are clearly important factors in determining possible routes between trees.

Ganzhorn (1989) in his study of lemurs in Madagascan rain forest showed that segregation of sympatric lemur species was achieved by the existence of structurally and phenologically distinct microhabitats. Similarly, Gautier-Hion *et al.* (1981) depicted forest structure and the availability of fruits as complementary factors influencing the habitat utilization of *Cercopithecus* monkeys. Other studies have shown that body size has influenced habitat choice by regulating the use of different sized supports (Mittermeier & van Roosmalen 1981; Fleagle & Mittermeier 1980; Harcourt & Nash 1986b) and that different morphological and behavioural adaptations are linked to choice of locomotory supports (Fleagle & Mittermeier 1980; Gittins 1983; Crompton 1984). Choice of food also influences habitat preferences for primates (Chivers & Hladik 1980; Rodman & Cant 1984; Crompton 1984; Fleagle 1985). However, until this study, these preferences have not been meaningfully quantified for any prosimian in comparison to the choices available within the habitat. This study has shown that the frequency of observations of both species on supports with particular qualities does not usually coincide with the frequency of these supports in the environment. Both species showed a preference for small sloping and horizontal branches, but they select them at different heights in the forest and with varying degrees of preference and avoidance for the other available supports. These variations in detail of support preferences will certainly aid the maintenance of species segregation. The high preference by both species for horizontal branches is surprising in species assigned to the VCL category, but it may be biologically important, and highly critical for the animals' adaptability to the environment. Even more striking in this context is the preference by both species for more sloping supports.

4 Ranging and Social Behaviour

4.1 Introduction

Most primates restrict their activities to a familiar, measurable area of the environment in which they live (DeVore 1963, Jay 1965). The chosen area must have food and shelter to sustain the animals. This utilized area has been termed the 'home range'. The home range of a species is the area which will provide all the necessities for survival (Jewell 1963). A 'complete' home range is the area utilized by the animals over the entire year. A home range is not defended from incursions of other animals; a defended home range is referred to as a 'territory' (Burt 1943). The animal does not usually visit all parts of its home range during one day or one night (Bearder 1974; Whitten 1982; Ganzhorn 1985; Crompton 1987; Pagès-Feuillade 1988). Home ranges in some animals change seasonally if resources, such as food, are limited (*e.g.* hamadryas baboons: Dunbar & Dunbar 1974a; macaques: Wada & Ichiki 1980; squirrel monkeys: Terborgh 1983). Because of this, the terms 'seasonal' and 'nightly' ranges are also used.

A home range is not used to the same extent throughout its area. Within a site there is often a patchy distribution of food and sleeping sites which encourages the animals to favour certain parts above others (*e.g.* Whitten 1982; Crompton & Andau 1986). Kaufmann (1962) therefore recognised 'core areas' within the home range. These are the most utilized areas containing the major food sources and sleeping sites. They can be identified by defining the area which is used more than would be expected from a uniform distribution of activity. Core areas can be exclusive to individual social groups, as is observed in *Indri indri* (Pollock 1979), *Propithecus verreauxi* (Richard 1978) and *Aotus trivirgatus* (Wright 1986), although some primates such as gorillas do not have exclusive core areas (Schaller 1963). A home range may overlap with that of other individuals or groups of the same species, as is the case in *Galago* *senegalensis* (Bearder and Martin 1979), *Galago garnettii* (Harcourt 1984), *Perodicticus potto* (Charles-Dominique 1977), *Tarsius bancanus* (Niemitz 1984) and *Eulemur mongoz* (Tattersall 1978).

There is no measure of home range to date able to take into consideration the possible vertical as well as horizontal dimensions of the home range for an arboreal animal. While using horizontal range as a convenient shorthand, the vertical dimension of home range must always be borne in mind.

Most species benefit from moving in a fairly defined area rather than by being totally nomadic. This allows familiarisation with food sites, sleeping sites and the best routes between them. The size of the area needed by the animals to ensure sufficient energy input is determined by several influences a) the body mass of the animal; b) the number of animals foraging together; c) the type of food; d) the quality of the food; and e) its location in time and space. These factors influence the distance travelled in a daily or nightly bout, the overall density of the species and the home range size (Dunbar 1988). These general variables are further complicated by metabolic rate, activity patterns and the seasonal fluctuation of food resources at any given site. Species which feed on a food source which is widely distributed tend to have longer daily/nightly travel distances and larger annual home ranges. Such tree-borne food resources will tend to be more 'clumped' than those on the ground. Terrestrial species for this reason tend to have larger home ranges than do arboreal primates; and similarly frugivores tend to have larger home ranges than folivores (Sussman 1977; Mace & Harvey 1983; Oates 1986). Folivores tend to have higher population densities than frugivores because fruits are more patchily distributed than are leaves. Thus, 'herbivorous' gelada baboons can maintain population densities which are three times those of 'frugivorous' olive baboons in the same habitat (Dunbar & Dunbar 1974b). Comparative studies based on nutritional quality of food sources have shown that population density declines as habitats become increasingly impoverished, and groups of similar sizes require larger ranges in poorer habitats than in rich ones (*e.g.* orangutans:

MacKinnon 1974; sifakas: Richard 1978; baboons: Anderson 1981). Pough *et al.* (1989) suggested the 'resource dispersion hypothesis' which takes these general principles one step further. The hypothesis predicts that the size of the home range of an individual will depend primarily on the resource needs of the individual and the distribution of resources in the environment.

Home range sizes have been shown to be related to body mass (Milton & May 1976), so that larger bodied primates have proportionally larger home ranges. The area of the home range can also be related empirically to the body mass of the animal (Harestad & Bunnell 1979) using the equation

$$H = a\ W^k$$

where H represents the home range size and W is the body mass of the animal. The constant k varies for herbivores (1.02), omnivores (0.92) and carnivores (1.36). If energy requirements determine home range size, one would expect the home range to increase by the power of 0.75, since metabolic rate scales with body mass to the power of 0.75 (Kleiber 1961, for further discussion of this relationship see Chapter Six). Home range size does indeed increase, but at a rate faster than expected. Explicit treatment of energetic requirements of animals and the productivity of their habitat gives a value of $k > 0.75$, because of the declining ratio of productivity per unit area of habitat to metabolic energy needs with increasing body mass (Harestad & Bunnell 1979). Therefore, home range size increases with respect to body mass, but not with the same power relationship as does metabolism. Also, although density of food resources influences this relationship, the influences of body mass account for 75-90% of the interspecific variation in size of mammalian home ranges. Importantly, mass alone may account for a large portion of the differences between male and female, or subadult and adult, home ranges (Harestad and Bunnell 1979).

Because body mass is positively correlated with home range area and because specialist feeders tend to have larger home ranges than do generalists of equivalent body mass, it has been widely accepted that species differences in home range size are related to differences in the metabolic needs of the animals concerned. Work by Harvey and Clutton-Brock (1981) suggested that primate home range size is a function of the metabolic needs of the animals and also of the quality of the diet. However, when they tested this hypothesis using data from the literature, the results, while showing trends towards the predicted values, were not exactly as predicted. Incomplete agreement with the resource dispersion hypothesis and the various factors that influence home range size have suggested that the concept of home range is a complex one. For example, Damuth (1981) pointed out that an individual's home range area is a function of the way in which the local population of a species, not just the individual, exploits the environment. From an overall ecological perspective, the distribution of resources needed by the animals is a major influence in determining its social structure.

Some form of group living is found in nearly all vertebrates. All non-human primates show some form of social grouping which allows for the two sexes to meet for mating at oestrus. Social behaviour interacts with food gathering, locomotion, predator avoidance, the physiology and morphology of the species, and with the distribution of resources within the habitat.

Three ecological factors seem to influence the social system of a primate particularly strongly:

1. **Defensibility of given food resources**. A primate may respond to this problem by: a) not defending the resources, b) defending a territory individually, or c) joining with other animals and defending the territory as a group.
2. **Overall distribution and availability of the food** will limit group size and stability.
3. **Predator avoidance** will influence behaviour of the animals. A larger group is better able to defend the young from predators but causes more intraspecific competition.

Three main social groupings are recognised in primates. These are:

1. multi-male groups with several females and their young,
2. one male groups with several females and their young,
3. family groups consisting of a mated pair and their young.

Lepilemur edwardsi has been thought to be solitary, sometimes sleeping with two or three other individuals, but moving around separately at night (Albignac 1981b, Petter *et al. 1977*). *Lepilemur* lives in 'neighbourhoods' where a single adult male has a home range which overlaps those of several females (Hladik & Charles-Dominique 1974, Russell 1977). The females, in turn, have home ranges which overlap considerably those of other females. 'Satellite' or 'vagabond' males lack home ranges. They live on the periphery of a neighbourhood, and fill a vacancy if a resident male dies (Charles-Dominique & Hladik 1971). *Avahi* on the other hand has been considered to be monogamous, living in family groups consisting of a pair and offspring (Albignac 1981; Ganzhorn 1985; Harcourt 1991). As each offspring reaches maturity, it encounters hostility from one or both of the parents and it is forced to leave. Darwin in 'The Descent of Man' (1871) suggested that monogamy is often seen in species where there is little sexual dimorphism (*e.g.Avahi laniger*: Harcourt 1991; gibbon: Robbins Leighton 1987; *Aotus trivirgatus*: Robinson *et al.* 1987). It has also been suggested that monogamy can exist when a single male is unable to defend more than one female (*e.g.* Kleiman 1977; Rutberg 1983). Again, a low level of predation is thought to favour small group size and hence monogamy (*e.g.* van Schaik & van Hoof 1983). However, it seems likely that *Lepilemur edwardsi* is under the same predation pressure as is *Avahi occidentalis* at Ampijoroa. The reasons why these two apparently similar species adopt two different social systems still remain unclear.

Primates are either diurnal (*e.g. Hylobates klossii*, Whitten 1982), cathemeral (*e.g. Eulemur mongoz*, Sussman & Tattersall 1976) or nocturnal (*e.g. Galago crassicaudatus*, Harcourt 1984). Diurnal animals are day active, nocturnal animals are night active and cathemeral animals can be active either day or night, and each of these patterns of activity may occur seasonally or year round (Tattersall 1988, Engqvist & Richard 1991). Nocturnality is considered to be the primitive condition for primates: over three quarters of the prosimians are nocturnal including both *Lepilemur edwardsi* and *Avahi occidentalis* (Martin 1990).

Activity patterns for primates are often of a biphasic nature, with peaks of activity at dusk and dawn and a resting period in the middle of the active part of the cycle (*Eulemur fulvus fulvus* and *Lemur catta*: Sussman 1977; *Hylobates*: Raemaekers 1978; *Galago crassicaudatus*: Bearder 1974; *Galago demidovii*: Charles-Dominique 1971). However, in other nocturnal prosimians, no consistent pattern is apparent (*Galago crassicaudatus* and *Galago senegalensis*: Harcourt 1980, *Euoticus elegantulus, Galago alleni, Perodicticus potto* and *Arctocebus calabarensis* : Charles-Dominique 1971 and *Lepilemur mustelinus:* Hladik & Charles-Dominique 1974). The functional significance of the biphasic nature of activity in diurnal primates may be a reaction to a peak in day temperature, or may allow maximum intake of food ingested per day (Clutton-Brock & Harvey 1977). Clutton-Brock and Harvey (1977) suggested that to maximise the bulk of leafy material taken in, it would be best for the animal to feed at the beginning of the day, then to take a period of rest and digestion, before feeding again, when the stomach is emptying, towards the end of the day, since food can be digested throughout the night. Presumably the same argument applies for a nocturnal animal, with peaks of feeding at the beginning and end of the night. External conditions such as seasonality, ambient temperature, and food type and availability would be expected to influence the temporal patterning of activity of a species.

Both *L.edwardsi* and *A.occidentalis* are small folivorous primates, which energetic considerations suggest will have a relatively high metabolic rate per unit body mass (Kleiber 1961, Pough *et al.* 1989). To gain access to proteins in leaves, utilizing symbiotic bacteria in the gut, fermentation of the cellulose within the leaves has to take place (Bauchop 1978). This form of digestion takes time and it therefore seems likely that these small but folivorous primates will have tight energy budgets. Activity patterns are crucial in managing energy and time budgets to minimize energy expenditure, particularly in species, such as *L.edwardsi* and *A.occidentalis*, with a high metabolic rate.

4.2 Aims

The aims of this part of the project were to study the ranging and social behaviour of *Lepilemur edwardsi* and *Avahi occidentalis* over a complete year, including for the first time, complete all night 'follows'.

4.3 Methods

4.31 Field methods

The animals were caught and tracked using the method described in Chapter Two, section 2.3. Dates of capture, and additional metric information are summarized in Appendix 2.

At five minute intervals throughout the night 'follow', a piece of forestry flagging was left at shoulder height at the approximate position of the animal. These flags were consecutively numbered from 1 to 144 and were placed in numerical order. The approximate position of the flag within the quadrat was recorded onto a cassette to assist in finding the flags the next day. After the data had been transcribed from the tape, the site was surveyed by locating the numbered flags sequentially and measuring distances and angles between them using a compass and tape measure. Thus, the nightly distance travelled and, ultimately, the home range could be plotted. Throughout the 18 months of field work, efforts were made to track both *Lepilemur edwardsi* and *Avahi occidentalis* on nights evenly scattered through the calendar, but field conditions made a statistical sampling of seasonality impossible.

4.32 Data analysis

The compass bearing and the distance between points were entered into a ranging programme written by Mr.R.Savage (HACB, Liverpool University). This programme plotted the nightly distances travelled, and calculated the home ranges by fitting an envelope around all known sightings of an individual (Bearder & Martin 1979). The programme also measured distances travelled and the area of the home range (to two decimal places).

4.4 Results

4.41 Social Behaviour in *Lepilemur edwardsi*

Calling

Vocalisations of *Lepilemur edwardsi* were very frequently heard but were difficult to record and analyze. It was hard to pin down the exact number of calls as there were several repertoires that seemed to be 'mixed and matched' on different occasions. The most common call was a loud, long screeching "weeeeek" with increasing pitch which was usually made on emerging from the day's rest in a tree hole. This was usually repeated several times, and a call sequence could last for several minutes (30 minutes is the maximum duration recorded). This call was also made throughout the night, and before entering the sleeping tree at daybreak, although these are not the only occasions on which it occurs. It was not uncommon during the 'follows' that on emerging from the sleep tree, an animal would call and another *L.edwardsi* would soon join the calling animal and they would move off together. This might suggest that this call was not purely a territorial or defence call, but rather an 'advertisement' of the animal's whereabouts. Sometimes a call was heard from elsewhere apparently in reciprocation, but this was not always the case.

If another *L.edwardsi* was in the vicinity there appeared to be one of two reactions by a calling individual. It either showed complete indifference, or gave a noisy "chirrup" which was repeated several times, followed by a low "chuck chuck chuck", all of which was then repeated with the individual elements in varying order and with varying frequency. This call sequence usually had the consequence of stimulating "chirrups" from other animals, estimated to be a distance of up to 500 *m from* the observer. This distance was estimated by standing under the calling animal and moving away from the site until only just in hearing range. The displaying animal might also take hold of any nearby branches and shake them energetically, and/or drum the branch on which it was sitting with its tail. The 'target' animal might also give a similar display, and a short and noisy chase ensue before one of the animals moved off in a rapid series of leaps. A third distinguishable call is the 'laugh': "he, he ,he, he", dropping in pitch. It did not appear to be an alarm or territorial call because it provoked no obvious reaction from other animals and was also only heard at a close range, but again its actual function was unclear. Fourthly, a high pitched screeching "eek eek eek" call was made later in the night than the initial "weeeek". This similarly seemed to be a statement of the animal's presence in an area. There might be a reply, but this was not always the case. Fifthly, an 'alarm' call; "cheek cheek" repeated several times was usually made when the animals were harassed for example by humans.

There are few other reports which describe the calls of *Lepilemur*. Charles-Dominique and Hladik (1971) reported *Lepilemur leucopus* to duet after they left the sleeping sites. Such duetting was not heard at Ampijoroa. Neither *Lepilemur ruficaudatus* nor *Lepilemur dorsalis*, (the two species geographically nearest to the range of *Lepilemur edwardsi*), have a call repertoire that is nearly as complex or nearly as frequently heard as that of *L.edwardsi* at Ampijoroa.

Social Behaviour and Grooming

Lepilemur edwardsi is usually classed as a solitary animal, unlike the monogamous *Avahi* (Albignac 1981). However, there were considerable interactions during the night with other animals. During the study the animals were seen to sleep with one or two other individuals, move at night with other individuals for several hours, and have long allo-grooming sessions. During this study, I was unable to capture and identify all *L.edwardsi* in the area, and it is therefore not possible to analyze fully the relationship between individuals. Due to time constraints, only qualitative data on social behaviour were obtained. It is worth noting that none of the individuals in the study area was known to have given birth during the project.

During only one out of the 23 all night 'follows' of *L.edwardsi* was no social contact recorded. During the dry season, when the feed trees were more restricted, there would often be three or four animals feeding in the same tree, with no aggression apparent. During the wet season, the animals were more dispersed, with multiple animals in the same tree a rare observation. Generally, if another animal passed through the same area it was ignored. Auto-grooming occurred at a frequency of observation of 3% of activity and allo-grooming 1.1%, making up considerably larger proportions of bout observations than for *Avahi occidentalis* (1.9% and 0.1% respectively). The first groom of the night very often took place before vacating the tree hole (such grooming was often viewed through cracks in the tree, or simply could be heard). If, (as in some cases), the hole was relatively small, the animal would sit on the edge of the hole and groom there before moving off. The grooming was thorough, starting with the stomach, pushing the tooth comb through the fur, then going on to the limbs and head. The head was groomed with the feet. The inside of the thighs was groomed by lifting the leg up with one arm and bending down to the crotch from a sitting position. (It might be thought that this posture is evidence in *L.edwardsi* of the caecotrophy that Charles-Dominique and Hladik [1971] believed to occur in *Lepilemur leucopus*. However, no evidence of caecotrophy was visible in this study.) 'Greeting' of two animals normally involved the animals first grooming each others heads and then the backs, interspersed with intermittent auto-grooming. On some occasions three animals were involved in allo-grooming. Other activities associated with 'greetings' included each animal sniffing and licking the other's face, and smelling the anal region of the other, usually before grooming took place. On one occasion the animals interspersed the mutual grooming with the cuffing and slapping of each other, but there appeared to be no aggression involved. Grooming is clearly an important element of social behaviour in *L.edwardsi.*

Sleeping Sites

Lepilemur edwardsi spent the day in naturally occurring tree holes in the forest.

The holes were not exclusively held: more than one *L.edwardsi* may be in the same hole. In this study, up to five different tree holes were found within an individual's home range, but not all are frequently used. For example, in two cases an adult female and a juvenile male were regularly found together in one hole; and another, (with three entrance holes) occasionally had three animals in it (sexes and age were unknown). In one case, *L.edwardsi* was seen to come to a hole which was already occupied, at the end of the night's activity. It left immediately, suggesting that occupancy of a hole is not challenged. An animal may visit its sleeping hole several times during the night for periods of up to an hour before travelling again. During the day the animals were never seen completely out of the holes, and never changed sleeping site, except for one occasion when the animal kept vacating and returning to the hole giving alarm calls, suggesting that a predator had occupied the hole. During the day, the animals became active several times, and were seen at the entrance to the hole, although they generally re-entered it if any threat was sensed.

Marking

Possible 'marking behaviour' in *Lepilemur edwardsi* was observed on only three occasions. In each case, the animal climbed down a trunk to a height of 0.2-1 m before urinating and defecating on the trunk, or an adjacent trunk. Both sexes were observed to show this behaviour. There was no evidence that particular trees were repeatedly used, as was observed by Harcourt at Berenty (pers. comm.).

Interaction within the local population

Data on all animals captured are given in Appendix 2. It was not possible to capture the entire local population, which appeared to be in excess of ten individuals. It is therefore impossible to give details of social interactions, as the age and sex structure of the population is unknown. It is perhaps worth recording, however, that all collared individuals interacted with each other on several occasions, apart from *Lepilemur edwardsi* 1 (LL1) and *Lepilemur edwardsi 2* (LL2) (the social content of these interactions is summarized above). Interactions between collared and non-collared individuals were also frequently observed, but do not form part of this study.

4.42 Social Behaviour in *Avahi occidentalis*

Calling

Avahi occidentalis, at Ampijoroa, was heard to produce only two types of calls but these were very distinct. The first, a piercing "ava hee", gives them their onomatopoeic name. This was made on average only twice a night. On some nights the target individual made no such calls. The maximum number of such calls heard in one night was seven. Both sexes made these calls, and the animals were usually positioned high in the canopy when calling. While they appeared to act as 'advertisement', these calls were also made when the whole family were travelling together, and the position of others is thus already known. Petter and Charles-Dominique (1979) interpret this call as a strong alarm call and a grouping call for the family, allowing animals to locate one another. From observations of the animals whilst they were making these calls and their prominent positions in the trees crowns, I would suggest that these calls are rather an advertisement of the individual's presence both to members of its own family group and to other groups around it. Only once when this call was made did another group respond by calling. Similarly, when other groups were heard to call during the night, the animals treated the vocalization with complete indifference. When the two study groups were in nearby trees and could be heard moving around in the branches, there was still no vocal response from either group. A grouping and personal advertisement role, rather than alarm or territorial threat, thus seems most likely for this distinct call.

The second call was a relatively quiet purring made by the vibration of the nostrils. It thus cannot be considered a vocalization intended for other groups of *Avahi occidentalis* to hear, but rather seemed to be a means of communication between animals which were travelling and foraging together. This gentle purring was made on-and-off most of the night, when the animals were together, or in nearby trees, but only during active periods. Both members of a pair, or a whole group would purr intermittently. No reciprocity, or other inter-individual coordination of calling was evident.

Harcourt (1991) reported that the *Avahi laniger* at Ranomafana made two calls, one of which was a whistle, (which *A.occidentalis* at Ampijoroa do not appear to make), and the other was, "ava hee" calls made when groups met on the border of their ranges. This once again, did not occur at Ampijoroa.

Monogamy

Within the study quadrat, two groups of *Avahi occidentalis* were found. These appeared to consist of a monogamous pair of animals, their offspring from the study year, and the previous year's offspring. This is exactly as found in other studies (Albignac, 1981a,b, at Ampijoroa; Harcourt, 1991 at Ranomafana; and Ganzhorn *et al.*, at Perinet, 1985) . The pair that lived in the north of the study site was seen to lose two offspring in the 1992-93 season: one juvenile male at the end of July 1992, and a two week old baby that was born around the 20th of September 1992. No cause of death was obvious for either of these two individuals. The other family, in the south of the study site, consisted of a pair of adults and a juvenile female from the previous year that, at the start of the study was not yet fully grown. Despite being more than half the size of the adult female, it would attempt to ride on its mother's back. The adult female gave birth on the 22nd of September 1992. For the first four weeks of life the infant travelled on the ventral surface of the adult female and it was never seen to leave the mother, or travel on another individual of the family group. After this period, the young *A.occidentalis* travelled on the dorsum of its presumed mother. In another family group at Ampijoroa, not intensively studied, a neonate was seen as early as mid August.

The northern pair spent the majority of their nights travelling together. However, on two nights they were only seen together at the beginning and the end of the night, in the sleeping tree. On three nights they were separate for the first couple of hours, (*i.e.* the period when the majority of feeding took place) but met later in the night and stayed together until morning. The behaviour of the southern group was slightly different. The adult male and juvenile female were always seen together throughout the entire period of the study, both travelling and feeding together. The adult female with the infant, however, remained separate from them, although all four were sometimes seen together during the night. When tracking the juvenile female or male, on several occasions, after an hour's ranging, the male and juvenile female would return to a tree where the female and baby had been left. When the young was big enough to travel itself, and the juvenile female fully grown, the group was observed to travel as a foursome for the entire night during three of the eight complete nights that this family was followed. The family was observed until the end of September 1993. At this time there had been no further offspring, and neither juvenile had left the family group.

Sleeping Sites

During the day *Avahi occidentalis* at Ampijoroa was seen to rest within its home range in trees with dense foliage. Each family group had several possible sleeping sites. Fifteen sites were recorded for the southern family, compared with fourteen for the northern family. These are low estimates, as these sleeping site locations were recorded only on all night 'follows'. As social structure does not form the core of this study, no attempt was made to record all sleeping sites used. The height range for these sites was 3.5m to 13m. The northern pair were always in physical contact with each other in the same tree; however the southern group were sometimes in adjacent trees, but were always in vocal contact. It is worthy of note that it was always the male and juvenile female that were separate from the mother and her infant. *A.occidentalis* sometimes moved to other sleeping sites during the day, if the first site became particularly exposed to the sun. During the dry season, when a large proportion of the trees lose their leaves, the availability of shadowed sleeping sites was greatly reduced, and *A.occidentalis* was typically seen in one of a few evergreen locations.

Grooming and Marking

Avahi occidentalis would habitually groom itself at the beginning of the evening, before leaving the sleeping site, and then occasionally during the night (but not for long periods). Only 1.9% of activity observations was auto-grooming. Allo-grooming was even rarer, only being seen on four occasions. The animals have visually obvious dark scent glands under the chin which were more conspicuous in the males, but marking was only seen once when a male *A.occidentalis* was seen to wipe the glands across a branch.

Territoriality

There was no evidence of territorial battles, and instances of chasing such as Harcourt (1991) described for *Avahi laniger*. However, the small degree of overlap of home ranges of the *Avahi occidentalis* in this study, in comparison with the *Lepilemur edwardsi*, may be significant in this context.

4.43 Ranging in *Lepilemur edwardsi*

Figures 4.4a - d show the annual home range for each individual *Lepilemur edwardsi* in the study, defined as an envelope enclosing all five minute sightings over the whole period of the study. The different coloured points represent the different nights of observation, and each dot is the location where an animal was observed for one or more five minute intervals. The mean home range size was 1.09 ha ± 0.6. Figure 4.4e shows the annual home ranges of all the individuals studied. It is clear that there was considerable overlap of home ranges in this species. Table 4.4a shows values for the annual home range for each individual *L.edwardsi* in the study and also the mean nightly home range. The mean nightly home range is the mean home range area used each night. It is worthy of note that the home range used for a single night was much less than the home range used by an animal over the year.

Table 4.4a: The annual home range, nightly home range and mean travel distance covered by *Lepilemur edwardsi* (LL) at Ampijoroa

Animal	N nights followed	Sex	Adult (ad) or juvenile (jv)	Annual home range (ha)	Mean nightly home range (ha)	Mean horizontal travel distance (m)
LL1	5	♀	ad	1.70	0.50	463
LL2	4	♀	ad	1.18	0.77	492
LL3	9	♂	ju	0.67	0.33	277
LL4	7	♀	ad	0.81	0.27	258

Note: Five-minute marker locations were measured to the nearest 0.5 m, but the ranging program rounds these to two decimal places.

The one male that was caught in this area started the study as a juvenile. For the first year, he had a correspondingly small home range: 0.47 ha. Over the following year the animal put on weight (Table 4.4b) and his home range increased to 0.67 ha. This is still the smallest home range of any individual followed. Considerable attempt was made to catch other animals in the vicinity but despite this, only this male was caught.

Table 4.4b: The change in mass of the male *Lepilemur edwardsi* caught within the study quadrat over the study period

Individual	Date measured	Mass (g)
LL3	18.6.92	558
LL3	11.11.92	680
LL3	8.9.93	728

4.44 Ranging in *Avahi occidentalis*

Figures 4.4f - i show the annual home ranges for each individual *Avahi occidentalis* in the study. The different coloured points represent the position of the lemur on different nights. The mean home range size was 1.6 ± 1.2 ha. Figure 4.4j shows the annual home ranges of all the individuals studied. It is clear that there was only a small area of overlap at the edge of the home range of the two families. Table 4.4c shows values for the annual home range for each individual *A.occidentalis* in the study, and also the mean nightly home range. The mean nightly home range is the mean home range area used each night. It is interesting to see that the difference between the annual home range and the nightly home range was less for *A.occidentalis* than it was for *L.edwardsi*, suggesting that *A.occidentalis* covered much more of its total (annual) home range during a single night.

Table 4.4c: The annual home range, nightly home range and mean travel distance covered by *Avahi occidentalis* at Ampijoroa

Animal	N nights followed	Sex	Adult (ad) or juvenile (jv)	Annual home range (ha)	Mean nightly home range (ha)	Mean horizontal travel distance (m)
Av1	5	♂	ad	2.42	2.28	1859
Av2	3	♀	jv	2.23	1.88	1430
Av3	6	♂	ad	1.15	0.66	824
Av4	4	♀	ad	0.76	0.55	655

Fig. 4.4a Home range of *Lepilemur edwardsi* (LL1, female) at Ampijoroa

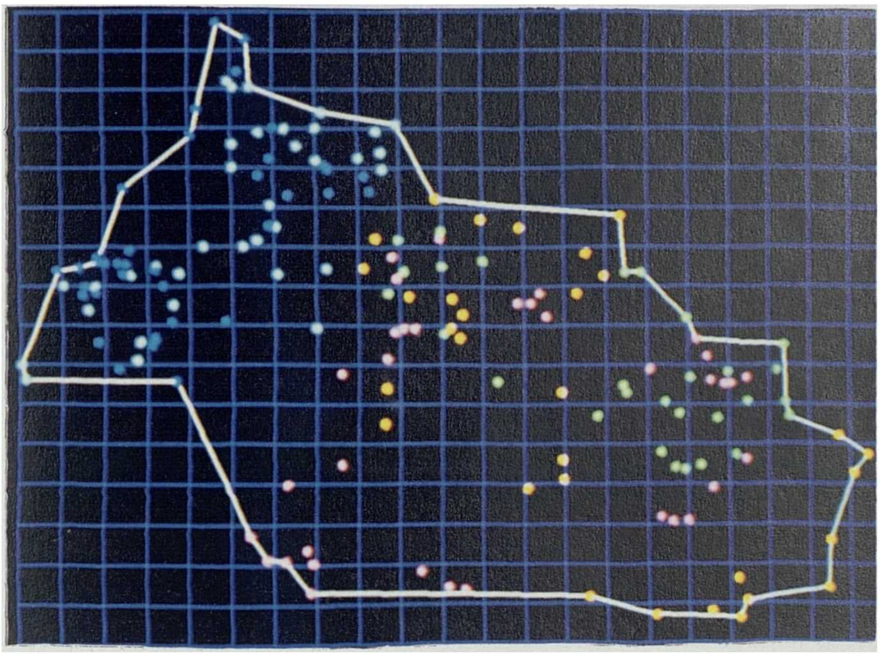
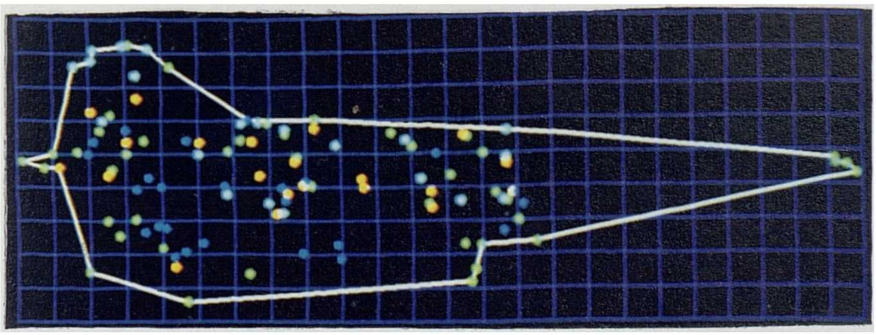


Fig. 4.4b Home range of *Lepilemur edwardsi* (LL2, female) at Ampijoroa.



Key: Fig. 4.4a and 4.4b
Grid squares represent 10 m by 10 m sections of the quadrat. Observations of different nights are coded in a different colour. Each dot represents a location where an animal was observed for one or more five minute intervals. Five full night follows are displayed in Fig. 4.4a, and four full night follows are displayed in Fig. 4.4b. **N.B:** The computer programme will only display a maximum of five nightly home ranges overlaid. In those cases where more than five nightly home ranges were available, those with the largest ranges were used.

Fig. 4.4c Home range of *Lepilemur edwardsi* (LL3, male) at Ampijoroa

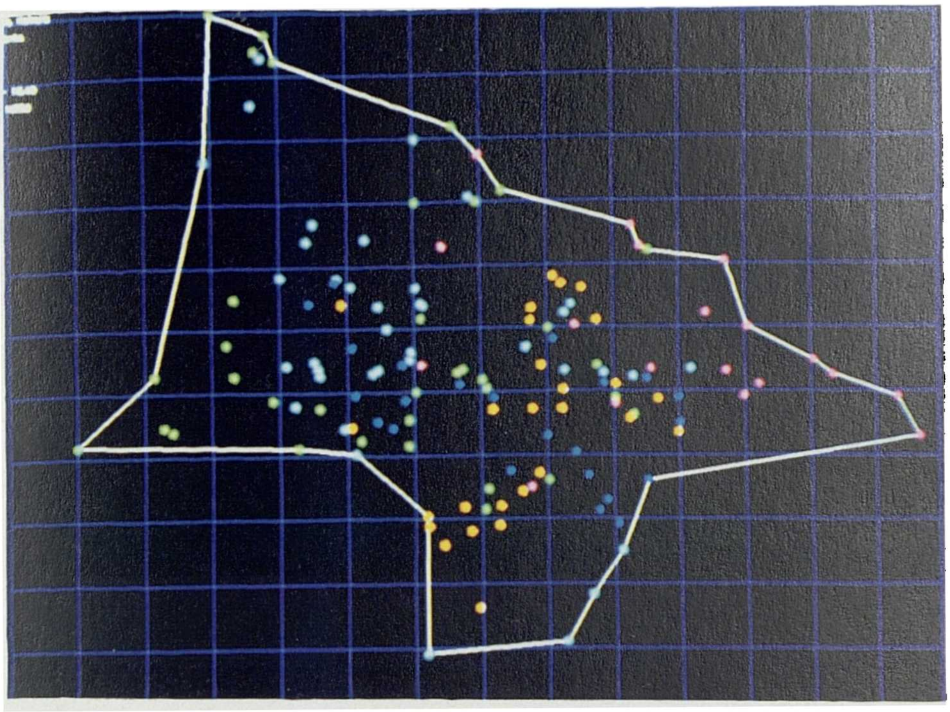
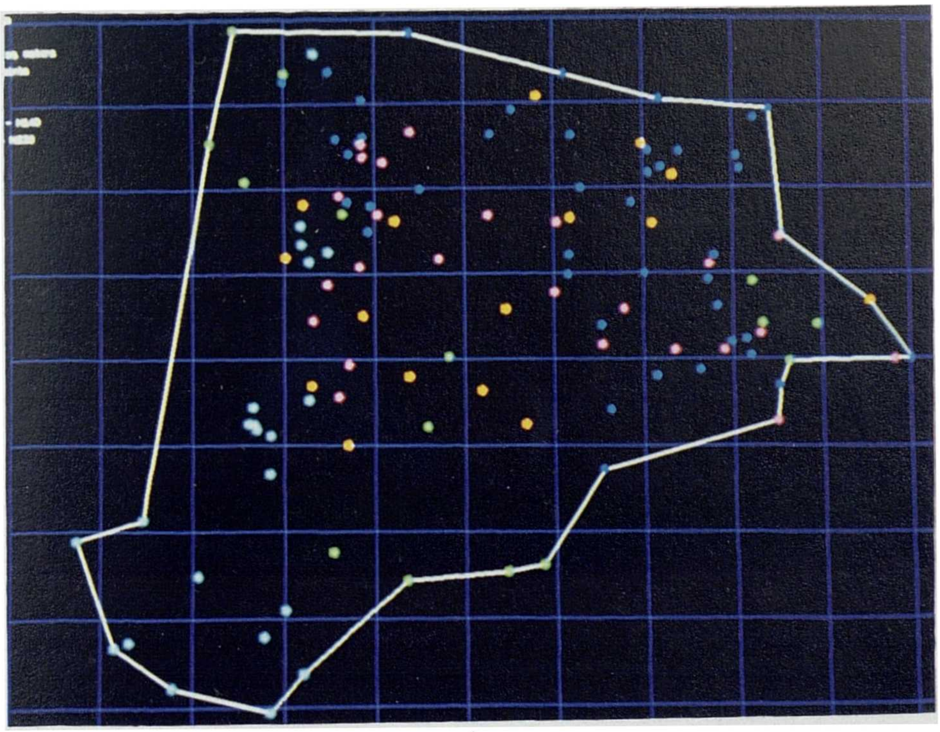


Fig. 4.4d Home range of *Lepilemur edwardsi* (LL4, female) at Ampijoroa.



Key: Fig. 4.4c and 4.4d
Grid squares represent 10 m by 10 m sections of the quadrat. Observations of different nights are coded in a different colour. Each dot represents a location where an animal was observed for one or more five minute intervals. Five full night follows are displayed in Fig. 4.4c, and five full night follows are displayed in Fig. 4.4d.

Fig. 4.4e Home range of all four individual *Lepilemur edwardsi* studied at Ampijoroa.

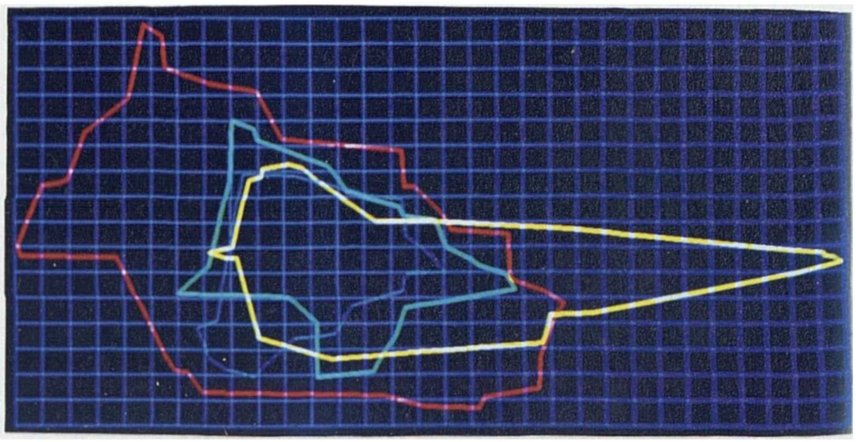
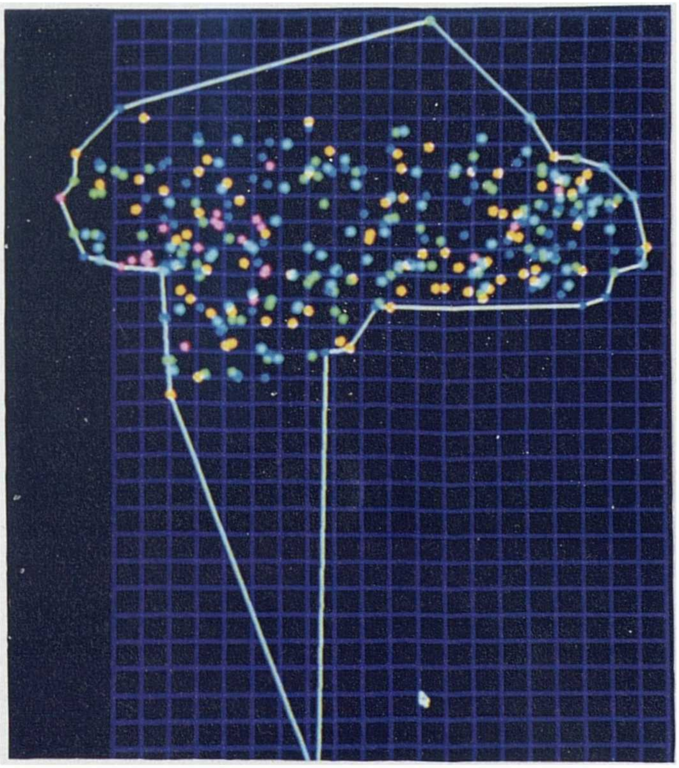


Fig. 4.4f Home range of *Avahi occidentalis* (Av1, male) at Ampijoroa



Key: Fig. 4.4e
Grid squares represent 10 m by 10 m sections of the quadrat. The annual home range of each individual is displayed; each individual home range is represented as a different colour.

Key: Fig. 4.4f
Grid squares represent 10 m by 10 m sections of the quadrat. Observations of different nights are coded in a different colour. Five full night follows are displayed. Each dot represents a location where an animal was observed for one or more five minute intervals.

Fig. 4.4g Home range of *Avahi occidentalis* (Av2, female) at Ampijoroa

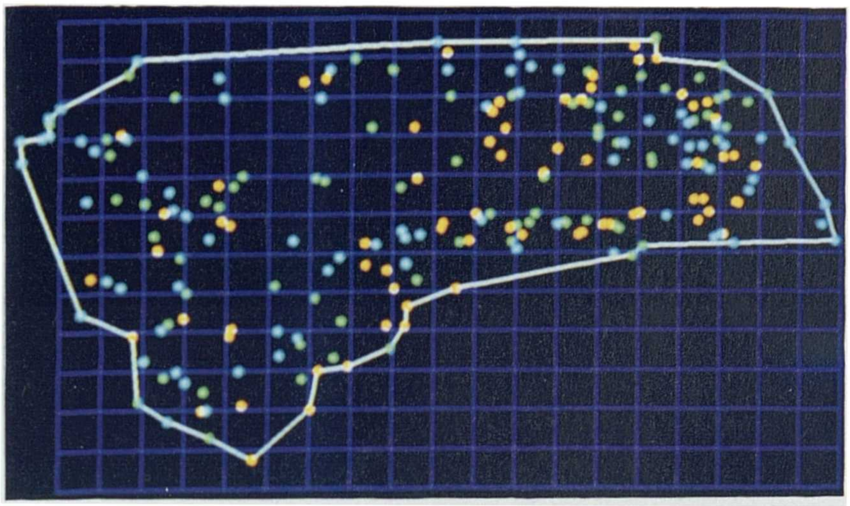
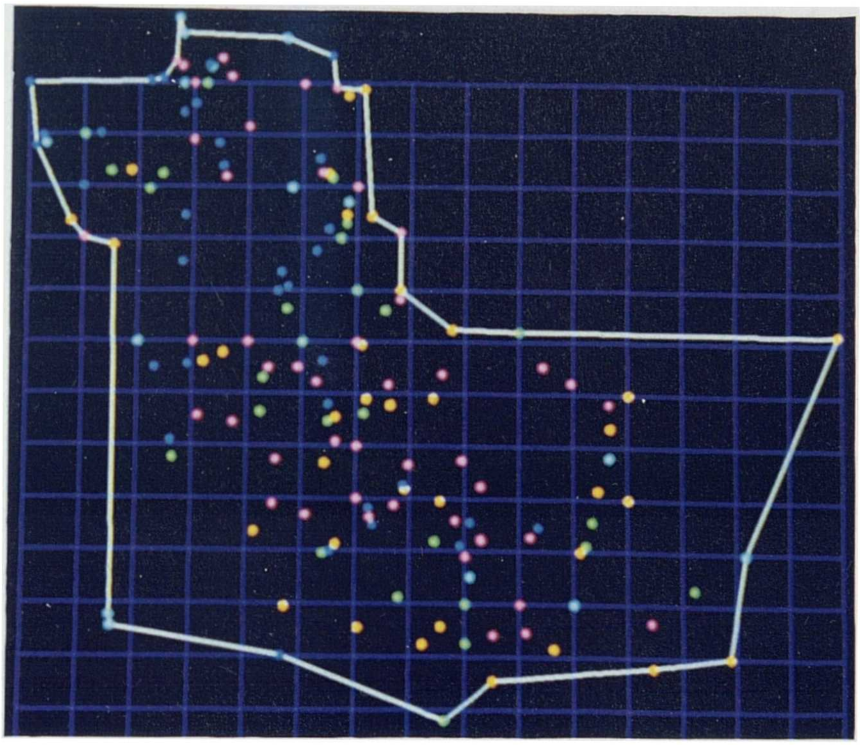


Fig. 4.4h Home range of *Avahi occidentalis* (Av3, male) at Ampijoroa



Key: Fig. 4.4g and 4.4h
Grid squares represent 10 m by 10 m sections of the quadrat. Observations of different nights are coded in a different colour. Each dot represents a location where an animal was observed for one or more five minute intervals. Four full night follows are displayed in Fig. 4.4g, and four full night follows are displayed in Fig. 4.4h.

Fig. 4.4i **Home range of *Avahi occidentalis* (Av4, female) at Ampijoroa**

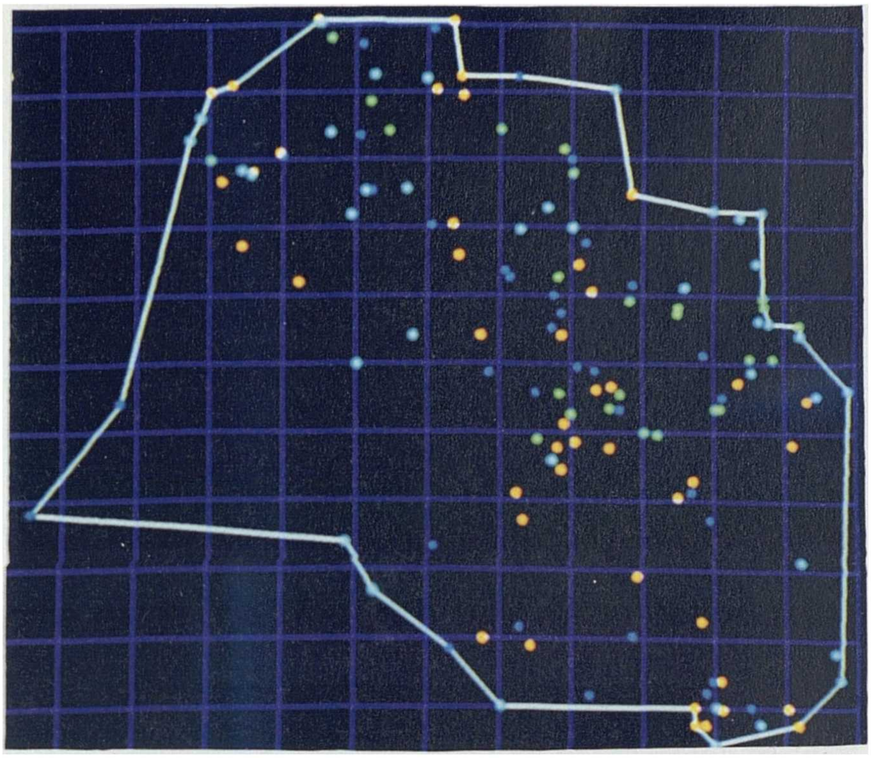
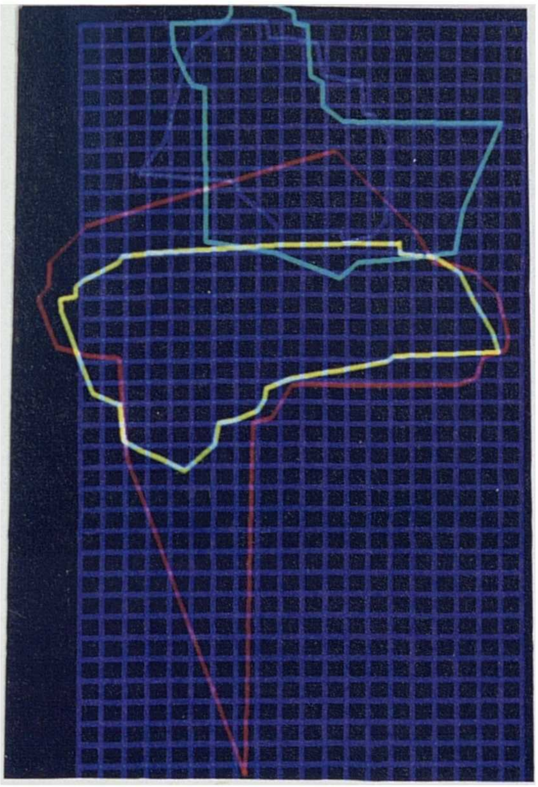


Fig. 4.4j **Home range of all four individual *Avahi occidentalis* studied at Ampijoroa**



Key: Fig. 4.4i
Grid squares represent 10 m by 10 m sections of the quadrat. Observations of different nights are coded in a different colour. Each dot represents a location where an animal was observed for one or more five minute intervals. Three full night follows are displayed in Fig. 4.4i.

Key: Fig. 4.4j
Grid squares represent 10 m by 10 m sections of the quadrat. The annual home range of each individual is displayed; each individual home range is represented as a different colour.

4.45 Activity of *Lepilemur edwardsi* and *Avahi occidentalis*

Lepilemur edwardsi

The onset of activity in the evening seemed to be triggered by ambient light levels since *Lepilemur edwardsi* became active in the evening at about the time that it became difficult to read. This is in agreement with work by Charles-Dominique & Hladik (1971) who found animals left their sleeping sites at 'nightfall', and that of Pages & Petter-Rousseaux (1980) who reported *Lepilemur ruficaudatus* to become active at 'dusk' throughout an artificially created yearly cycle. Similarly, the animals returned to sleep sites just before it was light enough to read, and, unlike *Avahi occidentalis*, were never seen to be active outside the sleeping site during full daylight. During the summer months (October to April) when the nights were about an hour shorter than in the winter months (May to September), the animals would habitually terminate their activities earlier, implying that light intensity was an important cue for the onset and termination of activity. From the data collected, the easiest way to quantify activity throughout the night was the frequencies of activity bouts observed. From the graph (Fig.4.4k), it can be seen that by far the majority of bouts observed fell between 1800 hours and just before 1900 hours. During this time period 16.2% of bouts were observed, the highest percentage for a single hour. Only four bouts were observed for *L.edwardsi* during the previous hour (1700 - 1800). From 1900 to 2000 hours 11.3% of activity bouts occurred, and from then on, the percentages drop to around the 8 or 9 % mark for most of the night, with a trough between midnight and 0200 hours, but a peak in the final hour of the night, when the animals are returning to their sleeping sites.

Cross-tabulation statistics on the frequencies of activity observed at each hour of the night, were calculated using SPSS/PC+ using the CROSSTABS procedure (Norusis/SPSS Inc. 1990). The null hypothesis that time and activity are independent of each other could be rejected (Pearson chi-squared value = 0.0, df = 72, N = 3429). This suggests that throughout the night, activities were more frequent at certain hours than at others. When the bouts observed are split up into the six separate activity categories (Fig.4.4l,m,n,o,p,q,), the peak of each of the activities was indeed seen to fall early in the night. There is another smaller peak at around 2200 to 2300; and another peak in activity just before dawn; so it appears to be a three peaked, triphasic activity pattern compared to the usual biphasic pattern (Charles-Dominique 1971; Bearder 1974; Sussman 1977).

Avahi occidentalis

Ambient light levels appear to trigger the activity of *Avahi occidentalis*, but it was noticeable that the threshold level for *A.occidentalis* was different from that which triggered *L.edwardsi*. *A.occidentalis* became active earlier in the evening (*i.e.* at stronger light intensities), and hence more of the animals were moving before 1800 hours, with 97 bouts of activity observed, compared to only 4 for *L.edwardsi*. The animals found suitable sleeping sites at dawn, and had shorter active periods during the summer months, when nights were an hour shorter. However, the animals were sometimes observed to be active later in the night than *L.edwardsi*, and were also seen travelling during the day. Observations of *A.occidentalis* activity during the day occurred predominantly around 1000 hr and 1100 hr, and were more frequent in the dry season, when the shelter produced by the sleeping site chosen was not adequate to shield *A.occidentalis* from the heat of the sun, or the light of the day, due to leaf-loss.

Cross-tabulation statistics were calculated on the frequency of activities observed at each hour of the night using SPSS/PC+ using the CROSSTABS procedure (Norusis/SPSS Inc. 1990). The null hypothesis that time and activity are independent of each other is rejected (Pearson chi-squared value = 0.0, df = 60, N = 3251). Given activities are therefore more frequent at specific times of the night. The statistic Cramér's V, a measure of association between variables, was calculated using SPSS/PC+ (Norusis/SPSS Inc. 1990) to allow for comparison of the cross-tabulation tables for *L.edwardsi* and *A.occidentalis*.

Cramér's V for *Lepilemur edwardsi* = 0.935, and for *Avahi occidentalis* = 0.966. These similar values suggest that both have a similar level of association between time and activity, but cannot indicate the direction or nature of the relationship.

From the graph (Fig.4.4k) of the frequency of nocturnal bouts of activity, it can be seen that there are three peaks of activity. One falls between 1800 to 1900, with the highest frequency of bouts observed occurring during this hour, at (17.9%). In the following two hours, up to 2100, there is a relatively high level of behavioural bouts (13.7% and 12.5% respectively), until the activity drops off considerably for the rest of the night. The second and third peaks of activity are smaller, and occur from 2200 until 2300, and from 0300 until 0400. When the activities are split into separate graphs (fig.4.4l,m,n,o,p,q,), a triphasic trend is again distinguishable, but it is less pronounced for *A.occidentalis* than it is for *L.edwardsi*. The travel bouts peak early on during the night and remain at a higher frequency than for *L.edwardsi*, and indeed they last for longer before dropping to a trough at 2400 until 0100 (when most activities seem to be less frequent). There is a further rise in travel activity between 0300 until 0400. Feeding activity has a large peak at 1800 - 1900, a small peak, at 2300 - 2400, a larger peak at 0200 - 0300 and (surprisingly) a fourth, but small peak in the last hour of the night. Auto-grooming has a large peak at the beginning of the night, a trough occurring at 2300 - 0100, a second peak at 0200 - 0300 and a small plateau at 0400 - 0500.

Fig. 4.4k Frequency of all activity bouts observed for each hour of the night and for each species

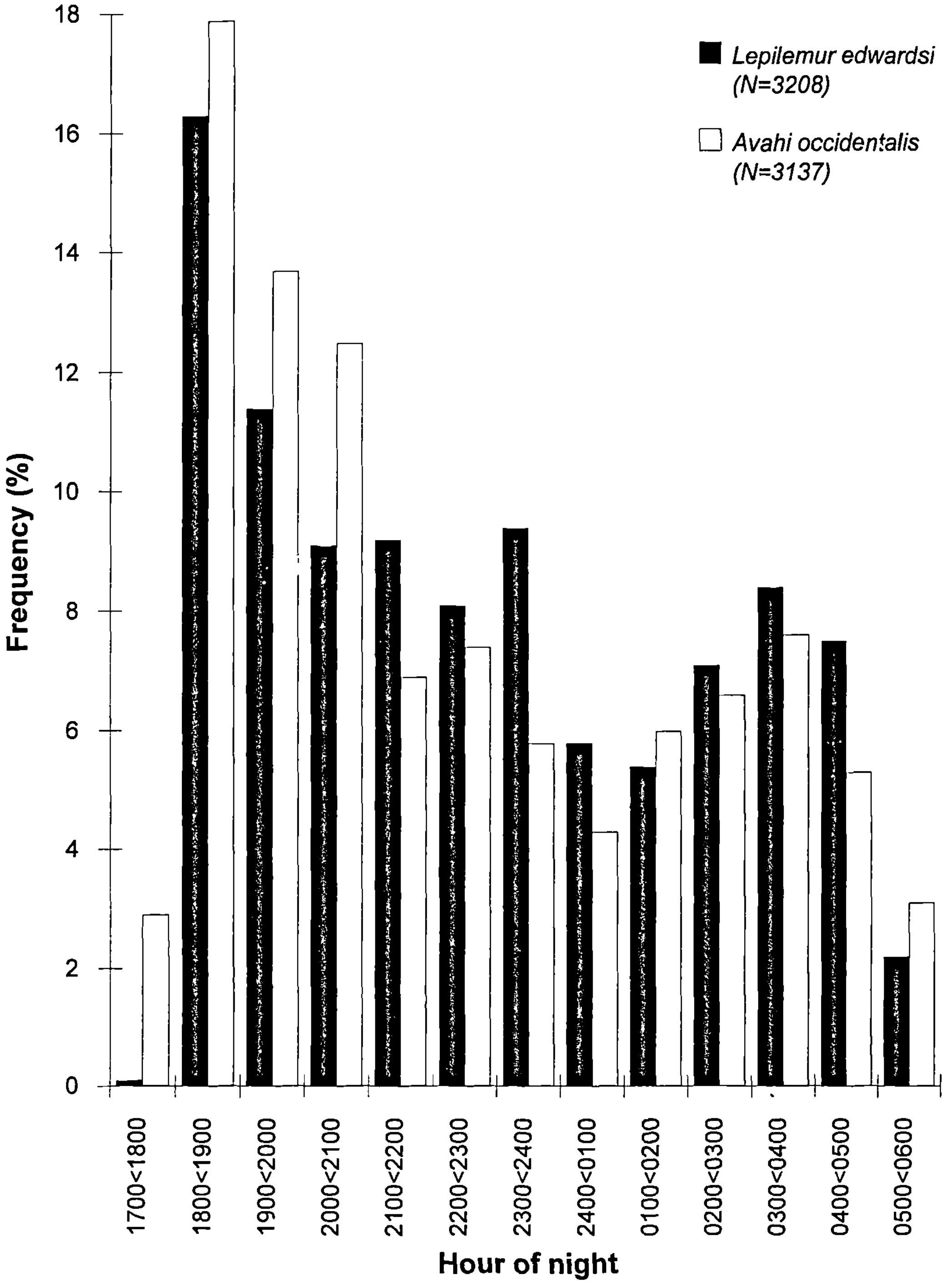


Fig. 4.4l Frequency of resting bouts observed for each hour of the night and for each species

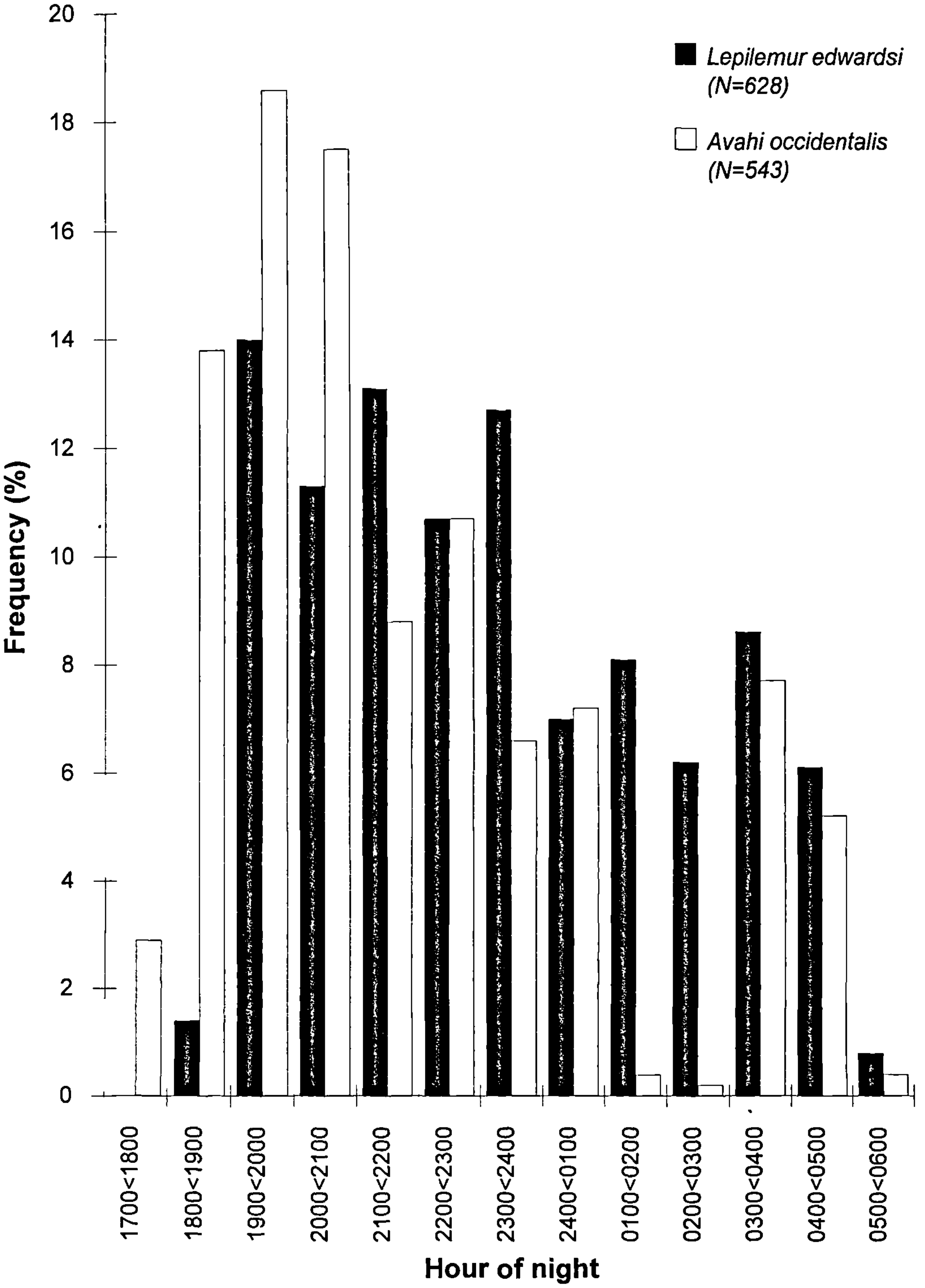


Fig. 4.4m Frequency of travelling bouts observed for each hour of the night and for each species

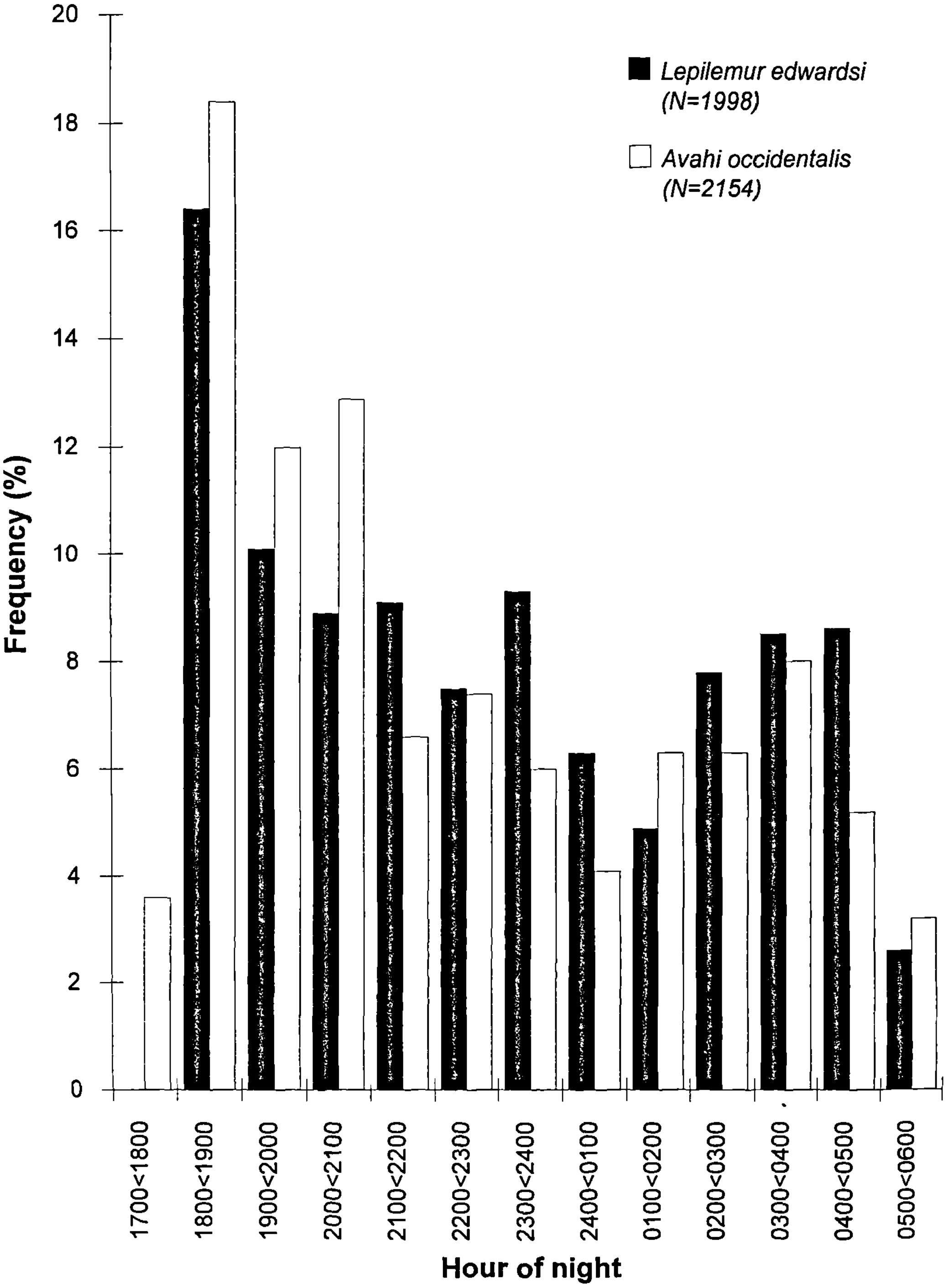


Fig. 4.4n Frequency of feeding bouts observed for each hour of the night and for each species

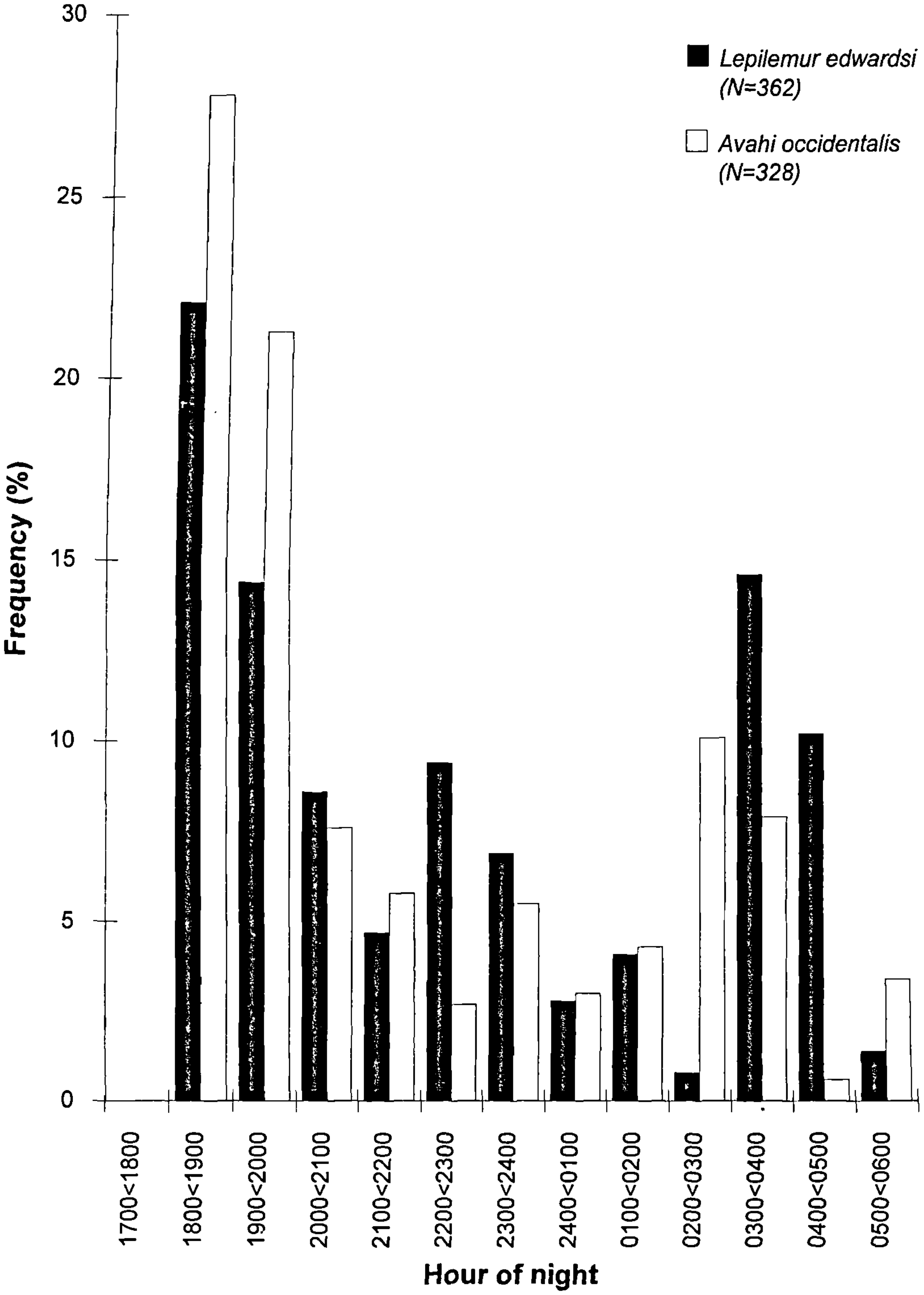


Fig. 4.4o Frequency of auto-grooming bouts observed for each hour of the night and for each species

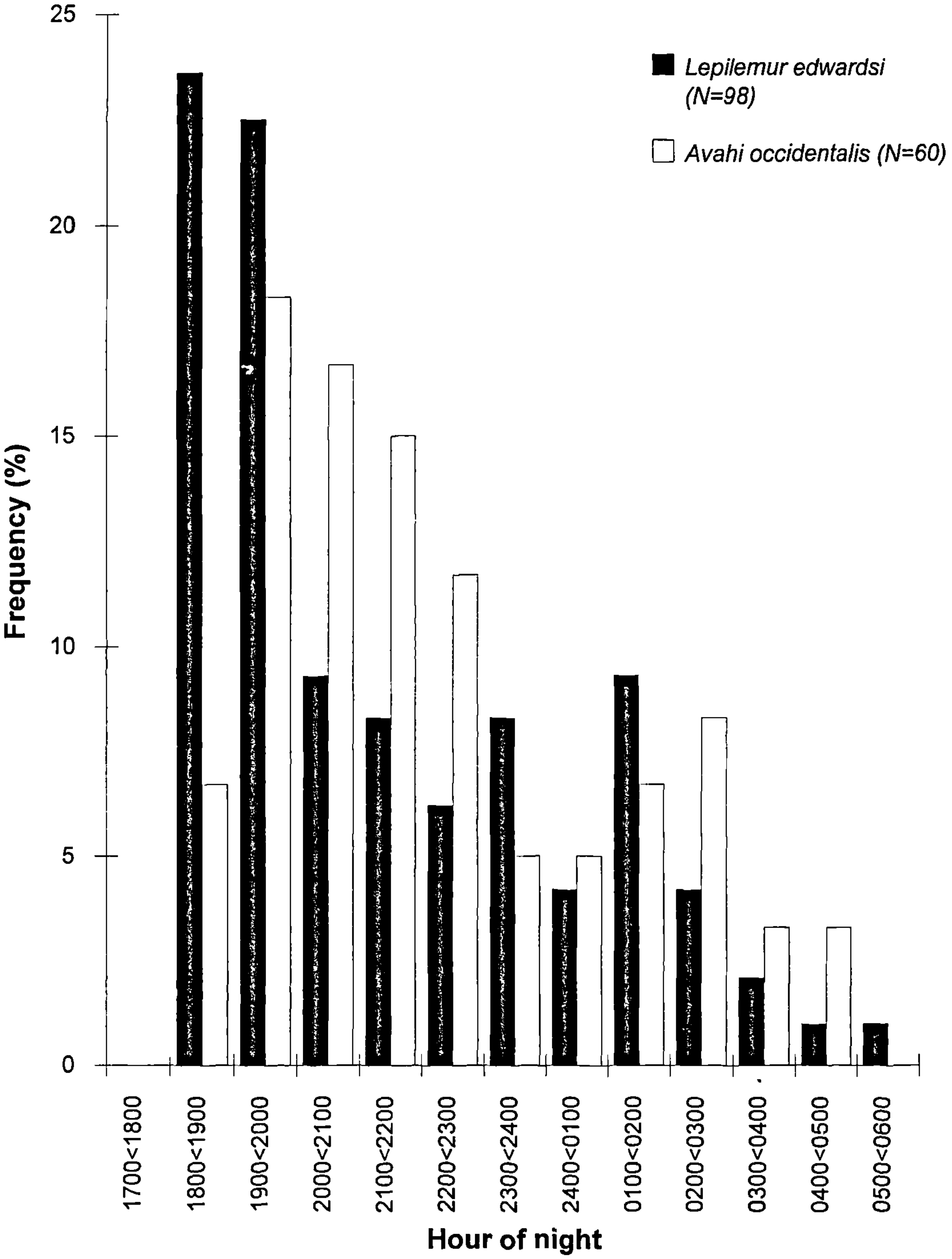


Fig. 4.4p Frequency of allo-grooming bouts observed for each hour of the night and for each species

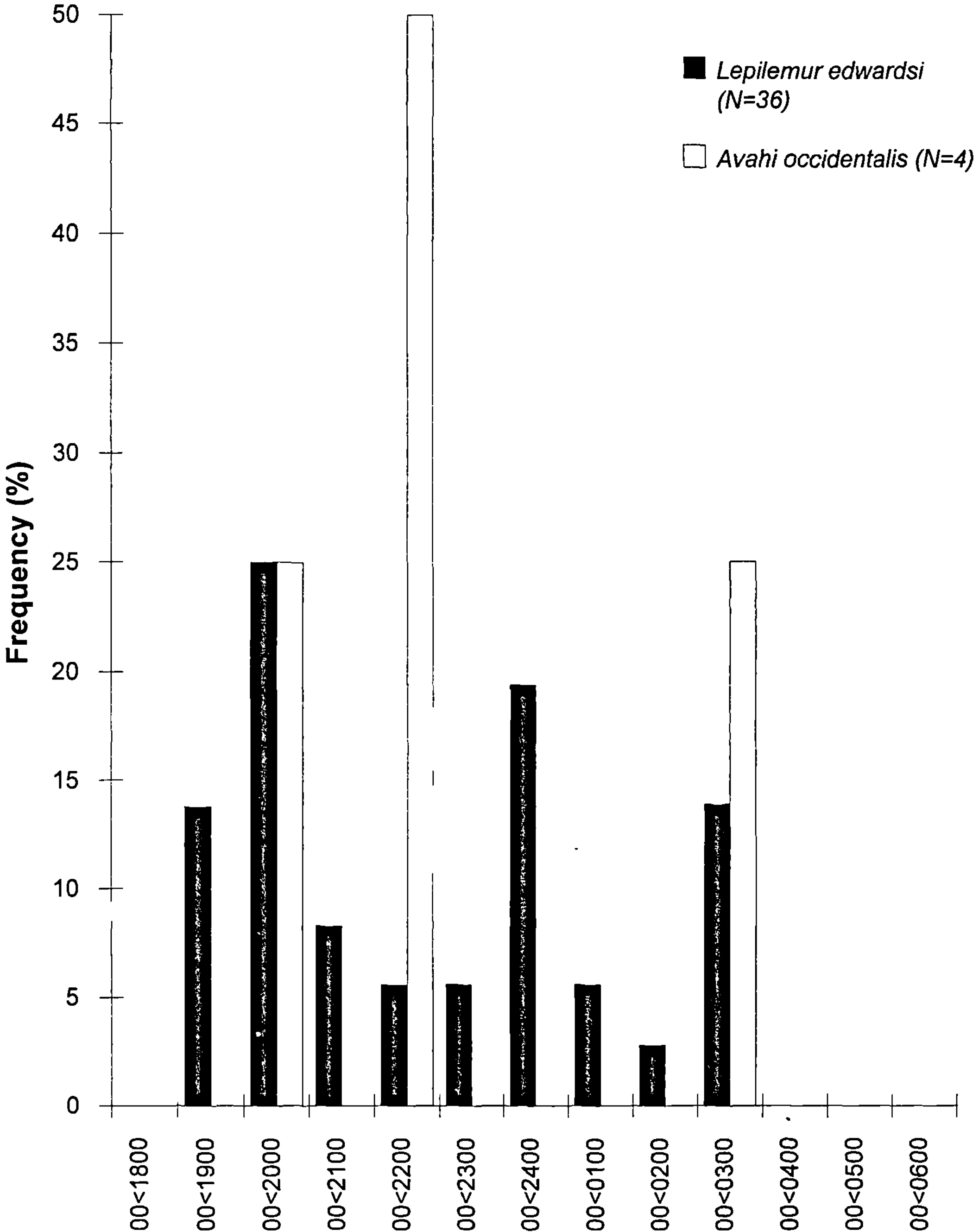
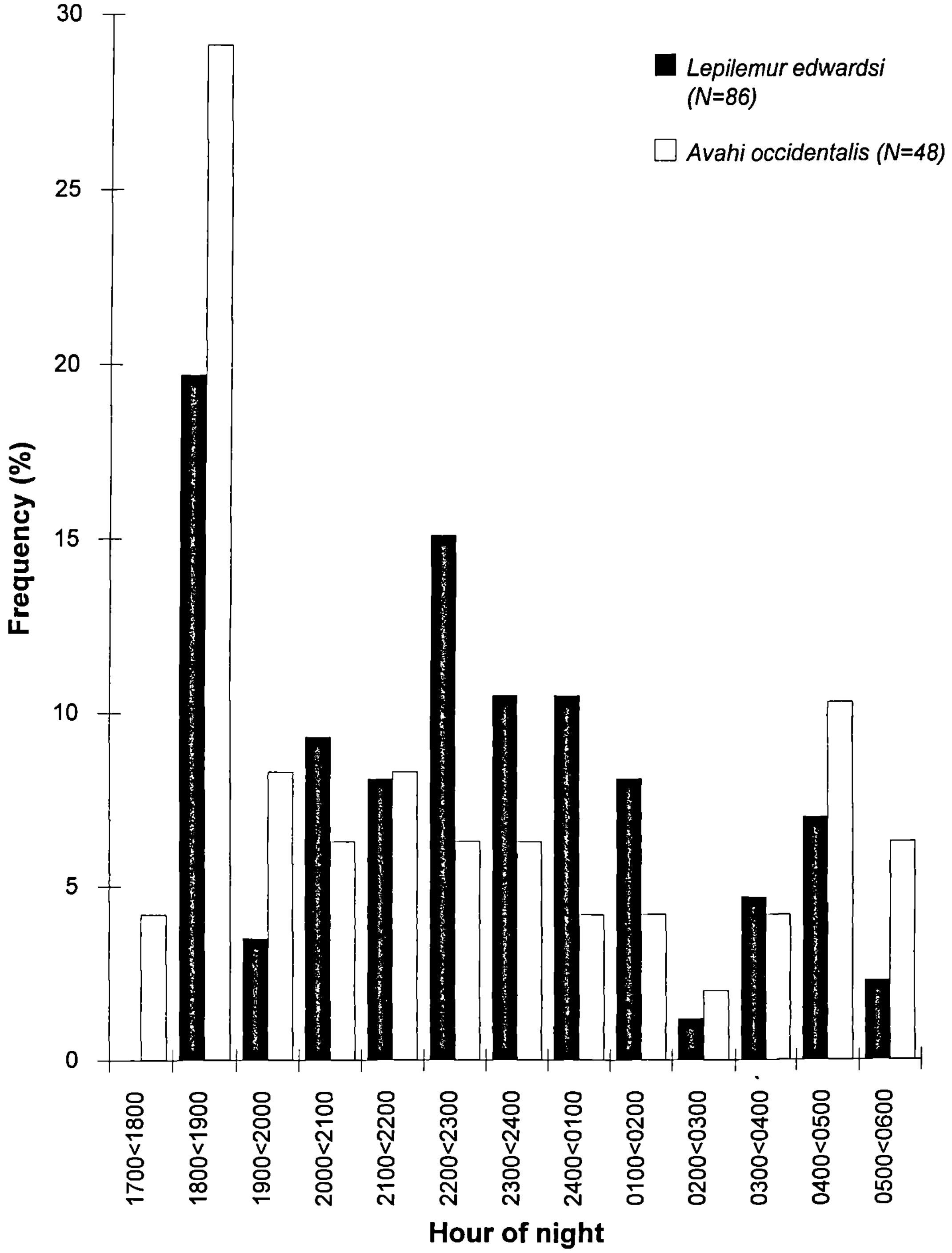


Fig. 4.4q Frequency of non-classified bouts observed for each hour of the night and for each species



4.5 Discussion

The findings on ranging behaviour of *Lepilemur edwardsi*: including a mean home range size of 1.09 ha., considerable overlap in individual home ranges, and non-exclusive core areas, agree with Albignac (1981b). Albignac found a home range of around 1 ha for *Lepilemur edwardsi* at Ampijoroa, although he only performed partial night follows. From the present study, it appears that there is no difference in home range size between the sexes. However, the sample size is small compared to the probable population of animals.

Lepilemur edwardsi has been described as a solitary animal, sometimes sleeping with two or three other individuals but moving around separately at night (Albignac 1981; Petter *et al.* 1977). However, there has to be some degree of sociality to allow for mating and rearing of offspring, and to coordinate such activities nocturnal solitary primates require complex systems of olfactory, visual and/or vocal communications (*e.g.* see *Tarsius bancanus*, Crompton 1987; *Galago moholi*, Bearder 1987; and *Mirza coquereli*, Richard 1987). The most common social system in nocturnal prosimians is the 'neighbourhood' system (also called the noyau system), in which a solitary male has a home range which overlaps those of several females. In this system the male has access to several females with which he mates. Females have a sufficiently large range to allow feeding throughout the year and seem to need no help with rearing of the offspring from the male. Mothers may share territories with adult daughters but as the daughters age, less overlap occurs. However, there may still be sharing of sleep sites and critical food sources during limiting periods (Bearder 1987). While female home range areas are correlated with food requirements, especially during pregnancy, male home ranges are far bigger than would be predicted on body size alone (Bearder & Martin 1979). Young males emigrate from the maternal home range at puberty and become 'satellites' or 'vagabonds' waiting for opportunities to mate with females or invade home ranges when sexually mature males are absent (Charles-Dominique 1978). Bearder (1987) states that the latter defend their territories with scent marking and vocalisations, but may tolerate the younger males to some degree. Territories are defended all year round and there are areas of overlap where territorial communication occurs. The males regularly visit the females to check their sexual receptiveness. This social system is that adopted by most bushbabies excluding *Galago zanzibaricus* (Bearder 1987).

This 'neighbourhood' system seems adequate to describe the social system of the *Lepilemur edwardsi* (as observed at Ampijoroa), at least on the basis of the behaviour of the four individuals caught and followed. In a description of social structures of prosimians by Charles-Dominique (1978), he states that *Lepilemur leucopus* has a similar type of social organization to that of the galagines, but home ranges are modified for a folivorous diet; they have very small borders and territories that 'seldom overlap'. Results from the present study, however contrast markedly with those reported for *Lepilemur leucopus* (Tattersall 1982). A mean home range size of 0.24 ha. for *L.leucopus* (c. 550g), compares to 1.09 ha for *L.edwardsi* (c. 800 g); and considerable overlap of home range of *L.edwardsi* compares with ranges which 'seldom overlap' for *L.leucopus.*

The only male *L.edwardsi* caught, at its first capture, lacked mature genitalia (Table 4.4b). By the summer of the study period, its genitalia were mature. It may be assumed that we were unable to find and catch the dominant 'adult' male in this area. If, in the case of these animals, the dominant male has a larger home range than the females, it may be that his sleeping site was not located within the chosen quadrat area. The male captured was observed to make what appeared to be territorial calls and 'branch-bashing' displays. The same sleeping sites were the preferred resting places for this individual during the day throughout the study period. When originally caught, this male shared sleeping sites with one of the females which I suspected to be its parent. If this was the case, this male may at some point have to emigrate (possibly as a result of expulsion by the hypothesized dominant male), to a new area. All three females studied had a home range which overlapped with this male, as well as two other females in the immediate area, whose sleeping sites were within the male's range. The overlap of female home ranges was considerable. This result may be a consequence of a matriarchal system in which the females, sharing home ranges, sleeping sites and food sources, may all be related to each other. Without further information, including genetic data, on the other local members of the population, it is difficult to construct the true social system of this species. Possibly, an extensive overlap of home ranges is tolerated because of the relative shortage of available feeding trees during the dry season, when many of the trees lose their leaves, leading to patchiness of the food sources (Ramangason 1986). These remaining patches are heavily exploited by all individuals in the area. This seems possible especially as the Bearder (1987) model suggests that these patches are exploited by mother-daughter groups.

Avahi occidentalis in this study had a mean home range size of 1.6 ha, which is less than that reported for this sub-species by Albignac (1981). There was a small area of overlap of the ranges of the two groups (see Fig.4.4k), and there were other *A.occidentalis* on all sides of the animals' home ranges. The northern group's home range covered a large path on the edge of the quadrat which allowed extra space for expansion of the canopy. These trees were particularly big, and it may be that these more productive trees (in terms of biomass), provided a concentrated source of food. If this was the case, the family might only need a small home range from which to gather sufficient food (Pough *et al.* 1989). However, the smaller home range of the northern group, (0.96 ha), might also be explained by its smaller group size. Despite the need for suitable leafy sleeping sites, there seemed to be sufficient possible sites within the smaller home range even in the dry season, when approximately 50 % of the trees lose their leaves (Ramangason 1986). There was no marked difference between the sexes in the home range size, and indeed, when the young were independent, it appeared that both *Avahi* study groups usually moved as units throughout the night.

Albignac (1981a) reported that group sizes of *Avahi occidentalis* at Ampijoroa were between two and five individuals. The maximum observed in this study was four, but it may be possible that if the home range was rich enough in food, a family would cope with the offspring staying on for the third year after birth, despite its being fully grown. Ganzhorn *et al.* (1985) at Perinet noted a group size of one to four with a mode of two for *Avahi laniger*.

The majority of nocturnal prosimians are solitary. This form of social system may be favoured as most prosimians rely on concealment, rather than rapid flight, to escape from predators and an individual can hide more effectively than can a group. Solitary species tend to feed on food sources that are evenly or randomly distributed, while increased group size has been thought to be explained by increasingly 'patchy' food sources (Terborgh & Janson 1986). It is as yet unclear why *A.occidentalis* is monogamous rather than solitary, as are the majority of nocturnal prosimians. At Ampijoroa, the only night predator is *Cryptoprocta ferox* and there are no nocturnal raptors, and only a very small owl unlikely to prove a threat. If *A.occidentalis* is to be regarded as monogamous, such monogamy might have the advantage that the male call acts as a predator warning for females (Dunbar 1988). However, in this study when the female was lactating, the male did not travel with the female and Dunbar's theory, thus, cannot be a satisfactory sole cause. Monogamy has also been associated with the concentration of food, (particularly fruit), in small, predictable patches (Wright 1986). Large groups, she argues, cannot feed in a small tree crown as there is insufficient food available, but smaller social units, such as monogamous pairs are however, able to exploit such sources efficiently. Wright (1986) also suggested that monogamy is associated with male help in rearing the offspring, particularly in infant carrying. However, male *Indri*, which are also monogamous and of the same family as *Avahi*, do not show this behaviour (Pollock 1979) and neither do gibbons (Tenaza 1975).

Lepilemur edwardsi and *Avahi occidentalis* are exclusively nocturnal but neither appears to show a clear biphasic activity pattern during the night (Fig. 4.4 k - q). Throughout the year, nightly temperatures varied, with the lowest temperatures occurring in winter, and at the end of the night. However, these temperatures could not directly affect food availability for the animals, as they might have done if the subject species had been feeding on insects. It appeared to be ambient light levels which triggered the commencement and cessation of the nocturnal activities, as the lengths of the active periods shortened correspondingly with shorter nights. Charles-Dominique (1977) found that the prosimians at Makoukou, Gabon started their period of activity with a long bout of grooming, as was seen in *L.edwardsi* and *A.occidentalis.* The galagines at Makoukou began to move around at dusk conditions *(Euoticus elegantulus* 300 to 100 lux, *Galago alleni* 50 to 20 lux, and *Galago demidovii* 150 to 20 lux). *Perodicticus potto* and *Arctocebus calabarensis* became active later on, under full nighttime conditions (Charles-Dominique 1977). The two lemurs studied therefore are like the galagines at Makoukou, as they too become active under crepuscular conditions. It did, however appear that the *A.occidentalis* responded to a higher luminance threshold level than *L.edwardsi*, as they were active earlier in the evening and later in the morning.

The period of greatest activity for both species was the first few hours of the night. Within this time there were the biggest peaks in travel, feeding and grooming. This is similar to the findings of Crompton and Andau (1987) for *Tarsius bancanus.* They found that the greater proportion of the distance travelled was in the first half of the night. However, they also found the highest percentage of leaping, climbing and clinging at around 2200 - 2400, later than the travel frequency peaks for *L.edwardsi* and *A.occidentalis.* At around midnight there were long periods of rest when *L.edwardsi* appeared almost 'torpid'. On some occasions, there was complete inactivity for several hours, the maximum length of time for resting observed for *L.edwardsi* was 2 hours 4 minutes, and 47 minutes for *A.occidentalis.* Hence, *A.occidentalis* seemed to show more consistent levels of activity throughout the night. Pagès & Petter-Rousseaux (1980) also found a large reduction in the activity of captive *Microcebus murinus, Microcebus coquereli, Cheirogaleus medius, Phaner furcifer* and *Lepilemur ruficaudatus* in the second half of the night, as did

Crompton and Andau (1987) for *Tarsius bancanus*.

L.edwardsi and *A.occidentalis* are folivorous, and are thus presumably under broadly similar dietary constraints. A folivorous diet requires fermentation of the leaf material to gain access to the nutrients within the cellulose cell walls. Fermentation is a slow process (Bauchop 1978). For a relatively small folivore, such as *L.edwardsi* and *A.occidentalis*, with a small gut size, and a proportionally faster metabolic rate than a large folivorous primate such as a gorilla, gaining sufficient energy from leaves may be presumed to be a problem (Chivers & Hladik 1984). Hence food intake has to be maximised to gain adequate energy. Clutton-Brock and Harvey (1977) proposed that for maximum efficiency, an animal should feed at the beginning and end of the active period, when the stomach is empty, *i.e.* biphasically. They suggest that the functional significance of a biphasic pattern of activity for diurnal primates may be a reaction to a peak in temperature, or may allow the maximum intake of food that can be ingested per day. However, work by Penry and Jumars (1987), modelling an animal gut as a reactor, suggested that the most efficient feeding strategy would be to have frequent small inputs of food throughout the active period. Optimization of time and energy budgets for animals suggests that there is a conflict between constant food collection, and demands of other activities, such as defence of the territory, search for a mate and so on. The relative ease of finding leaves (all other things being equal), suggests a low energy cost of food collection. For small nocturnal folivorous primates, feeding would probably be a strong influence on their activity and behaviour. The small home ranges observed would soon be covered and it seems likely that the majority of the travel activity bouts observed were linked with moving to a new feeding tree, rather than patrolling the perimeter of the territory. A triphasic pattern of feeding activity may be the compromise position between the two strategies reviewed above, which maximises digestive efficiency and allows time and energy for other necessary behaviours.

Nocturnality seems to offer the benefits of predator avoidance and avoidance of direct competition with the diurnal folivores such as (at Ampijoroa) *Propithecus verreauxi* and *Eulemur fulvus*. Seasonality may affect the activity of these animals as a consequence of the deciduous nature of the forest. Food sources may thus be changed (from the animals' perspective), from a ubiquitous to a patchy distribution. This change may, in turn, limit the populations in the area. The effects of seasonality on the behaviour and the activity pattern of *Lepilemur edwardsi* and *Avahi occidentalis* need to be further investigated in a study which explores explicitly the cause and effect of external environmental pressures.

5 Feeding

5.1 Introduction

Variation of food choice across the order Primates influences all aspects of primate lifestyles and morphology. The different diets are usually classified on the criterion of the most commonly eaten food. Broad categories are 'insectivores', eating primarily insects; 'gummivores', eating gum and sap; 'frugivores', eating fruit; 'gramnivores', eating seeds; and 'folivores', eating leaves. Several researchers have demonstrated that body size of a primate predicts the broad category of food eaten (Gaulin & Konner 1977; Gaulin 1979; Kay & Hylander 1978; Hladik 1975; Hladik & Chivers 1978; Chivers & Hladik 1980; Clutton-Brock & Harvey 1977a,b). The reason for this seems to be the way that metabolic rate scales with body mass. Kleiber (1961) surveyed metabolic rates for mammals of different masses, and found that the data could be described by an allometric equation where the metabolic rate is a function of body mass with an exponent of 0.75. This exponent varies for warm and cold blooded animals, and even varies depending on the main diet of the animal (folivores have a lower exponent, Nagy 1987). Generally speaking, however, this allometric equation states that as body mass increases, the metabolic rate per unit mass of an animal decreases. Therefore, small animals have high energy requirements per unit body mass and large animals have low energy requirements per unit body mass (Schmidt-Nielsen 1984). Insects have a high calorific value per unit mass and are extremely protein-rich (Hladik 1979). However, larger species may not be able to catch enough insects during their active period to obtain sufficient energy, although it seems likely that the chances of finding a prey item in a specific habitat are the same for both small and large primates (Charles-Dominique 1977; Hladik & Hladik 1969). Since insect food sources are cryptic, the mass caught may be sufficient for a small primate but not for a larger primate. Thus, larger primates often supplement their insect eating with fruit, or use a different feeding strategy (*e.g.*

folivory [Richard 1985]). Smaller primates have a higher protein requirement relative to body mass (Brody *et al.* 1934) and within primates there tends to be a negative correlation between body mass and the proportion of protein ingested (Gautier-Hion 1978, Hamilton & Busse 1978).

Leaves are neither cryptic nor rare. However, the protein which they contain is locked up within indigestible cellulose cell walls, and some plants have developed toxins to protect themselves from predators (Glander 1982). Compared to an insects or fruits, leaves are low in energy per unit mass, so that an animal has to eat a substantial amount of leaves to gain sufficient energy (McNab 1986). Kleiber's relationship for metabolic rate shows that small mammals have high energy requirements per unit body mass, although their total requirements are small. This means that they need to feed on easily digestible, high calorific food sources, but these food sources do not have to be particularly abundant, since they are not needed in large quantities. Large primates can afford a longer digestion time as their metabolic rate per unit body mass is less, but the food is needed in larger quantities (Chivers & Hladik 1984). Gut size is also important as digestion of leaves relies on a symbiotic relationship with bacteria which have the enzymes necessary to ferment such food (Bauchop 1978). This fermentation takes time, and the time that food takes to pass through the gut is roughly proportional to the gut length (Parra 1978). Therefore, an animal with a short gut has less opportunity to gain sufficient energy from fermentation. Longer and slower guts also seem better able to detoxify some of the poisons (Chivers & Hladik 1980). There is no reason to expect the symbiotic bacteria of small primates to ferment cellulose faster than those of large ones. Therefore, fermentation rate should be proportional to gut volume, and thus also to body mass: whereas metabolic rate is proportional to body mass$^{0.75}$ (Kleiber 1961). Thus, there is a physiological threshold at approximately 700g below which there are no obligate primate folivores, and above which there are no exclusive insectivores, set by restrictions of digestion and metabolic demands (Kay & Hylander 1978).

Primate folivory has encouraged increased complexity of the alimentary tract, involving either an enlargement of the fore-stomach or of the hind-gut (Bauchop 1978). Folivory is associated with the presence of symbiotic bacteria in the gut which help the digestion of polysaccharides; these are otherwise unavailable to most higher animals because of lack of the specific digestive enzymes (Parra 1978). The two major types of alimentary specialization for processing leaves involve either an enlarged caecum and colon, or an enlarged stomach (Hladik 1978). An enlarged caecum and colon is found in the genera *Lepilemur, Avahi, Indri, Propithecus, Alouatta* and *Gorilla* amongst others (Hladik 1978). Fore-stomach fermentation on the other hand, is found in *Presbytis, Colobus* and *Nasalis.* Fore-stomach fermentation has the advantage that after leaving the stomach, fermentation products, including the bacteria themselves can be digested and absorbed in the normal functional sites of the small intestine. However, some of the potential energy produced by fermentation is lost to microbial metabolism. Hind-gut fermenters digest and absorb most the digestible components of the food before it reaches the fermentation chamber, thereby reducing loss to the gut flora. The amount lost to the microbial biomass is only regained if the microbes are digested on leaving the fermentation chamber (Prins & Kreulen 1990). Microbes from fore-gut fermentation can be digested further down the alimentary canal, but microbes lost from the chamber in hind-gut fermentation are lost in the faeces. The relative value of fore-gut or hind-gut fermentation depends on the quality of the food; food with a large proportion of digestible components is preferable for a hind-gut fermenter, while poorer quality food can be utilized by fore-gut fermenters (Alexander 1993). Some hind-gut fermenters have overcome the problem of the loss of microbial energy in the faeces by reingesting the nitrogen rich faeces in a process called coprophagy or caecotrophy (Hörnicke & Björnhag 1980). Examples of mammals using this method of digestion are rabbits and some rodents. Coprophagy however is highly complex, involving the production of two types of faeces, only one of which is eaten again (e.g Schmidt-Nielsen 1990). Re-ingestion of faeces then allows for digestion of gut flora.

The alimentary canal of the Indriidae is both capacious and complex (Hill 1953). The stomach is large, and the intestine relatively long: 9 times body length for *Propithecus* and 14 times body length for *Avahi*, and the abdomen is further characterised by a large sacculated caecum (Hill 1953). The complex blood supply found in *Propithecus* and *Avahi* allows for absorption of bacterial fermentation products (Bauchop 1978). *Lepilemur*, on the other hand, has a simple stomach, but the caecum is particularly enlarged, with a spiral of 2.5 turns (Hill 1953). Work by Charles-Dominique and Hladik (1971) on *Lepilemur leucopus* in the xerophytic forest in the south of Madagascar over a period of six weeks suggested that this species practises caecotrophy. The animals are said to produce two forms of faeces, one of which is reingested to pass through the alimentary canal a second time. However, Russell (1977) studied this population for four months and did not witness a single bout of coprophagy. It is possible that coprophagy is only utilized during the dry season, when good quality food is scarce.

Razanahoera-Rakotomalala (1981) showed that *Lepilemur edwardsi* and *Avahi occidentalis* at Ampijoroa have two different anatomical morphologies for folivorous digestion. The percentage of mucous cells in the large intestine of *L.edwardsi* is said to approach values typical of folivores, whereas *A.occidentalis* has a percentage of mucous cells midway between that expected with a folivorous diet and an insectivorous diet. *A.occidentalis* has a small intestine three times the length of that of *L.edwardsi*, but *L.edwardsi* has tree like villi within the caecum whereas *A.occidentalis* has few or none at all. Also, within the small intestine, the villi become diminished towards the proximal end in *A.occidentalis* but the contrary is observed in *L.edwardsi*. Razanahoera-Rakotomalala (1981) suggested that *L.edwardsi* is better adapted to folivory than *A.occidentalis*, which has less well-adapted (intermediate) characteristics.

Ganzhorn (1988) worked on a sympatric guild of lemurs in Madagascar to see if plant chemicals could explain niche separation of seven lemurs with apparently grossly similar dietary preferences. He compared his findings to those he found during a brief study on *L.edwardsi* and *A.occidentalis* and other lemurs at Ampijoroa. Although differences in height of feeding, patch sizes, body mass, and activity patterns went a long way to explain coexistence in most study species, chemical composition of food plants helped to explain distinctions in seemingly analogous species. For example, at Ampijoroa, *A.occidentalis* ate fewer alkaloid containing leaves than did *L.edwardsi*. But *A.occidentalis* did not discriminate against tannins, whereas the opposite was found for *L.edwardsi*, possibly explaining some of the anatomical differences in the alimentary canal of the two species. As alkaloids are more common in woody plants in the understorey, than in plants of the canopy, the higher levels of alkaloids in the diet of *Lepilemur* probably reflects the indiscriminant nature of its feeding (Ganzhorn 1988). Tannins, on the other hand, are more common in canopy plants than understorey plants, and as *Avahi* fed higher up at the Andasibé site of his study, the preponderance of tannins in their diet is probably a reflection of the height of feeding (Ganzhorn 1988). Ganzhorn went on to show that when *Avahi* were present, *Lepilemur* ate poorer quality food (such as old leaves), and suggested that this is best interpreted as a 'behavioral character displacement in the wake of interspecific competition' (Ganzhorn 1992,1993).

Folivory is associated with relatively small individual home ranges (Milton & May 1976). The foodstuff on which the two study species, *L.edwardsi* and *A.occidentalis*, are primarily feeding is ubiquitous, so it seems unlikely that large home ranges are necessary to supply sufficient food within the home range (Sussman 1977, Mace & Harvey 1983. For further discussion see Chapter Four.) Folivory in mammals tends to be associated with a low basal metabolic rate (McNab 1978). Possible reasons for this include the low available calorific value per unit mass, placing a limit on the maximum bulk that can be processed within one day. It has been suggested that the secondary chemicals which have developed in many plants as a response to predation by insects, are also toxic to mammals, and that a low basal metabolic rate may reduce the intake of toxins and the cost of detoxification (McNab 1978). Also, arboreal mammals have a low muscle mass compared to terrestrial species (McNab 1978), and low muscle mass in turn is associated with low metabolic rate. It is not clear how the low calorific value of leaves per unit mass, the plant toxins and the low muscle mass interact to determine the low basal metabolic rates of arboreal folivores, but Schmid & Ganzhorn (in press) have found that *Lepilemur ruficaudatus* has the lowest resting metabolic rate so far recorded for a folivorous mammal.

5.2 Aims

The *L.edwardsi* and *A.occidentalis* measured in this study, had mean body masses of 819 g ± 226 and 708 g ± 126 respectively. It can be seen that the masses of these two species lie on the threshold for folivory in primates. Since it is therefore likely that their energy budget and dietary behaviour are under close constraint, this part of the study sought to identify the major food items of *Lepilemur edwardsi* and *Avahi occidentalis* over an 18 month period. This is the first time that diet has been assessed in these species over an annual cycle. Food choice and preference were also observed, the feeding activity throughout the night examined, and a comparison made between the two species.

5.3 Methods

5.31 Field Methods

The animals were caught and tracked during complete night follows (see Chapter Two). Details of support use whilst feeding were collected using the same branch categories as for the locomotion data (Table 5.3a) and the same three categories of sitting, clinging or standing (Table 5.3b). Each time an animal was observed to feed on a tree, the tree was marked with forestry flagging giving a number and the date. Where possible, samples of the leaves, fruit and flowers were collected later from each tree so marked. Descriptions of its approximate height, characteristics of its bark and any other distinguishing features, were recorded for each tree. The samples were then placed in a botanical press and left to dry in the sun, before being taken to the herbarium of the Parc Botanique et Zoologique de Tsimbazaza for identification.

Table 5.3a: Schedule of Feeding Observations

1	Date
2	Animal species and identification number
3	Time
4	Feeding posture
5	Support diameter (cm)
6	Support orientation:vertical (81-90°); angle (46-80°); oblique (11-45°); horizontal (0-10°)
7	Height (m)
8	Position of feed tree

Table 5.3b: Feeding postures

1	sitting
2	standing
3	clinging

Descriptions of the feeding categories were:

Sitting: the animal was stationary and supported under the rump by a branch.

Standing: the animal was stationary and the trunk held upright on the two hind limbs.

Clinging: the animal was stationary and the trunk was held upright, with the animal holding onto a vertical or angled support with both fore and hind limbs.

5.32 Data analysis

Jacob's D preference values were calculated for substrate use while feeding (see Chapter Three). Frequencies of support use and the frequency of feeding bouts at each hour of the night were calculated and plotted for both species. The results are presented in the from of figures for ease of reading and comparison. The frequency of feeding bouts for each species at different metre-interval heights from the forest floor were tested using SPSS/PC+ (Norusis/SPSS Inc. 1990) using the routine CROSSTABS. Pearson's *chi-square* was used to test whether the variables were independent.

5.4 Results

5.41 Feeding behaviour of *Lepilemur edwardsi*

Lepilemur edwardsi fed almost exclusively on leaves, although it was observed to feed on flowers, fruit, and also on moths; these were caught opportunistically, at the periphery of the tree crowns, by the lemurs grabbing them with their hands as the insects flew past. *L.edwardsi* would typically feed by pulling a branch towards its mouth with its hands, and then indiscriminantly consuming the leaves before letting the branch go and reaching for another. The feeding at the beginning and end of the night could only be described as 'frenzied'. While old leaves were eaten, dying leaves were generally avoided, but it is noteworthy that the animals were seen to feed on dead and dying leaves of *Tabernaemontana modesta* (family Apocynaceae) when these leaves were the last available of this particular plant species at the end of the dry season. This suggests that the leaves may hold some kind of nutrient that is difficult to obtain elsewhere. Flowers and fruits were eaten in the same way as the leaves. The animals were never observed to feed exclusively in one tree for the entire night; they would always move on, despite the fact that more food might still be available in the feeding tree.

5.42 Feeding behaviour of *Avahi occidentalis*

The feeding behaviour of *Avahi occidentalis* was completely different from that of *Lepilemur edwardsi* in terms of both speed and the discrimination involved. *A.occidentalis* also fed predominantly on leaves. When feeding, it would typically pull a branch towards its mouth and nip the leaves off. Sometimes, it would bite the leaves off without steadying the branch with its hands. However, the animal would only eat leaves after close inspection, and would typically only eat one or two of the leaves from the branch before looking around for another suitable source. While visibility was not adequate for qualification of leaf choice by the observer, the leaves that *A.occidentalis* was choosing appeared to be younger than those typically eaten by *L.edwardsi.* At no time of the night could the feeding behaviour of *A.occidentalis* be described as 'frenzied'. It also fed on fruit and flowers but never on insects, (despite the description of the *Avahi* gut as intermediate between an insectivore and folivore, Razanahoera 1981), or on dying leaves. If a tree was flowering the animals would typically strip the tree within two or three nights, suggesting that flowers are a very important element of *Avahi*'s diet.

5.43 Height preference for feeding

In both species, the results of CROSSTABS using SPSSPC+ (Norusis/SPSS inc. 1990) gave a Pearson's *chi-square* value of 193.22 with 13 degrees of freedom, $p < 0.001$ showing that certain heights within the forest were utilized more than others.

5.44 Support use and feeding activity

Figures 5.4a - h illustrate the frequency of support use by both species, the Jacob's D preference value for use of these supports, and the percentage frequency of feeding activity throughout the night at hourly intervals, for all nights taken together.

5.45 Plant species eaten

Tables 5.4a - c shows the list of the plant species eaten by each species.

Table 5.4a: List of plant species eaten by *Lepilemur edwardsi* at Ampijoroa

Family	Species	Part of plant	Frequency
Anacardiaceae	*Protorhus deflexa*	leaves	1
Anacardiaceae	*Protorhus sp.*	leaves	1
Annonaceae	*Monanthotaxis pilossa*	leaves	1
Apocynaceae	*Tabemaemontana modesta*	leaves	1
Bignoniaceae	*Stereospermum euphorioides*	leaves	1
Canellaceae	*Cinnamosma fragrans*	leaves	1
Capparidaceae	*Thilachium sangustifolium*	leaves	1
Cesalpineae	*Baudouinia flaggeiformis*	leaves	2
Clusiaceae	*Ochrocarpus sp.*	not known	1
Dichapetalaceae	*Dichapetalum perrieri*	fruits, leaves	3
Dichapetalaceae	*Dichapetalum sp.*	leaves	2
Euphorbiaceae	*Acalypha reticulata*	leaves	1
Euphorbiaceae	*Securinega seyrigii*	old leaves	1
Flacourtiaceae	*Scolopia sp.*	leaves	1
Hypericaceae	*Psorospermum sp.*	young leaves, fruit	1
Loganiaceae	*Strychnos decussata*	leaves	1
Loganiaceae	*Strychnos madagascariensis*	leaves	14
Mimoseae	*Albizzia fastigiata*	leaves	1
Mimoseae	*Albizzia irridis*	leaves	1
Moraceae	*Bosqueia boiviniana*	young leaves	1
Oleaceae	*Linociera tropoophylla var. angustata*	leaves	1
Oleaceae	*Linociera tropophylla*	leaves	3
Oleaceae	*Noronhia boinensis*	leaves	2
Oleaceae	*Noronhia seyrigii*	flowers, leaves	2
Papilionaceae	*Dalbergia eurybotrya*	leaves	2
Papilionaceae	*Dalbergia sp.*	leaves, flowers	4
Ptaeroxylaceae	*Cedrelopsis grevei*	leaves	1
Ptaeroxylaceae	*Cedrelopsis rakotozafyi*	leaves	1
Ptaeroxylaceae	*Cedrelopsis trivalvis*	leaves	4
Rhamnaceae	*Colubina faralaotra*	leaves	1
Rubiaceae	*Breonia sp.*	fruit, leaves	2
Rubiaceae	*Canephora sp.*	old leaves	1
Rubiaceae	*Canthium sp.*	old & young leaves	3
Rubiaceae	*Genipa sp.*	young leaves	2
Sapindaceae	*Allophyllus sp.*	leaves	1
Sapotaceae	*Sideroxylon sp.*	leaves	1
Sphaerosepalace	*Rhopalocarpus similis*	leaves	1
Sphaerosepalace	*Rhopalocarpus similis veluntinus*	leaves	1
Verbenaceae	*Clerodendrum involucratium*	leaves	1
Verbenaceae	*Premna lepidella*	leaves	1
Verbenaceae	*Premna longiacuminata*	old leaves	2

Table 5.4b: List of plant species eaten by *Avahi occidentalis* at Ampijoroa

Family	Species	Plant part eaten	Frequency
Bignoniaceae	*Stereospermum euphorioides*	leaves	2
Boraginaceae	*Cordia varo*	leaves	1
Canellaceae	*Cinnamosma fragrans*	leaves	1
Chlaenaceae	*Schizolaena sp.*	leaves	1
Dichapetalaceae	*Dichapetalum sp.*	leaves	1
Dichapetalaceae	not identified	leaves	2
Euphorbiaceae	*Securinega perrieri*	flowers, buds, leaves	4
Euphorbiaceae	not identified	leaves	1
Flacourtiaceae	*Scolopia sp.*	leaves	4
Meliaceae	*Malleastrum antsingyensis*	fruits	2
Mimoseae	*Albizzia arenicola*	leaves	2
Mimoseae	*Albizzia sp.*	leaves	1
Moraceae	*Bosqueia boiviniana*	leaves	7
Moraceae	*Bosqueia calcicola*	leaves	1
Moraceae	*Bosqueia dangnyana*	leaves	1
Moraceae	*Bosqueia occidentalis*	young leaves, leaves	6
Ochnaceae	*Diporidium ciliatum*	leaves	2
Papilionaceae	*Dalbergia sp.*	leaves	1
Papilionaceae	*Varighania perrieri*	leaves	1
Rhizophoraceae	*Cassipomea lanceolata*	leaves	3
Rhizophoraceae	*Cassipomea lanceolata variety boinensio*	green flowers	1
Rhizophoraceae	*Cassipomea macrocarpa*	fruit	2
Rhizophoraceae	*Macarisia pyramidata*	leaves	5
Rubiaceae	*Canthium sp.*	leaves	4
Rubiaceae	*Genipa sp.*	leaves	1
Rubiaceae	*Ixora sp.*	leaves	2
Sapotaceae	*Mimusops sp.*	flowers, fruits	1
Sapotaceae	*Sideroxylon sp.*	leaves	1
Sphaerosepalaceae	*Rhopalocarpus similis*	leaves	4
Sphaerosepalaceae	*Rhopalocarpus similis veluntinus*	leaves	2
Sphaerosepalaceae	not identified	leaves	1
Steraculiaceae	*Nesogordonia stylosa*	leaves	4
Verbenaceae	*Vitex beraviensis*	leaves	1

Table 5.4c: List of plant species eaten by both *Lepilemur edwardsi* and *Avahi occidentalis*

Family	**Species**
Bignoniaceae	*Stereospermum euphorioides*
Canellaceae	*Cinnamosma fragrans*
Dichapetalaceae	*Dichapetalum sp.*
Flacourtiaceae	*Scolopia sp.*
Moraceae	*Bosqueia boiviniana*
Papilionaceae	*Dalbergia sp.*
Mimoseae	*Albizzia sp.*
Rubiaceae	*Canthium sp.*
Rubiaceae	*Genipa sp.*
Sapotaceae	*Sideroxylon sp.*
Sphaerospalaceae	*Rhopalocarpus similis*

5.46 Support preference while feeding

Figures 5.4a - h show the most frequently used postures, substrate use and substrate preference of the two study species while feeding.

Fig. 5.4a **Frequency of posture while feeding for the two species**

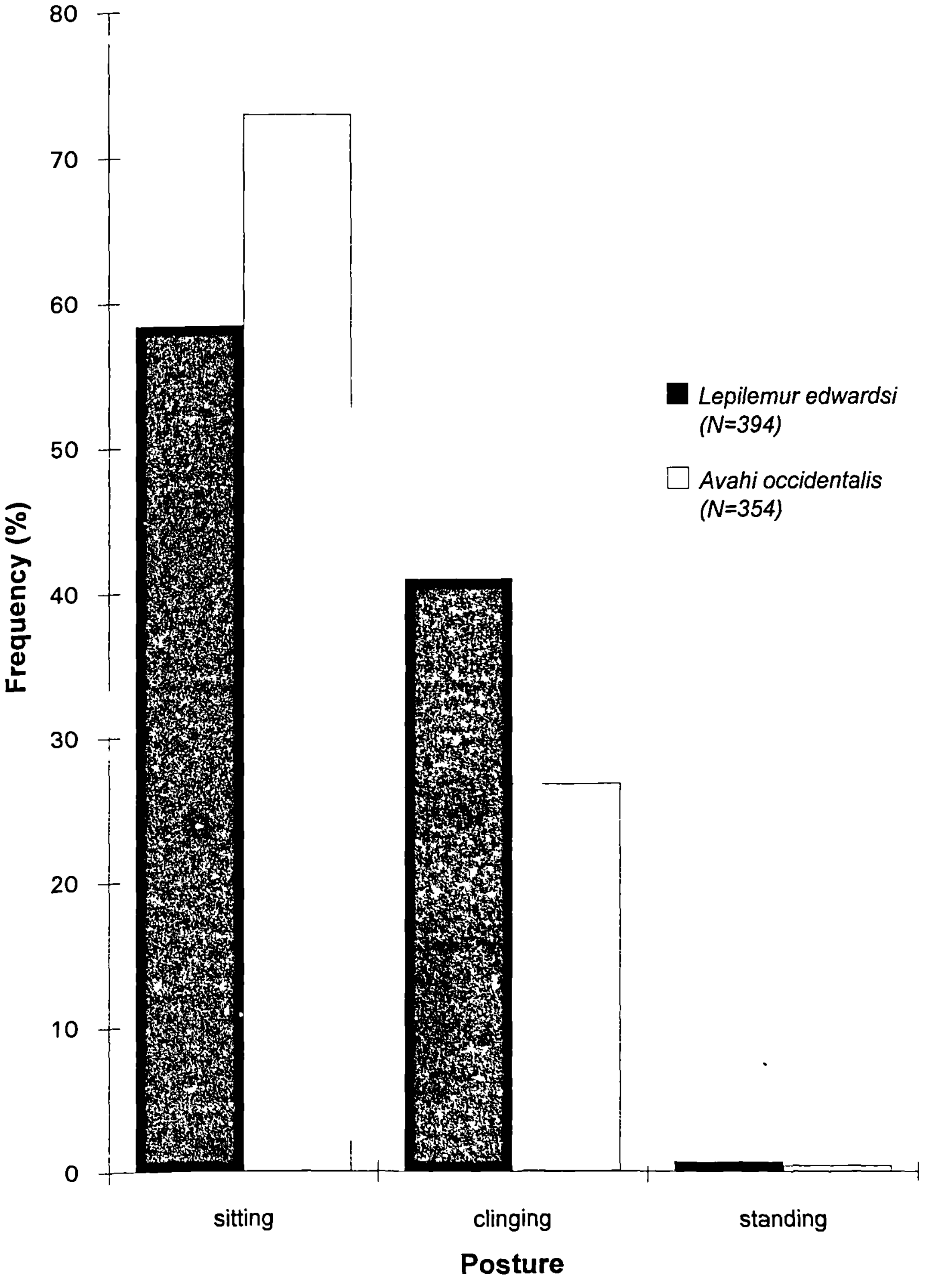


Fig. 5.4b Frequency of support orientation while feeding for the two species

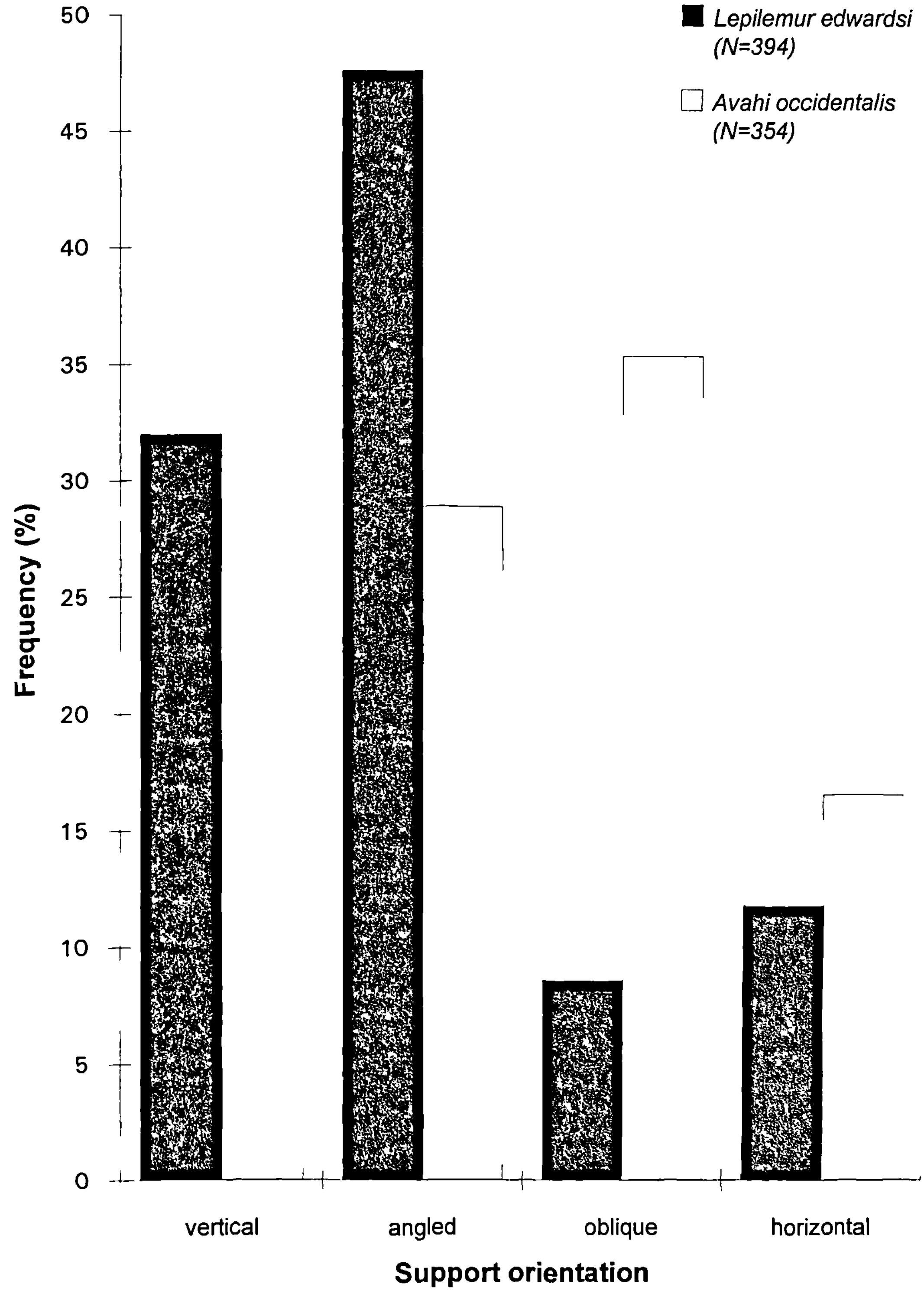


Fig. 5.4c Frequency of the support size used while feeding for the two species

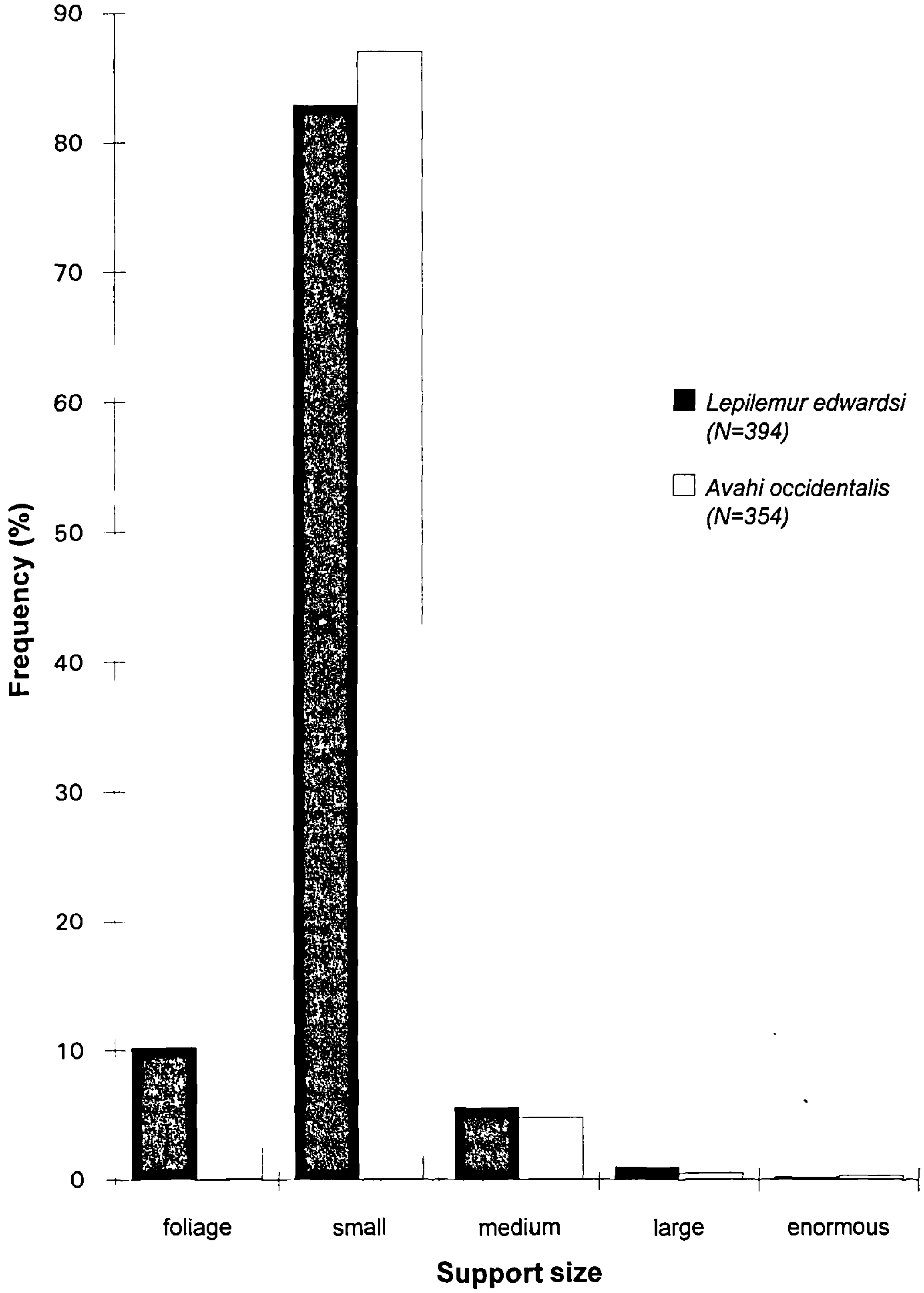


Fig. 5.4d Frequency of the height above ground used while feeding for the two species

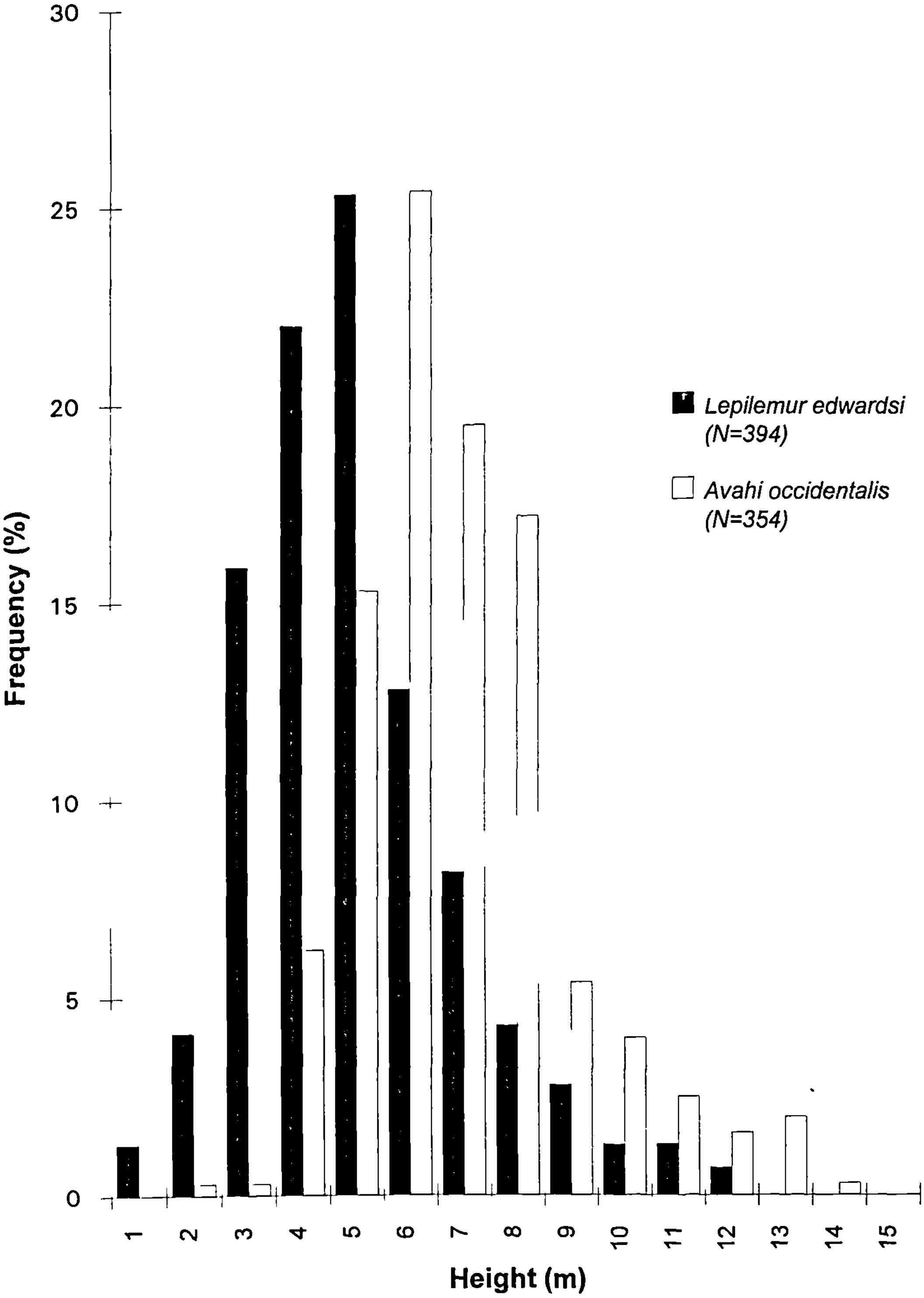


Fig. 5.4e The Jacob's D preference value for the support orientation when feeding

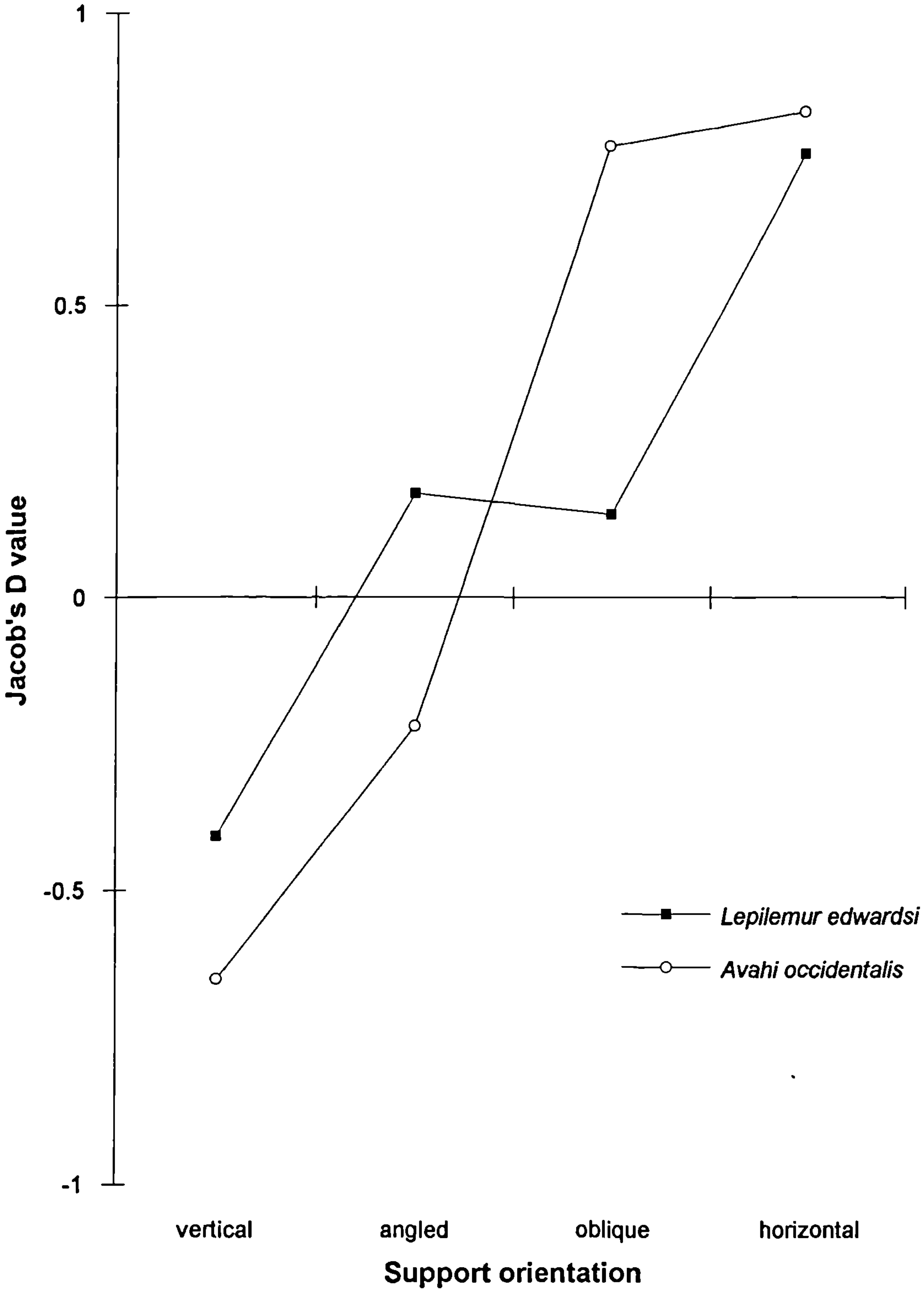


Fig. 5.4f The Jacob's D preference value for the support size when feeding

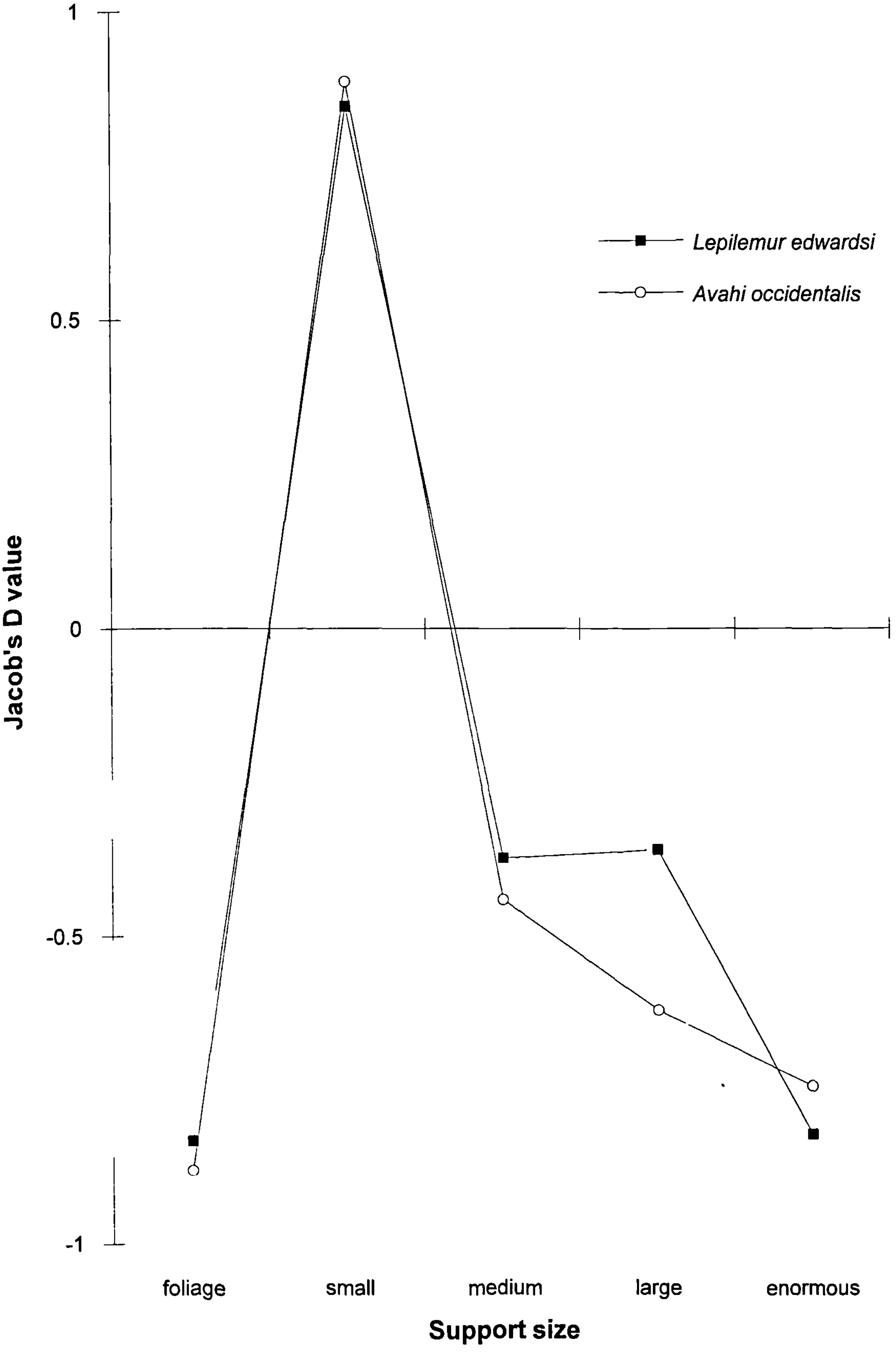


Fig. 5.4g Jacob's D preference value for the height above ground of the support when feeding

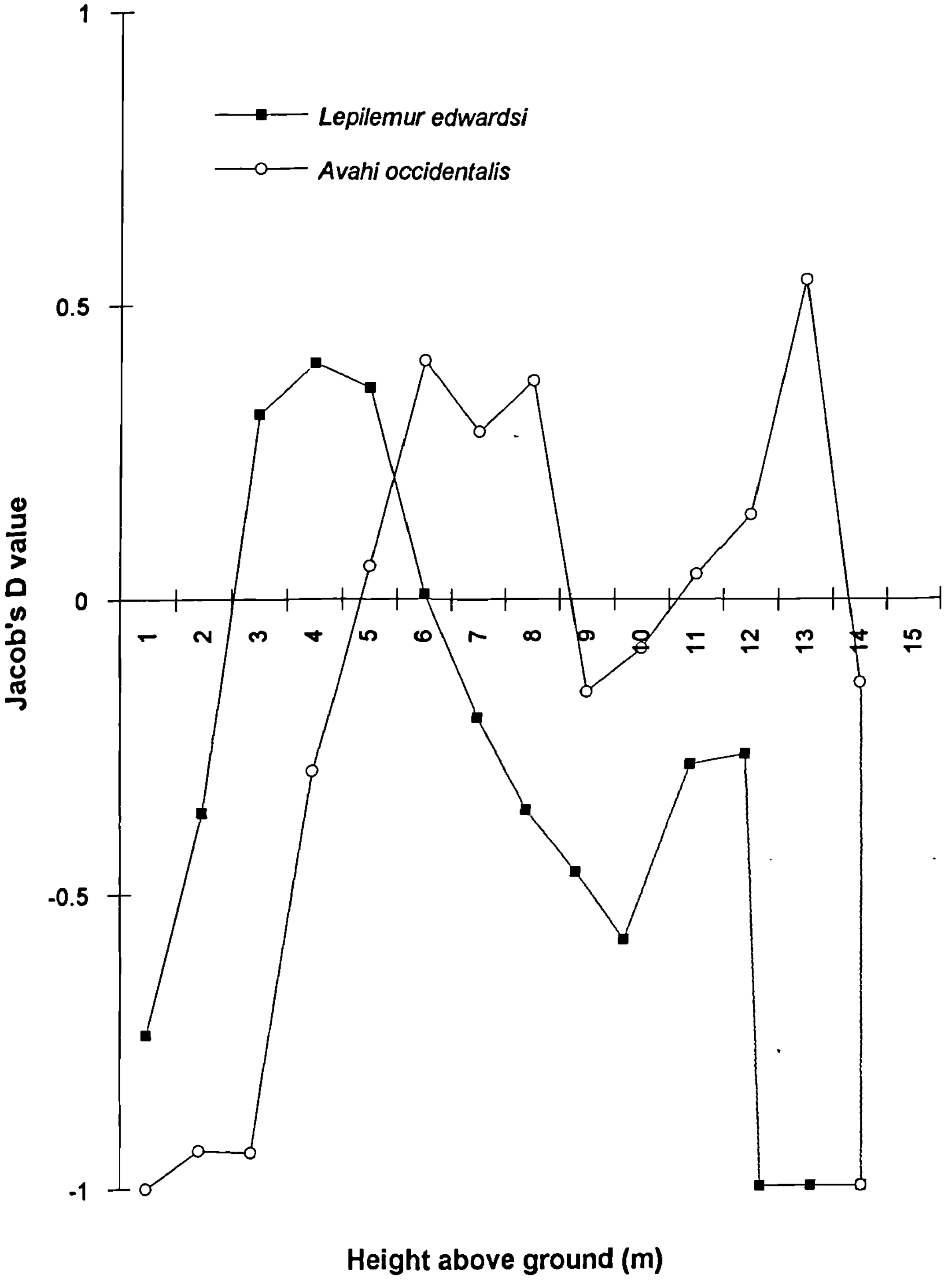
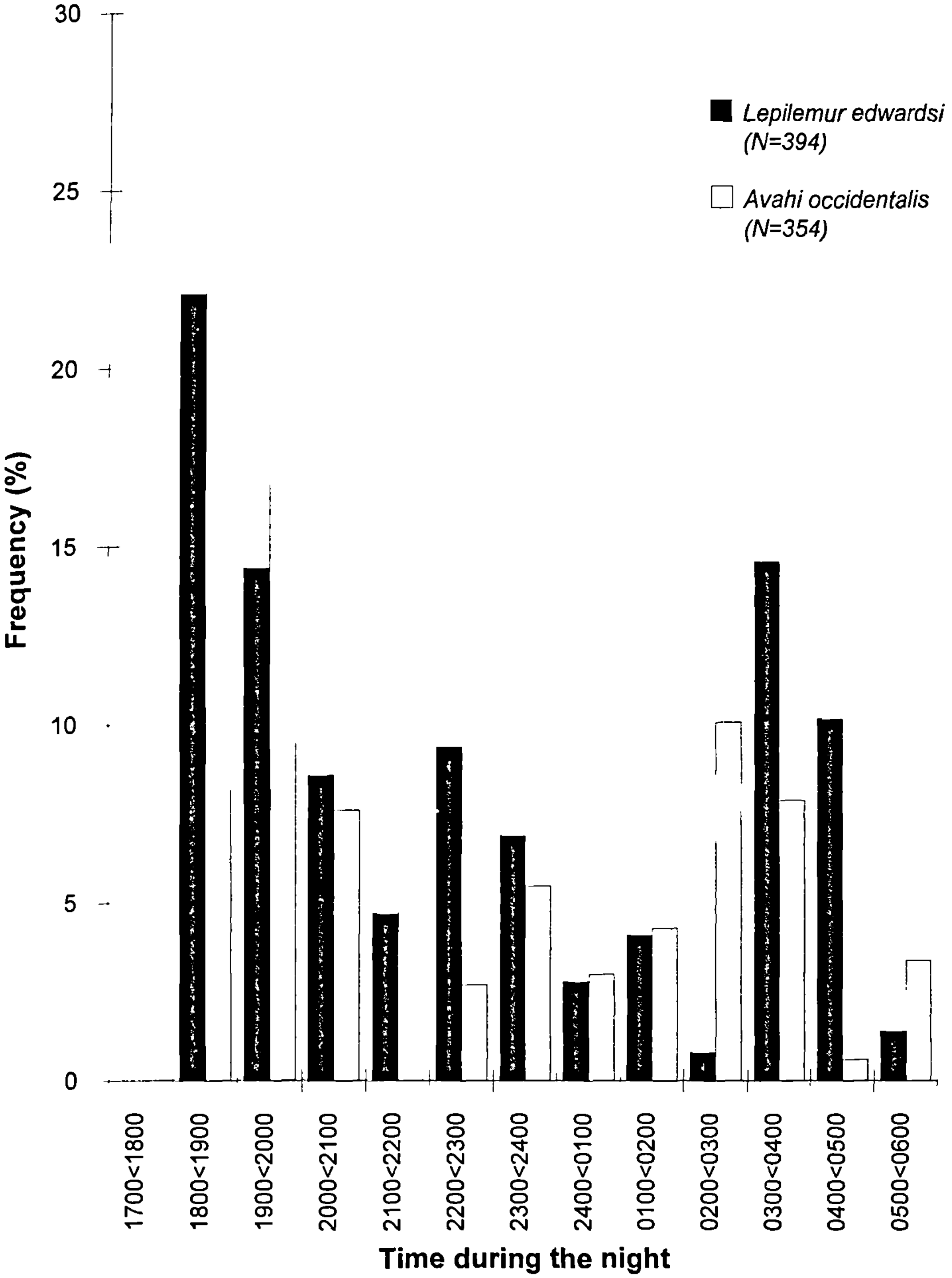


Fig. 5.4h Frequency of bouts of feeding activity for specific hours during the night for each species



5.5 Discussion

Both *Lepilemur edwardsi* and *Avahi occidentalis* preferred to feed whilst sitting, presumably so that the hands were free to reach for food (Fig 5.4a). Feeding from a clinging posture occured in both species, but interestingly, it appears that *L.edwardsi* showed a higher preference for feeding in this position. *L.edwardsi* also fed lower in the forest than did *A.occidentalis* (Fig. 5.4d), a result which was analogous to the locomotion preferences of these species (Chapter Three). The orientation of branches most frequently used for feeding was not the same for both species (Fig. 5.4b). *L.edwardsi* used angled supports more frequently than anything else, but it is noteworthy that *A.occidentalis* used oblique branches most frequently.

These results can now be compared to support availability using the Jacob's D value. This index is effectively asking whether the animals were using the support types to the same extent that they were available in the forest, or whether they actively sought branches with certain qualities. From Fig. 5.4e, we can see that both species were, in fact, choosing to use horizontal branches when possible. Both species avoided feeding from vertical supports, and *A.occidentalis* also avoided angled supports. This may explain why this species showed a higher frequency of sitting than of clinging, and also why *L.edwardsi* showed a higher incidence of clinging than did *A.occidentalis*. When the pattern of preference for feeding is compared to the preferences for branch orientation in locomotion (Fig. 3.4g), we can see that the animals had different sets of criteria for support choice. *L.edwardsi*, in particular, chose to feed from any branches other than vertical ones, whereas when travelling, this species avoided supports of all orientations apart from horizontal ones despite horizontal branches being rare (see Chapter Three, section 3.4). In all cases, both species were frequently choosing small branches of between 0.5 and 5 cm in diameter. The Jacob's D value for height above ground when feeding can be seen to resemble, (and thus to some extent mirrors), the overall height preferences for locomotion (Fig.5.4g and 3.4k), *L.edwardsi* preferring to feed at around 3-5 m above the ground (slightly lower than the locomotion preference of 4-6 m), and *A.occidentalis* preferring to feed and move at 6-8m. Therefore, in terms of feeding, there was an even more pronounced difference in the heights used by the two species. We might expect leaves nearer the ground to be of a lower quality, since less light will be available for production of sugars by photosynthesis. The height difference suggests therefore that there was also a difference in the quality of food taken by each species.

Observations made on *L.edwardsi* suggested that they did not discriminate between leaves and were, indeed, seen to feed on dying and dead leaves towards the end of the dry season, *A.occidentalis* on the other hand, was never observed eating old leaves or leaves that were dead or dying. Ganzhorn (1988) did not find a significant difference in height of feeding for the two species at Ampijoroa, but did for *A.laniger* and *L.mustelinus* at Andasibé, Madagascar. This study found a significant difference in the feeding frequency of the two species at different heights in the forest at Ampijoroa. The difference between Ganzhorn's study and the present study is probably a consequence of Ganzhorn's relatively small data set compared to that obtained in this study. The study only consisted of twelve nights at Ampijoroa. He did find, however, a significant difference in food composition taken by the two species. *A.laniger* avoided leaves with alkaloids but showed no discrimination against tannins, whereas *L.mustelinus* did exactly the opposite. *A.laniger* also showed a preference for leaves with easily extractable protein, whereas *L.mustelinus* selected leaves where the protein was bound to the diverse fraction of hemicellulose, which effectively makes the protein difficult to extract. These choices may reflect morphologically different gut structures, but nevertheless effectively result in dietary partitioning of the two species. Ganzhorn (1988) noted that it was not clear whether these differences reflected food choice or merely a correlation of habitat use and the leaves available in particular forest strata. He found that at Ampijoroa, differences in dietary discrimination existed despite the similar heights of feeding he found for the two species.

Of the 27 different species identified for *L.edwardsi* (and the additional 14 which could only be identified to genus level), and of the 17 species identified for *A.occidentalis* (and the further 16 identified to genus level), only four were eaten by both species. (The other seven in Table 5.4c were not identified to species level). Ganzhorn (1988) identified 10 genera and species combined eaten by *A.occidentalis* and 11 genera and species combined for *L.edwardsi* at Ampijoroa. Only two of these were duplicated in the present study for *L.edwardsi*, and then only where the species had not been fully identified in one or other of the data sets. None of the plant species eaten by *A.occidentalis* during this study was recorded by Ganzhorn, nor did Ganzhorn find any tree species eaten by both species of lemur. It seems apparent, therefore, that in the present study only a small proportion of the species potentially eaten by these two lemurs at Ampijoroa was identified. Given the high diversity of the forest at Ampijoroa (Ramangason 1986), it seems likely that different individuals of each of the two lemur species studied at Ampijoroa will feed on different species even within the same forest. Two of the four 'duplicate' tree species eaten were seen to be eaten at the same time of year by both lemurs just before the rains fell (*Stereospermum euphorioides* and *Bosqueia boiviniana*). The other two tree species 'duplicated' were seen to be eaten throughout the year.

The following section will enlarge on the discussion of activity cycles with respect to feeding provided in Chapter 4. Fig. 5.4h shows the peaks of feeding activity throughout the night for the two species. Clearly the most marked peak is at the beginning of the night, with a smaller peak at the end of the night. However, there is another smaller peak in feeding activity at around 2200-2400 for *L.edwardsi* and at 2300-2400 for *A.occidentalis*. We have noted that activity patterns in primates have often been found to be biphasic in nature, with a peak of activity at dusk and dawn with a resting period in between (*e.g. Eulemur fulvus fulvus* and *Lemur catta* - Sussman 1977, *Hylobates* - Raemaekers 1978, *Galago crassicaudatus* - Bearder 1974, *Galago demidovii* - Charles-Dominique 1971). However, in some nocturnal prosimians no consistent pattern is apparent (*Galago crassicaudatus* and *Galago senegalensis* - Harcourt 1980, *Euoticus elegantulus, Galago alleni, Perodicticus potto* and *Arctocebus calabarensis* - Charles-Dominique 1971 and *Lepilemur mustelinus* - Hladik & Charles-Dominique 1974). We have further observed that the biphasic nature of activity for diurnal primates may be a reaction to a peak in day temperature which decreases activity levels due to the extreme heat. Alternatively, it may help maximize the food that can be ingested in a day (Clutton-Brock & Harvey 1977). Clutton-Brock and Harvey suggested that to maximise the bulk of leafy material taken in, an animal should first feed at the beginning of the day, then take a period of rest and digestion, and then feed again, when the stomach is emptying, towards the end of the day so that food can subsequently be digested throughout the night. Presumably a similar argument would also apply for a nocturnal animal, with peaks of feeding at the beginning and end of the night. However, work by Penry and Jumars (1987) has suggested that the optimal way of feeding in terms of digestion is a slow graze maintained throughout the active period. They found that regular inputs of small amounts of fuel were more efficient than intermittent input of large amounts. Clearly, there is a payoff between meeting the cost of constantly collecting food and the conflicting demands of other activities such as defence of the territory, search for a mate and so on. A leafy diet relies on a ubiquitous resource and food is thus relatively abundant for the two study species, so that the energy cost of searching for food is likely to be small. As predicted by Penry and Jumars' model, feeding frequency is above zero throughout the night implying that feeding occurs throughout the night (Fig. 5.4h). However, on individual nights the animals did take long periods of rest (see Chapter Four) and thus, they are not perpetually eating.

These animals, then, may be using an intermittent strategy made possible by the low cost of food collection, and influenced by the absolutely small size of their gut. The latter is likely to cause problems in a folivorous diet, by limiting the bulk that can be ingested at any one time. Behavioural evidence for the importance of flowers in the diet of *Avahi occidentalis*, together with a substantial difference in the height at which the *Avahi* and *Lepilemur* fed, and clear evidence that only a few species form part of the diet of both lemurs, appears to identify key factors permitting sympatry of the two species at Ampijoroa.

6 The Energy Cost of Locomotion

6.1 Introduction

Locomotion is energetically expensive (*e.g.* Casey 1992). An animal gains its energy through the metabolism of food consumed. (Energy metabolism refers to the animal's overall use of chemical energy (Schmidt-Nielsen 1990)). The demands on this energy even when an animal is resting can be considerable. This available energy has to be shared between normal daily costs of body maintenance, including protein synthesis, circulation of body fluids and tissue repair. Substantial additional costs for reproduction and lactation occur in female animals and these factors have been shown to be of considerable importance in activity budgets, and, if anything, more significant than the effects of sexual dimorphism (Dunbar 1988). Clearly, an animal that needs to move throughout its active period will have to budget carefully to allow for all these demands. During increased physical activity, contraction of the skeletal muscles requires extra energy, and the respiratory and cardiovascular systems must increase in rate to supply these working muscles with oxygen. These factors again place extra demands on oxygen consumption and energy use (Bennett 1985).

Some principles of basic mechanics [from Alexander (1992)] need to be reviewed before we can attempt to understand the mechanical costs of animal locomotion. A force on a body will do work when it moves a body a distance along its line of action. Work done on a rigid body gives it kinetic energy (energy of movement) or gravitational potential energy (energy due to height) or both. The energy gained by a system when work is done on it is equal to the work. The Principle of Conservation of Energy states that energy cannot be created or destroyed but may be converted to another form, for example, work done against friction converts some of the work into heat. Positive work is done on a body when it moves in the direction of the force applied to it, and negative work when it moves in the opposite direction. A body can have positive and negative kinetic energy by accelerating or decelerating. Climbing up or down will cause positive or negative potential energy. The energy which the muscles use to do work is gained from food. Aerobic metabolism involves the combustion of the food with oxygen to give carbon dioxide and water and energy. Anaerobic metabolism releases less energy than the aerobic form, but the process can proceed quickly. However, an oxygen debt is soon built up, so that for air breathing animals, this level of energy output cannot be sustained. Only a small proportion of energy is utilized as work. This can be measured as the ratio of the energy output to the input of energy. Margaria (1976) measured oxygen consumption of people walking up and down gradients and calculated an efficiency of 0.27. Cost of transport is often used when comparing the energy costs of locomotion of different animals.

Both *Lepilemur edwardsi* and *Avahi occidentalis* are folivorous primates but have a low body mass for this diet (see Chapter Five), and the study species will have a higher metabolic rate per unit body mass than larger primates (Kleiber 1961). They eat a bulky, slowly digestible folivorous diet and both species lie on, or near Kay's threshold (Kay 1984). The low level of energy intake for these two species might imply that they have energy-limited lifestyles. In such situations it would be likely that the energy cost of locomotion would be of considerable importance in their activity budgets.

The energy costs of locomotion have often been measured using 'indirect calorimetry', involving the measurement of the exchange of respiratory gases and calculation of the energy equivalent. For terrestrial animals the subject is fitted with a mask while moving (often on a treadmill) (*e.g.* Goldspink 1977). Clearly, this necessitates the subject being placed in an artificial environment which may lead to stress in the animals. The doubly-labelled water technique can be used to assess the metabolic rate, but it is expensive and involves taking blood from the animals before and after a period of activity (Ulijaszek 1992). However, the energy cost of locomotion can also be calculated using mechanical equations to assess the kinetic costs of locomotion. Alexander *et al.* (1980) used biomechanical modelling to estimate the energy costs of different quadrupedal gaits. His model was successful in interpreting some of the energy costs of quadrupedal locomotion, but failed in some cases because such mathematical models usually involve assumptions which may not represent an animal moving precisely.

Terrestrial locomotion has been shown to be energetically more expensive than both flying and swimming (Schmidt-Nielsen 1972). A large quantity of the energy input is spent on raising the centre of mass and accelerating and decelerating the limbs during a stride (Alexander 1977). Arboreal animals use comparable gaits within the trees to those used by terrestrial species. However, the branches bend under the weight of the animals, and are left vibrating when they jump from them. (Indeed, distinct oscillation of some branches was observed at take-off and landing of the two study species). A typical sequence of arboreal locomotion would involve an animal jumping onto a branch, walking along it and jumping off again. The animal would typically lose kinetic or potential energy at several stages along this route, which would have to be made good later on. To begin with, when an animal lands on a compliant branch, it loses most of its kinetic energy. The branch will be depressed by body weight, and the animal will therefore have to regain height. Also, if the branch is slender it will be left vibrating with kinetic energy on landing and take-off. All of these complications will increase demands on the available energy. The flexibility of branches and the need to jump from branch to branch thus makes arboreal locomotion more expensive of energy than running on rigid ground (Alexander 1991).

The distance s travelled over level ground by a projectile taking off at speed v at an angle α to the horizontal is:

$$s = \frac{v^2}{g} \sin 2\alpha$$

(*e.g.* Alexander 1983). The kinetic energy required for a jump if body mass is M_b is:

$$E_{KE} = \frac{1}{2} M_b u^2 = \frac{1}{2} M_b \frac{s g}{\sin 2 \alpha}$$

and the energy required to move the unit mass of an animal unit distance is:

$$C = \frac{E}{M_b\ s} = \frac{g}{2\ \sin\ \alpha} \propto \frac{g}{2}$$

[if α is reasonably near 45^0, the optimum angle for a projectile (*e.g.* see, Norton 1987)]. C is the mechanical cost of transport. Since g is about 10 m/s^2, this argument will give a cost of transport for vertical clinging and leaping of about 10/2 = 5 joules per kilogram metre. Heglund *et al.* (1982) show that the rate at which a running mammal (running on level ground) does work (watts) is about 0.69 x speed (m/s) x body mass. This implies that the cost of transport for level running is 0.69 joules per kilogram, only one seventh of the cost of vertical clinging and leaping. Thus vertical clinging and leaping is a very expensive way of travelling if kinetic energy is not carried over from one leap to the next (as may occur in richochetal leaping). Mechanical equations will therefore allow us to discover whether locomotion is indeed a major component of energy expended over 24 hours.

Taylor *et al.*(1982) have expressed the cost of running and walking in the form of an allometric relationship

$$10.7\ M^{-0.316}$$

in which the slope of the regression between rate of expenditure and velocity is the net cost, or incremental cost, in J/m, and is independent of velocity. They considered the y intercept to be the energy expenditure while standing, but Paladino & King (1979) argued that laboratory stresses were associated with the power increments. In many terrestrial animals, an increase in speed brings about a change in gait and hence different associated intercepts and slopes (*e.g.* Heglund & Taylor 1988, Hoyt & Kenagy 1988).

One of the most rigorous calculations of the relative costs of locomotion on daily activity costs and the field metabolic rate (FMR) has been made by Kenagy and Hoyt (1990). Hoyt & Kenagy (1988) measured the energy expended by the golden-mantled ground squirrel, whilst it was running on a treadmill. They then went on to measure field metabolic rates (FMR) and resting metabolic rates (RMR) of this species in the wild (Kenagy *et al.* 1989) and in 1990, Kenagy and Hoyt measured running speeds of the same squirrel under field conditions. They calculated that the daily energy costs of locomotion accounted for 15 % of the FMR. However, Karasov (1981) found this value to be 4 % for a different species of ground squirrel; while Gettinger (1984) obtained a value of 3.6 % for pocket gophers, and Nagy and Milton (1979) obtained a value of 2 % for mantled howler monkeys. Clearly, the value obtained by Kenagy and Hoyt (1990) is much larger than the latter values. However, in the absence of standardized methods, these various values are not closely comparable. The studies do agree in finding that locomotory costs account for less than 50 % of total daily activity costs of these mammals [that is the cost expenditure of metabolism plus the expenditure associated with food assimilation (Karasov 1992)]. Garland (1983) performed a similar allometric analysis and concluded that locomotor costs were only a small proportion of the total energy expenditure of wild mammals, but that the proportion increased with body size. Garland's work was, however, refuted by Altmann (1987) and Kenagy & Hoyt (1990), who found the cost of locomotion to be a considerable proportion of the available energy. Estimations of the cost of transport using allometry for energy expenditure while running, and travel distances, probably underestimate the real costs due to change in direction and changes in height which are not taken into account.

Most measurements of locomotion costs have been made using treadmills. These, however do not take into account the effect of spongy or compliant surfaces (McMahon 1984). Daily movement distances have also often been underestimated, especially when based on periodic sightings or trigonometrical fixes using radio-transmitters. Moreover, animals with long daily movement distances (DMD) tend to have greater relative costs of transport which cannot readily be predicted from treadmill studies. For example, mustelids have DMDs about 80% greater than similar sized canids and about 240% larger than similar sized felids (Goszczynski 1986). Particularly high additional costs for locomotion were reported by Karasov (1992), who found locomotion in winter to add 37 - 55 % to the daily standard metabolism of a 1 kg pine marten and 158 - 237 % to that of 15 kg wolverines.

Both *Lepilemur edwardsi* and *Avahi occidentalis* are folivorous. As we have seen, folivory is often associated with a depressed metabolic rate (McNab 1978), which may be a consequence of high fibre and cellulose content of leaves. As a response to predation on leaves by insects and other folivores, high quantities of secondary chemicals and toxins may exist, which might further encourage low metabolic rates. Such secondary chemicals impose additional costs of detoxification (McNab 1978, Ganzhorn 1992). *Lepilemur edwardsi* and *Avahi occidentalis*, with similar body mass will have similar high energy requirements per unit body mass, but their small gut capacity imposes a limit on bulk intake. Given high energy requirements, they must ensure rapid turnover of food stuffs, and cannot allow for increased digestive effectiveness by increasing the passage time through the gut as larger animals can do (Robbins 1983).

6.2 Aims

The aims of this element of the study were to calculate the locomotor energy costs of the two study species, using biomechanical equations combined with first hand observations of the locomotor behaviour of the animals. Complete all night 'follows' were made on the animals to give accurate measures of nightly distances travelled horizontally, and both horizontal and vertical components of the locomotor bouts were recorded. Locomotor energy costs were calculated for leaping, 'standard' climbing and 'ladder' climbing, and walking. For the first time, this allows reliable estimations of locomotor costs of these two nocturnal lemurs and adds another piece to the 'jigsaw' relating animal form and function to their biological role within the wild.

6.3 Methods

6.31 Field Methods

Data were collected on locomotor frequencies as explained in Chapter Two and for nightly travel distances as explained in Chapter Four.

6.32 Kinetic analysis

The distance *s* travelled over level ground by a projectile taking off at speed *v*, at an angle α to the horizontal is

$$s=\frac{v^2}{g}\sin 2\alpha \qquad (1)$$

where *g* is gravity (Alexander 1983). The kinetic energy required for a jump, if body mass is M_b , is

$$E_{KE} = \frac{1}{2}M_b v^2 = \frac{1}{2}M_b\frac{sg}{sin 2\alpha} \qquad (2)$$

However, if there is a change in height either up or down the equation has to be modified to take this into account. Figure 6.3a shows the parameters used in these calculations. If we consider a jump which gains height *h* (the y component) and travels a distance *s* (the x component), from equations of motion ($s = ut + at^2$),

$$h = v \sin \alpha\ t - \frac{1}{2}\ g\ t^2 \qquad (3)$$

where *t* is the time taken for the jump and *g* is gravity (acceleration in the equations of motion). For the horizontal axis

$$s = v \cos\ \alpha\ t \qquad (4)$$

This equation can be rearranged to give:

$$t = \frac{s}{v \cos \alpha} \tag{5}$$

Equation 5 can be substituted into equation 3:

$$h = s \tan \alpha - \frac{\frac{1}{2} g s^2}{v^2 \cos^2 \alpha} \tag{6}$$

Rearranging equation 6 using trigonometrical equations gives:

$$h = s \tan \alpha - \frac{g s^2}{2 v^2} (\tan^2 \alpha + 1) \tag{7}$$

Equation 7 is rearranged to calculate v^2

$$(s \tan \alpha - h) = \frac{g s^2}{2 v^2} (\tan \alpha - 1) \tag{8}$$

$$v^2 = \frac{g s^2}{2} \times \frac{(\tan \alpha + 1)}{(s \tan \alpha - h)} \tag{9}$$

Substituting equation 9 into equation 2 :

$$E_{KE} = \frac{M_b g s^2}{4} \frac{(\tan^2 \alpha + 1)}{(s \tan \alpha - h)} \tag{10}$$

This gives a kinetic energy value for a specific leap in joules. The angle α was calculated by differentiating equation 10. The differential of this equation would allow us to minimize the value of E_{KE} for any given *s*, by placing the differential equal to zero and solving the equation.

$$\frac{dE}{d(\tan\alpha)} = \frac{M_b g s^2}{4} \times \frac{(s \tan\alpha - h)\, 2 \tan\alpha - (\tan^2\alpha + 1)}{(s \tan\alpha - h)^2} \tag{11}$$

$$= \frac{m\,g\,s^2}{4} \times \frac{2\,s\,\tan^2\alpha - 2\,h\,\tan\alpha - s\,\tan^2\alpha - s}{(s\,\tan\alpha - h)^2} \qquad (12)$$

$$= \frac{m\,g\,s^2}{4} \times \frac{s\,\tan^2\alpha - 2\,h\,\tan\alpha - s}{(s\,\tan\alpha - h)^2} \qquad (13)$$

which is zero when

$$s\,\tan^2\alpha - 2\,h\,\tan\alpha - s = 0 \qquad (14)$$

Solving this quadratic equation gives:

$$\tan\alpha = 2\,h \pm \frac{\sqrt{4\,h^2 + 4\,s^2}}{2\,s} \qquad (15)$$

$$= \frac{h \pm \sqrt{h^2 + s^2}}{s} \qquad (16)$$

tan α must be positive, therefore

$$\tan\alpha_{opt} = \frac{h \pm \sqrt{h^2 + s^2}}{s} \qquad (17)$$

Equation 17 was applied to every leap by *Lepilemur edwardsi* and *Avahi occidentalis* recorded in this study. Its mean value for a leap of one metre was calculated, and adjusted to give a mean value of the kinetic energy for a one metre leap. To convert this value to metabolic energy, an efficiency of 0.2 was taken from Wunder and Morrison's (1974) paper on the metabolic costs of squirrels running on an incline.

As was described in the introduction, the energy costs of walking and running were calculated using the equation from Taylor *et al.* (1982),

$$E_{metab} / M_b = 10.7 \, M_b^{-0.316} \, v_g + 6.03 \, M_b^{-0.303} \qquad (18)$$

which is the same as,
rate of energy use = (energy cost / distance) * speed + cost of staying still. The gradient of this equation ($10.7M^{-0.316}$) is used to calculate the metabolic cost of running (Joules/kg m).

Climbing was calculated using the equation for potential energy

$$E_{PE} = m \, g \, h \qquad (19)$$

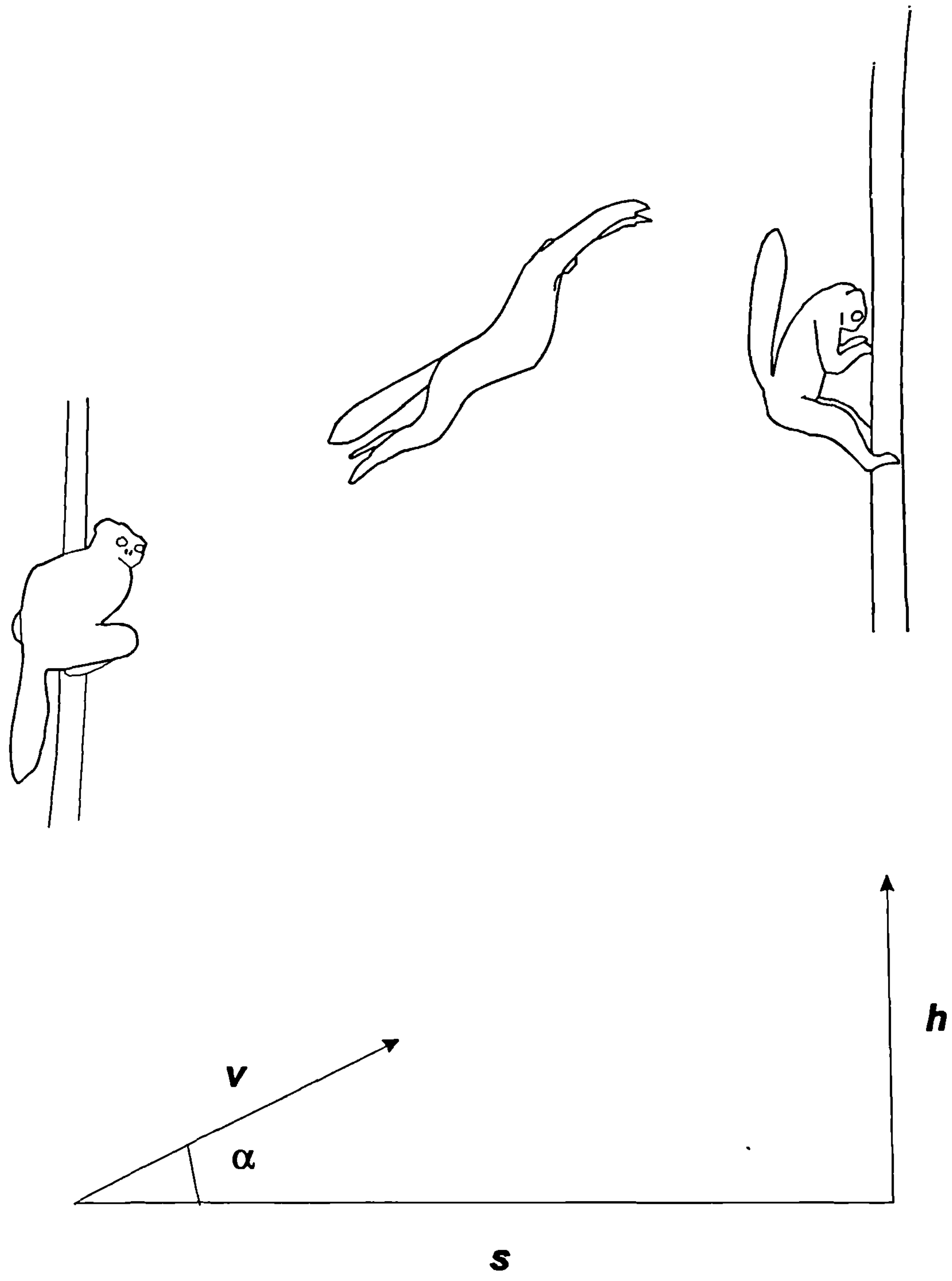
where *m* is the mass in kilograms, *g* is gravity and *h* is the height change. Once this is calculated, it is converted to metabolic energy by dividing by an efficiency of 0.2 (Wunder & Morrison 1974) for climbing up, and -1.2 (Margaria 1976), with *h* negative, when climbing down.

Therefore the energy cost for locomotion over a night
= (total distance jumped * mean (energy/distance) for jumps)/efficiency
+ (total distance climbed up * weight) / efficiency
+ (total distance climbed down * weight) / efficiency
+ total distance walked/run * metabolic cost of walking/running

Any horizontal component of climbing was added into the calculation for walking and similarly, any vertical component of walking was included in the climbing calculations. The mean nightly travel distance was then calculated from the ranging data for each species. The metres per kilometre (m/km) of the horizontal distance travelled, climbing down, and climbing up, were calculated from mean bout lengths and frequencies of observation. These were then used to calculate in metres, the proportion of the nightly distance travelled for each of the locomotor modes. Only leaping, running, walking, climbing and ladder climbing were included as the other locomotor modes were of relatively low frequency.

The estimated energy cost of locomotion calculated was then compared to the resting metabolic rate (RMR) of *Lepilemur ruficaudatus* measured by Schmid and Ganzhorn (in press), and the energy cost of locomotion was also compared to the field metabolic rate (Nagy 1987).

Fig.6.3a A diagram to show the parameters used in the kinetic analysis of leaping



6.4 Results

The mean kinetic energy cost and its standard error for each one metre jump for *Lepilemur edwardsi* is 4.240 ± 0.119 J. The mean cost and standard error of kinetic energy for each one metre jump for *Avahi occidentalis* was 3.304 ± 0.089 J. The mean distance travelled by *L.edwardsi* per night was 343.47 ± 33.74 m (N = 25) and the mean distance travelled by *A.occidentalis* per night was 1174.89 ± 164.57 m (N= 18). Figures 6.4a, b and c show the number of metres per kilometre travelled by each of the two species, using each of the ten locomotor modes identified (see Chapter Two). Table 6.4a shows the major components of the metabolic cost of locomotion for the two species when their mean nightly travel distance is used; 6669 J for *L.edwardsi* and 22168.14 J for *A.occidentalis*.

Table 6.4a The energy cost for a mean nightly travel distance

Locomotor component	**Energy cost for *Lepilemur edwardsi* (J)**	**Energy cost for *Avahi occidentalis* (J)**
leap	5014	19409
climb up	438	211
climb down	72	65
walk/run	1145	2483
Total	**6669**	**22168**

Schmid and Ganzhorn (in press) showed that *Lepilemur ruficaudatus*, (with a mass between 400g and 1 kg), has a resting metabolic rate which is 42.2% ± 10.2% of the Kleiber relationship (1961). They also found that the rate of metabolism when the animals were active was 79.9% ± 16.8% of the Kleiber relationship (1961). The Kleiber relationship (1961) can be expressed as:

$$P_{met} = 70\ M_b^{0.75}$$

where P is the symbol for power in kcal/24hr^{-1} and M_b is body mass in kg. Therefore *Lepilemur edwardsi*, with a mean mass of 0.819 kg, has a resting metabolic rate of 60.26 kcal/24hr. Converting this to kJ gives 253.09 kJ/24hr. I will use this same conversion rate for *Avahi occidentalis* as this is the closest calculation of metabolic rate for this species. Therefore, *A.occidentalis* with a mean mass of 0.708 kg has a resting metabolic rate of 54.03 kcal/24hr or 226.93 kJ/24hr. Possible available energy for the two species can be estimated using Nagy's (1987) equation for field metabolic rate (FMR) based on various measures on mammals in the field using doubly-labelled water

$$\log_{10} FMR = 0.774 + 0.727 \log_{10} M$$

where M is mass in grams and FMR is in kJ/24hr. Therefore for *L.edwardsi* the FMR is 779.75 kJ/24hr and for *A.occidentalis* is 701.41 kJ/ 24hr. The energy cost of locomotion for *L.edwardsi* is 0.03 of the resting metabolic rate and 0.009 of the FMR. For *A.occidentalis* the energy cost of locomotion is 0.01 of the resting metabolic rate and 0.03 of the FMR. The relative cost of locomotion can then be calculated using an equation adapted from Karasov (1992):

$$\frac{distance\ moved\ (km/24hr) \times cost\ of\ transport\ (kJ/24hr)}{resting\ metabolic\ rate\ (kJ/24hr)}$$

where RMR is used instead of the daily standard metabolism used in his paper. Table 6.4b summarises these results.

Table 6.4b: Summary of the energy cost and estimated metabolic rates for both species.

Energy measure	*Lepilemur edwardsi*	*Avahi occidentalis*
Energy cost of locomotion kJ/24hr	6.67	22.17
Resting metabolic rate (RMR) kJ/24hr	253.09	226.93
Field metabolic rate (FMR) kJ/24hr	779.75	701.41
Relative cost of locomotion	9.05	114.78

Fig. 6.4a Metres per kilometre travelled horizontally using each locomotor mode by each species

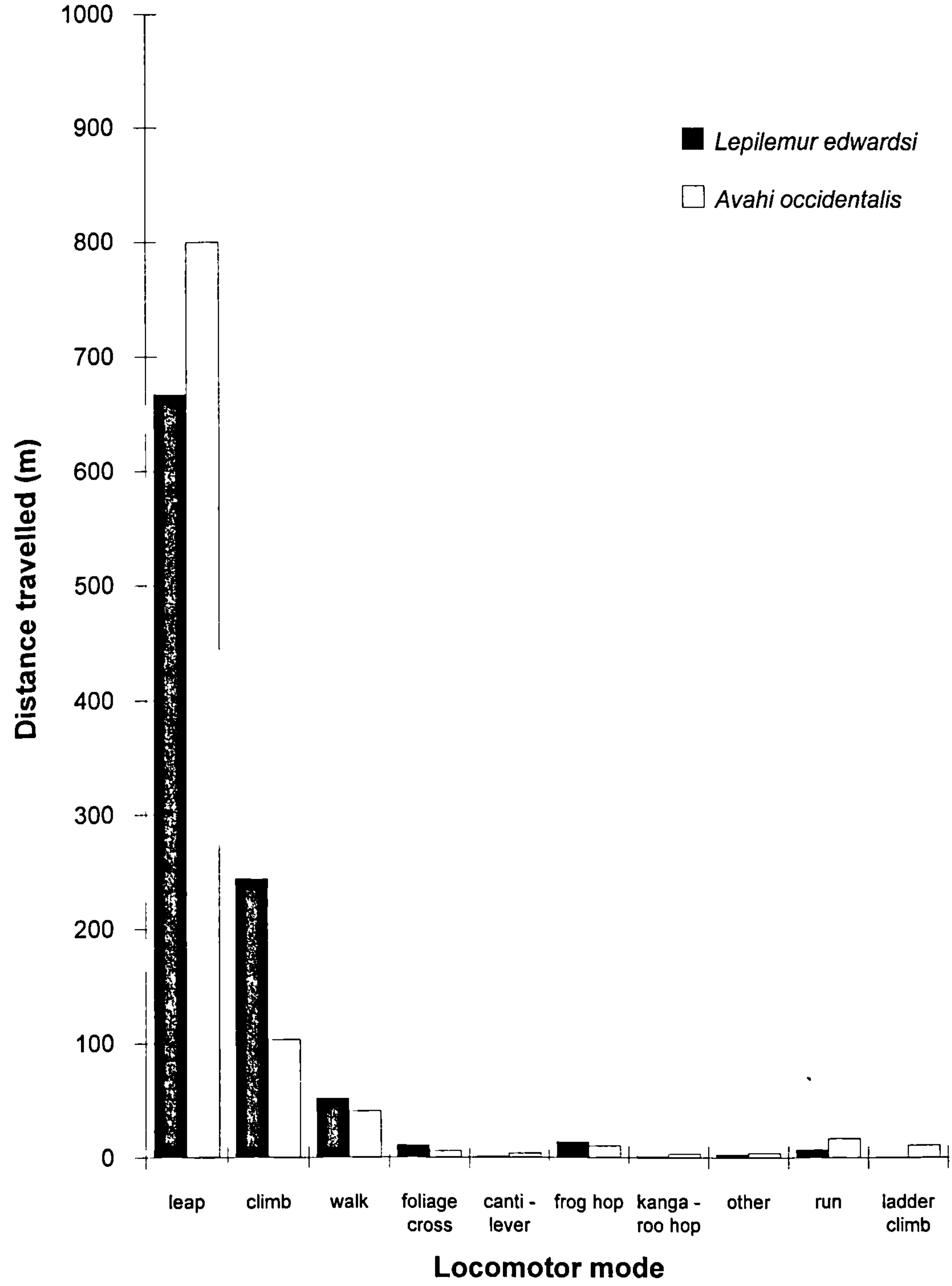


Fig. 6.4b Metres per kilometre of height gained using each locomotor mode by each species

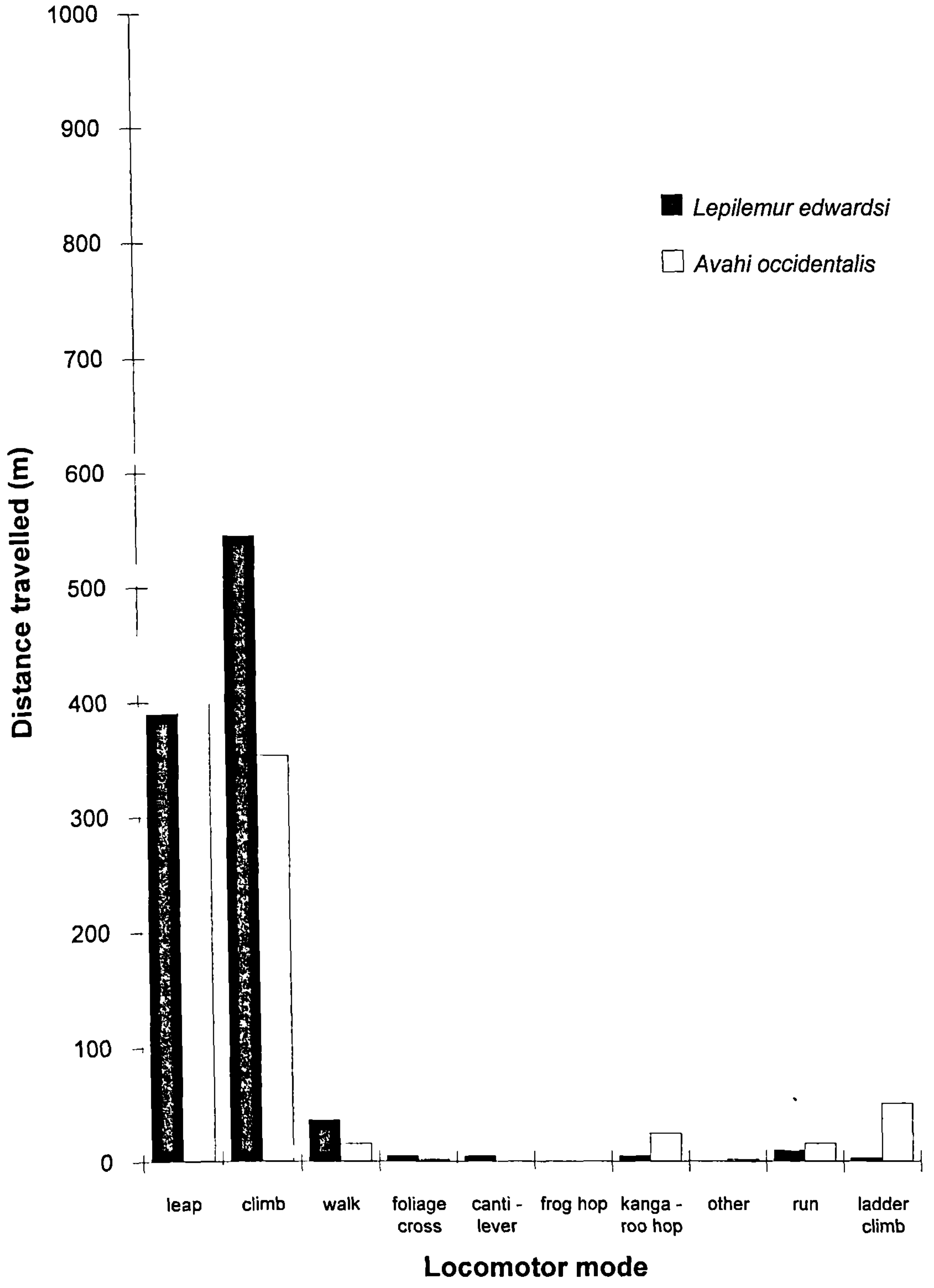
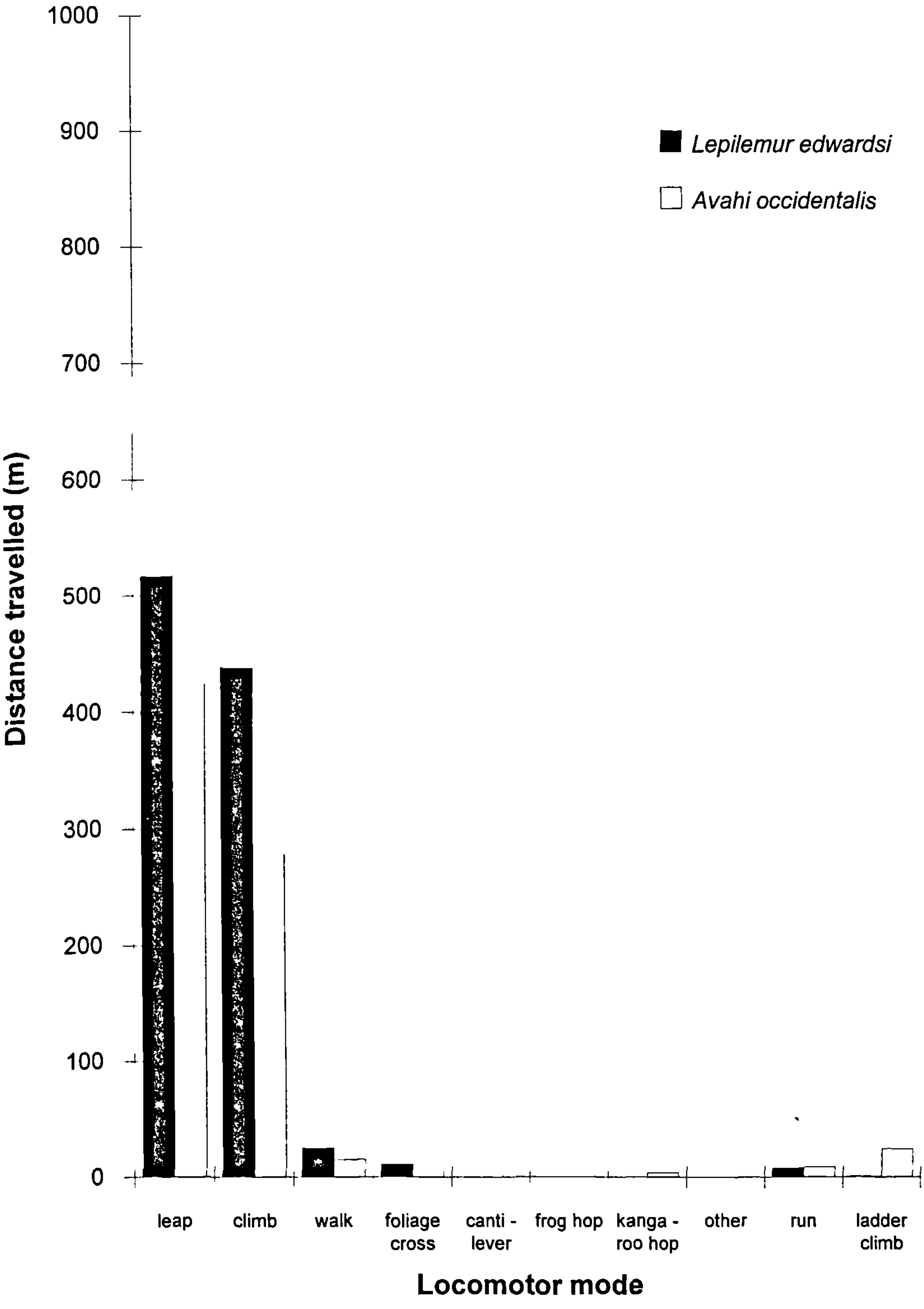


Fig. 6.4c Metres per kilometre of height lost using each locomotor mode by each species



6.5 Discussion

Avahi occidentalis uses more energy per night, and travels further, than *Lepilemur edwardsi*, despite being of lower body mass (mean of 708 g compared to 819 g). Correspondingly, its relative cost of locomotion is very much higher than for *L.edwardsi* at Ampijoroa. The apparent expenditure of energy for locomotion appears particularly low for *L.edwardsi* when compared to the field metabolic rate (FMR). Locomotion only accounts for 0.9 % of the FMR for *L.edwardsi* and 3 % for *A.occidentalis.* Comparing the value for *L.edwardsi* to the results of 4 % for ground squirrels (Karasov 1981), 3.6 % for pocket gophers (Gettinger 1984), 15 % for golden mantled ground squirrels (Kenagy & Hoyt 1990) and 2 % for mantled howler monkeys (Nagy & Milton 1979), it can be seen that the value of energy costs for locomotion in *L.edwardsi*, is very low even compared to that for other arboreal primates. On the other hand, *A.occidentalis* has a value which is not particularly different from the other mammals; although its locomotor costs are not a major component of the energy expended.

However, when comparing the energy cost of locomotion with a reasonable estimate of the resting metabolic rate, we have seen that for *L.edwardsi* the cost of locomotion is 0.03 of the resting metabolism, whereas for *A.occidentalis* the cost of locomotion is 0.01 of the resting metabolic rate. The main reason for this big difference in the energy cost of locomotion between these two species seems to be the large difference in the distances travelled nightly by an individual rather than the locomotor mode used. Indeed when the relative cost of locomotion is recalculated so that *L.edwardsi*'s nightly travel distance is set the same as that for *A.occidentalis*, the value (31) is still higher than that obtained for *A.occidentalis*. So it does appear that distances travelled are very important for the energy cost of locomotion.

Hladik and Charles-Dominique (1974), who studied *Lepilemur mustelinus* in the south of Madagascar, suggested caecotrophy as a means whereby these animals might obtain sufficient energy from their diet to maintain their activity levels. They suggested 30 kcal/24hr (about 126 kJ/24hr) as the value that could be obtained from food using caecotrophy, (basal metabolism requiring in the order of 20-30 kcal [about 84 -126 kJ/24hr] and the minimum cost of locomotion being 2.16 kcal [about 9.1 kJ/24hr]). Basal metabolic rate has not been considered in this study as it is very difficult to ensure that the animal's metabolic rate is at this level. Resting metabolic rate has been used instead. The cost of locomotion calculated by Hladik and Charles-Dominique (1974) is higher than that calculated for *Lepilemur* in this study. However, it seems unlikely that if *L.mustelinus* was so energy constrained that it found it advantageous to resort to caecotrophy, that *A.occidentalis*, which is of similar mass (708 g compared to 600 g for *L.mustelinus*), would be able to survive without caecotrophy, given its higher cost of locomotion and a similar folivorous diet (even if this diet is of a slightly higher quality). Certainly, *L.edwardsi* at Ampijoroa was never seen to eat its own faeces.

Another method of decreasing energy costs for these mammals is to depress the metabolic rate even further than is expected for other folivorous mammals. Indeed the value obtained by Schmid and Ganzhorn (in press) for *Lepilemur ruficaudatus* is the lowest metabolic rate of any folivorous mammal obtained so far. There is a marked difference in resting metabolic rate between the resting phase of the activity cycle (32.4 % of Kleiber's relationship [1961], see section 6.4) and the active phase of the activity cycle (92.9 % of Kleiber's relationship). This suggests active regulation of basal metabolic rates.

Energy could also be saved through locomotion using optimum take-off angles (Sellers 1992) and by storing energy in elastic tendons (Alexander 1991a,b). Tendons and ligaments in the feet of wallabies have been estimated to store and return 33% of the kinetic and potential energy lost and regained in slow hopping (Ker *et al.* 1986). Indeed both *Avahi occidentalis* and *Lepilemur edwardsi* were seen to use ricochetal leaping, in which bouts of leaping are not punctuated by pauses, so that the kinetic energy from the last jump can be used again on take-off. However, there was no evidence of the animals using the branches like springboards, giving an animal extra momentum when it leaps. While, as proposed by Günther *et al.* (1991), an animal could do this by making a small hop on the substrate to store energy to aid take-off, Alexander (1991) considers that the branch compliance is more likely to cause a loss of energy, due to the branch bending under the weight of the animal. Demes *et al.* (in press) found that larger vertical clingers and leapers such as *Propithecus* with a body mass of 2 - 5 kg, do not use the elastic energy stored in substrates, and further found that energy is wasted in deformation of compliant supports. Work by Crompton *et al.* (1993) on five prosimian leapers suggested that the theoretical optimum angle of 45^0 is in fact rarely used, and the use of lower angles are preferred, and these permit greater speed and render the trajectory more unpredictable in order to confuse predators.

This study has used an accurate measure of nightly distances travelled, horizontal distance and height lost and gained during the most frequent five out of the ten locomotor modes observed, in order to calculate a reasonable estimate of the energy cost of locomotion. The cost of locomotion, when considered as a percentage of the FMR, is low for both of the study species but particularly low in *L.edwardsi.* The difference in nightly travel distances, rather than the preferred locomotor modes, is suggested as the factor which accounts for a large proportion of the difference in energy costs. If available energy is a limiting factor, an adjustment of preferences for different locomotor modes would make only a very small difference. If both species are indeed under similar energy constraints as a consequence of habitat and diet, it would appear that *A.occidentalis* would have a smaller energy safety margin than *L.edwardsi*, unless the higher quality food consumed by *A.occidentalis* is sufficient to explain the difference in their activity levels. Further investigation into energy intake of these two animals needs to be done. Locomotor energy costs, however, do not seem to be limiting factors, despite the relatively high costs of vertical clinging and leaping compared to other modes of locomotion.

7 Summary and General Discussion

Lepilemur edwardsi and *Avahi occidentalis* have both been classed as vertical clingers and leapers (VCL) and have similar morphological adaptations for leaping; namely, an extended femur rather than the long foot which is the main morphological adaptation for leaping seen in tarsiers and galagos (Oxnard *et al.* 1990). Both study species move in the same forest, with the same supports available to them, and therefore, (perhaps unsurprisingly), the gross locomotor repertoires for each species were found to be similar.

However, *Lepilemur edwardsi* used a lower stratum of the forest than did *Avahi occidentalis*; and, as a consequence of the characteristics of available supports, the first and second support diameters were larger for *L.edwardsi* than for *A.occidentalis*. *L.edwardsi* used vertical and angled supports more frequently than did *A.occidentalis*, and branches of 0.5-5 cm in diameter were used more often than other categories. In the dry deciduous forest of Ampijoroa, *L.edwardsi* tended to travel between tree trunks rather than saplings, and accordingly used larger supports than does *A.occidentalis*, and *L.edwardsi* exploited angled as well as vertical branches. *A.occidentalis*, in contrast, lived predominantly in the tree crowns. Although the heights used by each species were not mutually exclusive, the species were effectively split spatially by the use of different stratum.

We have seen *A.occidentalis* had a higher frequency of leaping (66.2%) than *L.edwardsi* (55.1%) and covered 800 m of a typical kilometre by leaping, whereas *L.edwardsi* covered 667 m of a kilometre by leaping. Both these points suggest that *A.occidentalis* is a more committed leaper than *L.edwardsi*, which however had a greater emphasis on climbing (30.3%) than did *A.occidentalis* (17.2%). The mean leap length for *L.edwardsi* was 1.36 m, and for *A.occidentalis* was 1.51 m, which in both cases is much less than the mean inter-tree distance observed at Ampijoroa (2.55 m). It seems likely, therefore, that both species are conserving energy by restricting their leap length and using 'low cost' routes throughout the forest. Short leaps also have the advantage of being fast and a change in direction can be quickly implemented by taking off from the target support in a different direction, thereby confusing predators (Crompton *et al.* 1993).

Arboreal pathways did indeed seem to be used by *L.edwardsi* in particular, but close contact with the animals whilst travelling within the forest was infrequent, because of poor visibility at night. It seems highly likely that this species, with a small home range of 1.09 ± 0.6 ha, would be familiar with its home range and have a number of regularly used routes to go to preferred feeding or sleeping sites. Arboreal pathways were less apparent for *A.occidentalis*, although they would presumably offer it the same advantages as *L.edwardsi*. Reduced emphasis on regular pathways could, however, also be a reflection of the bigger home range (1.6 ± 1.2 ha), and greater distances travelled during the night by *A.occidentalis*.

One of the most interesting aspects of locomotor behaviour observed was the degree of suspensory postures and arm swinging seen in both species, but particularly in *A.occidentalis*. Tensile forces and forelimb tension created in this posture may be critical in terms of maximum imposed loading of anatomical structures and influence the animals' adaptedness to the environment. These forces may not be large when the animal is just hanging, but could be considerable if the animal leaps and lands by catching a branch in its hand, as was observed for *A.occidentalis* on a few occasions. Pollock (1975,1977) also reports a degree of suspensory postures seen for *Indri*, and Richard (1974,1977) reports that suspensory postures are common for sifakas. Certainly *Propithecus verreauxi coquereli* at Ampijoroa would frequently utilize suspensory postures and catch branches whilst leaping (pers obs). *Indri*, together with other large primates, are known to use their arms whilst leaping as they can contribute more effectively to the acceleration of the body with increasing size, as well as help initiate the rotation of the trunk while airborne to bring the hind limbs into the landing position (Demes & Günther 1989). Using tracings from the video of one leap from each species, (Fig.2.4k *A.occidentalis* leaping), we can see that *A.occidentalis* does use its arms when leaping. In comparison Fig. 2.4g, showing *L.edwardsi* leaping, indicates that the arms are held much lower, and almost passively, in front of the animal as it leaps.

The locomotor morphology of primates is characterized by the retention of a relatively primitive skeletal framework (Martin 1990). It is not clear if the suspensory behaviour seen in *A.occidentalis* is a preadaptation to arm use in leaping, in arm suspension or in both. Both *Megaladapis*, a sub-fossil member of the Lepilemuridae, and *Palaeopropithecus*, a sub-fossil indriid, have skeletal features suggesting suspensory habits (Tattersall 1982, Martin 1990). However, *Megaladapis* has robust limbs, suggesting a propensity to vertical clinging and climbing, rather like a koala, compared to the slim limbs of *Palaeopropithecus* which may have been the most suspensory of all strepsirhines, suggesting behavioural continuity between extant and extinct Indriidae (Jungers 1977, Jungers 1980). Fore limb suspension may thus represent the retention of a characteristic that is infrequently used but which permits *Avahi* access to the energetically important small branch niche. Cartmill (1972) observed that it is unlikely that the ancestors of extant primates were committed vertical clingers and leapers, rather, it is thought that the ancestors were more like a modern mouse lemur (Martin 1972). The retention of ancestral modes of locomotion evident in this study suggests, however, that ancestral primates possessed features that permitted, and possibly predisposed towards, the development of vertical clinging and leaping.

This study addressed the question of support preference of vertical clingers and leapers with reference to support availability. Ampijoroa was found to be a forest of predominantly vertical and angled supports of relatively small size. For efficient exploitation of such a forest, an arboreal animal should probably have a low body mass, in order to prevent extreme branch deformation. With a predominance of supports perpendicular to the forest floor, a quadruped might 'perceive' the forest as more discontinuous than might an animal which could utilize these vertical supports for leaping locomotion. It appears, therefore, that both *Lepilemur edwardsi* and *Avahi occidentalis* are well-adapted. It is not possible to judge, however, if the vertical clinging and leaping seen in these species is a result of adaptation to the present environment, or a preadaptation evolved under a different selection regime. This could perhaps be tested by surveying the structure of various forests with and without vertical clingers and leapers. A possible question to ask is: do VCLs only inhabit forests which have predominantly vertical supports, or can they exploit a large variety of forest types?

The Jacob's D preferences values obtained were an important measure of the ratio of support availability to support use. Neither of the two study species used the supports to the extent of their availability. Overall, both species surprisingly avoided vertical and angled supports in the forest, and rather choose to use sloping or horizontal supports. Despite the high frequency of branches of 0.5-5 cm in diameter, the two species both displayed a frequency of use of branches of this diameter greater than the frequency of occurrence. *A.occidentalis* strongly avoided branches over 10 cm in diameter, whereas *L.edwardsi* used these supports and only avoided branches over 15 cm in diameter. These bigger branches were most often vertical in orientation, matching *L.edwardsi*'s slight orientation preference for take-off and landing. *L.edwardsi* also prefered to travel lower in the forest than did *A.occidentalis*, corroborating other aspects of locomotor behaviour demonstrating spatial differentiation between the two species. Again, surprisingly, both species showed strong preferences for oblique and horizontal take-off supports rather than the vertical supports suggested by the locomotor category to which they are usually assigned. This may be a reflection of their hind limb morphology, since the extended femur system is less efficient for VCL than is an elongated foot (Alexander, *pers.comm.*). Preferences for oblique and horizontal branches may reflect better quality food found towards the edge of the canopy where leaves tend to grow. The high diversity of locomotor performances shown by both of these species might also reflect ancestry in a quadrupedal generalist that had a preference for oblique or horizontal supports. *Lepilemur edwardsi* and *Avahi occidentalis* may be morphologically adapted for leaping, but they still show a level of preference for oblique and horizontal supports that one might expect to see from a generalist such as *Eulemur fulvus.* To summarise, when compared to *A.occidentalis*, *L.edwardsi* prefered branches lower in the forest (predominantly vertical trunks); only avoided branches with diameters above 15 cm; showed a slight preference for leaping from and to vertical supports; showed a higher percentage of clinging when stationary; and used more supports vertical or angled in orientation.

The locomotion data suggest that *A.occidentalis* is a more committed 'leaper' with *L.edwardsi* being a more committed 'clinger'. Further consideration of *Megaladapis* supports this view. *Megaladapis* has been described as a '*vertical clinger and climber* ' (Jungers 1977). Indeed, *L.edwardsi* showed a higher percentage of climbing than did *A.occidentalis*, again indicating behavioural continuity between extinct and extant species. *Megaladapis* had a body mass of around 150 kg, and it may be that the cost of leaping would have been too high a proportion of its available energy. This would have been even more of a problem for an animal that may have had a relatively low metabolic rate per unit mass. The robusticity of the bones of this animal was probably a compromise between the expense of the bony materials and the risk of breaking.

This study has shown that the frequency of use of categories of supports was not the same as the availability of the various categories within the forest environment of Ampijoroa. Both species have shown a preference for small sloping and horizontal branches, but at different heights in the forest, and with varying degrees of preference and avoidance for the other available supports. These variations in details of support preferences certainly aid the maintenance of species segregation, and may also be related to the location of food within the environment. The high preference for horizontal branches by both species may be both biologically important and highly critical for the animals' adaptability to the environment. The preference by both species for more sloping supports, despite morphological adaptation for vertically-orientated supports, underlines the importance of studying not only the form-function relationships of the species but also the biological role that these play in their natural environment.

Lepilemur edwardsi has been shown to have a small home range of 1.09 ha, with a very high degree of overlap between individual home ranges. The social system seems to be of the noyau type, and the lemurs gave use of very vocal territorial displays, together with branch shaking by both sexes. *Avahi occidentalis* had a mean home range size of 1.6 ha, larger than that of *L.edwardsi*, despite lower body mass, suggesting that Harestad and Bunnell's (1979) theory of a straight-forward relationship of home range to body size is far too simple. Influences on home range size are likely to be multifactorial (social system, metabolism, food choice, food dispersal, amongst others). *A.occidentalis* was confirmed to be monogamous and throughout the 18 months of the study, pairings remained stable.

The height difference seen in data for overall locomotor modes is even more pronounced when these two species are feeding: *L.edwardsi* preferred to feed at 3-5 m whereas *A.occidentalis* preferred to feed at 4-6 m. Four species of plant were seen to be eaten by both species, indicating that food choices were not exclusive. However, sufficient numbers of tree species are certainly consumed by only one of the two study lemurs to permit the species to be sympatric, and moreover, *L.edwardsi* was found to be less discriminating than *A.occidentalis*, in its choice of leaves.

It appears that neither species shows any clear pattern of activity. Work by Penry and Jumars (1987) has suggested that the optimal way of feeding in terms of digestion is a slow graze maintained throughout the active period. But

Lepilemur edwardsi and *Avahi occidentalis* did not feed continuously throughout the night. These animals then, may have adopted an intermediate strategy between the typical biphasic pattern (*e.g. Eulemur fulvus fulvus* and *Lemur catta*, Sussman 1977), and Penry and Jumar's constant grazing. Such a strategy may have been made possible by the low cost of food collection, and necessitated by the absolutely small size of their gut.

Both *Lepilemur edwardsi* and *Avahi occidentalis* have locomotion costs which are extremely small. Field metabolic rates and resting metabolic rates measured for the two species are grossly similar, but it appears to be the differences in distance travelled by the two species which accounts for the big difference in the relative energy cost of locomotion. *A.occidentalis* clearly gains sufficient available energy from its diet to sustain a higher cost of locomotion. Sharing approximately the same diet, but with much lower total locomotor energy cost, it would appear likely that available energy is not a limiting factor for *L.edwardsi*. When calculating the energy cost of locomotion, energy optimal take-off angles were used. However, it seems more likely that the animals use a wide range of angles when leaping, and are not restricted to energy-optimal angles. Indeed, Crompton *et al.* (1993) found that, for five prosimians, the leap trajectory did not usually take the most energy-efficient path, so that the additional costs of leaping at non-optimal angles are not prohibitive. The energy cost of postures was not considered in this study, and calculations were based on simplified locomotor categories. But, the underlying message remains true, that distance travelled is critical when considering relative costs of locomotion.

A study of nocturnal prosimians inevitably encounters problems of visibility. Both species in this study were very tolerant of observers, but it was apparent that the longer sequences of locomotion were being missed due to the lack of light, and the impossibility of keeping up with the animals whilst radio-tracking. A study of only four individuals of each species is only a small sample of the population, and it would have been profitable to study animals in different areas of the forest. Further work, on social behaviour, in particular of *L.edwardsi* is necessary. Also, considering sample sizes of feeding data, it is probable that these data were still low on the 'discovery curve' and that many more species of tree are eaten by each species than are reported in this study. Calculations of energy cost gave an indication of the range of energy expenditure, but a more detailed analysis(using a method such as doubly-labelled water) would vastly improve understanding of the bioenergetics of these two species.

Lepilemur edwardsi and *Avahi occidentalis* are nocturnal sympatric lemurs with a similar body mass. Superficially, they appear very similar. However, detailed examination of their locomotor ecology has shown differences in the emphasis in locomotor repertoire, in the heights used, in support preferences, in home range sizes and nightly distances travelled, and food choices, and also vastly different values for the relative energy cost of locomotion.

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Appendix 1: Statistical results of locomotor data, Chapter Two.

Table App1a: GLM analysis comparing the horizontal distance moved with each locomotor mode by species (N=3516)

Source	Degrees of Freedom (DF)	Sum of Squares (SS)	F value	P>F
Model	19	642.37	48.91	0.00
Error	3496	2416.45		
Source	DF	Type III SS	F value	P>F
Species	1	0.03	0.04	0.83
Locomotor mode	9	559.69	89.97	0.00
Species * Locomotor mode	9	19.9	3.2	0.00

Table App1b: GLM analysis comparing the height gained per bout with each locomotor mode by species (N=955)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	19	17.63	3.22	0.00
Error	935	269.36		
Source	DF	Type III SS	F value	P>F
Species	1	0.11	0.37	0.54
Locomotor mode	9	14.4	5.57	0.00
Species * Locomotor mode	9	2.40	0.93	0.5

Table App1c: GLM analysis comparing equal heights and height lost per bout with each locomotor mode by species (N=2585)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	19	106.47	11.66	0.00
Error	2565	1233.20		
Source	DF	Type III SS	F value	P>F
Species	1	0.03	0.05	0.82
Locomotor mode	9	96.80	22.37	0.00
Species * Locomotor mode	9	2.06	0.48	0.89

Table App1d: Oneway anova of locomotor mode and horizontal distance per bout for *Lepilemur edwardsi* (N=1762)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	9	224.47	34.65	0.00
Error	1752	1261.14		
Source	DF	Type III SS	F value	P>F
Locomotor mode	9	224.48	34.65	0.00

Table App1e: Siginificant pairwise mean comparison (Scheffé's) of horizontal distance moved for locomotor modes of *Lepilemur edwardsi* (N=1762)

Significant comparisons of locomotor mode (0.05)		Lower confidence limit (95%)	Difference between means	Upper confidence limit (95%)
leap	walk	0.32	0.63	0.94
leap	climb	0.47	0.66	0.84
leap	frog hop	0.07	0.66	1.24
leap	other	-0.77	0.99	2.74

Table App1f: Oneway anova of locomotor mode and horizontal distance per bout for *Avahi occidentalis* (N=3405)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	9	407.21	68.3	0.00
Error	1744	1155.32	0.66	
Source	DF	Type III SS	F value	P>F
Locomotor mode	9	407.21	68.30	0.00

Table App1g: Siginificant pairwise mean comparison (Scheffé's) of horizontal distance moved for locomotor modes of *Avahi occidentalis* (N=1754)

Significant comparisons of locomotor mode (0.05)		Lower confidence limit (95%)	Difference between means	Upper confidence limit (95%)
leap	run	0.06	0.61	1.15
leap	walk	0.43	0.74	1.05
leap	frog hop	0.23	0.80	1.38
leap	other	0.05	0.98	1.91
leap	cantilever	0.20	1.00	1.80
leap	climb	0.80	1.00	1.21
leap	foliage cross	0.58	1.12	1.67
leap	ladder climb	0.92	1.40	1.89
run	ladder climb	0.08	0.80	1.51
walk	ladder climb	0.11	0.66	1.22

Table App1h: Oneway anova for locomotor mode compared with height gained per bout for *Lepilemur edwardsi* (N=2189)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	9	6.06	2.57	0.01
Error	540	141.73	0.26	
Source	DF	Type III SS	F value	P>F
Locomotor mode	9	6.06	2.57	0.01

There were no significant pairwise comparisons of the mean height gained with locomotor mode for *L.edwardsi* with Scheffé's test.

Table App1i: Oneway anova for locomotor mode compared with equal height and height lost per bout for *Lepilemur edwardsi* (N=1229)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	9	47.95	10.6	0.00
Error	1219	660.63		
Source	DF	Type III SS	F value	P>F
Locomotor mode	9	47.95	10.60	0.00

There were no significant pairwise comparisons of the mean height maintained or lost with locomotor mode with Scheffé's test.

Table App1j: Oneway anova for locomotor mode compared with height gained per bout for *Avahi occidentalis* (N=405)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	9	11.55	3.97	0.00
Error	395	127.63		
Source	DF	Type III SS	F value	P>F
Locomotor mode	9	11.55	3.97	0.00

Table App1k: Siginificant pairwise mean comparison (Scheffé's) of height gained for locomotor modes of *Avahi occidentalis* (N=1754)

Significant comparisons of locomotor mode (0.05)		Lower confidence limit (95%)	Difference between means	Upper confidence limit (95%)
walk	climb	0.09	0.52	0.96

Table App1l: Oneway anova for locomotor mode compared with equal height and height lost per bout for *Avahi occidentalis* (N=1356)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	9	57.58	13.88	0.00
Error	1346	620.51		
Source	DF	Type III SS	F value	P>F
Locomotor mode	9	57.58	13.88	0.00

Table App1m: Siginificant pairwise mean comparison (Scheffé's) of height lost for locomotor modes of *Avahi occidentalis* (N=1356)

Significant comparisons of locomotor mode (0.05)		Lower confidence limit (95%)	Difference between means	Upper confidence limit (95%)
climb	leap	-0.48	0.12	-0.72
climb	walk	0.38	0.72	1.06
climb	foliage cross	0.24	0.74	1.60
climb	cantilever	0.06	0.84	1.75
leap	walk	0.05	0.35	0.66

Table App1n: Oneway anova of species with equal height and height lost per leap with horizontal distance as covariate (N=1572)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	2	65.18	75.3	0.00
Error	1569	679.03		
Source	DF	Type III SS	F value	P>F
Species	1	0.45	1.03	0.31
Horizontal distance	1	63.16	145.93	0.00

Table App1o: Descriptive statistics for an analysis of covariance comparing species with equal height and height lost while leaping with horizontal distance as the covariant (N=1572)

Species	N	Height lost LSMean	Standard Error LSMean	P > |T| Ho : LSMeans=0
Lepilemur edwardsi	679	0.427	0.03	0.00
Avahi occidentalis	893	0.46	0.02	0.00

Table App1p: Oneway anova of species and height gained per leap with horizontal distance as covariate (N=334)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	2	8.15	42.70	0.00
Error	331	59.45		
Source	DF	Type III SS	F value	P>F
Species	1	0.03	0.16	0.69
Horizontal distance	1	8.13	45.29	0.00

Table App1q: Descriptive statistics for an analysis of covariance comparing species and height gained while leaping with horizontal distance as the covariant (N=334)

Species	N	Height gained LSMean	Standard Error LSMean	P > |T| Ho : LSMeans=0
Lepilemur edwardsi	192	0.657	0.03	0.00
Avahi occidentalis	142	0.639	0.04	0.00

Table App1r: Oneway anova of species and height gained per climbing bout with horizontal distance as covariate (N=383)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	2	48.74	92.06	0.00
Error	380	100.59		
Source	DF	Type III SS	F value	P>F
Species	1	1.51	5.72	0.02
Horizontal distance	1	48.28	182.40	0.00

Table App1s: Descriptive statistics for an analysis of covariance comparing species and height gained while climbing with horizontal distance as the covariant (N=383)

Species	N	Height gained LSMean	Standard Error LSMean	P > |T| Ho : LSMeans=0
Lepilemur edwardsi	249	0.674	0.03	0.00
Avahi occidentalis	134	0.806	0.04	0.00

Table App1t: Oneway anova of species with equal height and height lost per climbing bout with horizontal distance as covariate (N=567)

Source	DF	Sums of Squares (SS)	F value	P>F
Model	2	89.72	74.64	0.00
Error	564	338.98		
Source	DF	Type III SS	F value	P>F
Species	1	7.94	13.21	0.00
Horizontal distance	1	87.48	145.56	0.00

Table App1u: Descriptive statistics for an analysis of covariance comparing species with equal height and height lost while climbing with horizontal distance as the covariant (N=567)

Species	N	Height lost LSMean	Standard Error LSMean	P > |T| Ho : LSMeans=0
Lepilemur edwardsi	3441	0.681	0.04	0.00
Avahi occidentalis	226	0.925	0.05	0.00

Table App1v: Descriptive comparative statistics of equal height and height lost for *Lepilemur edwardsi* (1) and *Avahi occidentalis* (2)

Species	Locomotor mode	N	Mean	Standard error of mean	Significant difference between means (** 0.05, *** 0.01)
1	4	743	0.446	0.03	***
2		946	0.536	0.02	
1	5	449	0.626	0.04	***
2		288	0.809	0.06	
1	6	133	0.120	0.03	
2		124	0.097	0.04	
1	7	80	0.088	0.04	
2		37	0.081	0.05	
1	8	1	0.000		
2		17	0.000		
1	9	0			
2		0			
1	10	3	0.000	0.00	
2		9	0.333	0.17	
1	11	3	0.000	0.00	
2		14	0.143	0.10	
1	12	10	0.500	0.22	
2		35	0.200	0.08	
1	13	1	1.000		
2		33	0.606	0.10	

Table App1w: Descriptive comparative statistics for height gained for *Lepilemur edwardsi* (1) and *Avahi occidentalis* (2)

Species	Locomotor mode	N	Mean	Standard error of mean	Significant difference between means (** 0.05, *** 0.01)
1	4	131	1.140	0.03	
2		93	1.110	0.03	
1	5	167	1.252	0.04	
2		95	1.284	0.08	
1	6	12	1.167	0.11	
2		6	1.00	0.00	
1	7	2	1.000	0.00	
2		1	1.000		
1	8	2	1.000	0.00	
2		0			
1	9	0			
2		0			
1	10	2	1.000	0.00	
2		6	1.500	0.22	
1	11	0			
2		1	1.000		
1	12	4	1.000	0.00	
2		4	1.500	0.50	
1	13	1	1.000		
2		17	1.059	0.06	

Appendix 2: The morphometric data on each individual lemur caught throughout the study

Table App 2a: *Lepilemur edwardsi*

SPECIES (LL)	INDIVIDUAL	DATE CAUGHT	SEX	MASS (g)	TOTAL LENGTH (mm)	TRUNK (mm)	TAIL (mm)	EAR (mm) left	EAR (mm) right	TARSUS (mm) left	TARSUS (mm) right
L.edwardsi	1	31.5.92	f	1156	520		290			70	
L.edwardsi	5	1.6.92	m	908	565		290			80	
L.edwardsi	3	18.6.92	m	558	480		260			70	
L.edwardsi	4	21.6.92	f	837	585		295			80	
L.edwardsi	4	30.9.92	f	830	560	166	280	27	26	50	50
L.edwardsi	1	10.11.92	f	1124	610	180	315	30	32	60	62
L.edwardsi	3	11.11.92	m	680	515	160	275	29	31	43	45
L.edwardsi	5	26.3.93	m	508	500	152	222	31	29	39	37
L.edwardsi	2	31.3.93	f	838	625	209	310	32	31	65	64
L.edwardsi	6	20.8.93	f	1108	582	212	270	33	32	75	77
L.edwardsi	7	20.8.93	m	552	490	152	235	28	29	67	65
L.edwardsi	3	8.9.93	m	728	590	179	280	31	31	44	45
SUM				9827.00	6622.00	1410.00	3322.00	241.00	241.00	743.00	445.00
MEAN				818.92	551.83	176.25	276.83	30.13	30.13	61.92	55.63
VAR				51143.17	2407.61	559.64	758.52	4.13	4.13	212.81	179.98
SD				226.15	49.07	23.66	27.54	2.03	2.03	14.59	13.42

SPECIES (LL)	INDIVIDUAL	TIBIA (mm) left	TIBIA (mm) right	FEMUR (mm) left	FEMUR (mm) right	HAND (mm) left	HAND (mm) right	FORE ARM (mm) left	FORE ARM (mm) right	HUMERUS (mm) left	HUMERUS (mm) right
L.edwardsi	1	55		70		49		46		55	
L.edwardsi	5	100		105		50		60		50	
L.edwardsi	3	90		95		50		60		50	
L.edwardsi	4	110		100		60		70		50	
L.edwardsi	4	69	70	105	103	22	17	66	63	52	52
L.edwardsi	1	76	77	100	98	24	22	72	73	64	62
L.edwardsi	3	69	70	87	87	22	23	65	67	58	57
L.edwardsi	5	65	70	77	82	19	21	57	54	49	51
L.edwardsi	2	72	78	105	105	29	34	69	69	65	67
L.edwardsi	6	82	89	102	106	37	34	70	71	59	64
L.edwardsi	7	78	78	84	82	16	16	57	56	53	52
L.edwardsi	3	97	96	96	94	22	23	65	67	58	57
SUM		963.00	628.00	1126.00	757.00	400.00	190.00	757.00	520.00	663.00	462.00
MEAN		80.25	78.50	93.83	94.63	33.33	23.75	63.08	65.00	55.25	57.75
VAR		260.75	90.86	137.97	99.41	229.33	46.79	55.54	47.14	30.75	36.50
SD		16.15	9.53	11.75	9.97	15.14	6.84	7.45	6.87	5.55	6.04

SPECIES (LL)	INDIVIDUAL	NOTES
L.edwardsi	1	Natural nick in the ear, mark on forehead, 0.5 cm above the eyes. No parasites.White tipped tail. Trapped by noosing.
L.edwardsi	5	No white tip to tail, no parasites. Darted.
L.edwardsi	3	No parasites, tiny white tip to tail, caught by noosing, in tree hole with another LL.
L.edwardsi	4	Small white tip to tail, caught in the same hole as LL3 though not present. Grooved clit.
L.edwardsi	4	Recaught
L.edwardsi	1	Recaught LL1 decided female . Teeth very worn.
L.edwardsi	3	Recaught LL3
L.edwardsi	5	Found dead probably of exposure in the rain. The body was still warm and kept the body. Another animal in the same hole.
L.edwardsi	2	Caught in the same hole as LL3 and LL4 with noose. White tip to tail.
L.edwardsi	6	Pregnant (3cm foetus). Ragged ears, possibly previously marked but not by me (Albignac ?). No white tip to tail.In tree with another animal.
L.edwardsi	7	Caught E of N170W250. Another lepi in tree next door. No white tip to tail. Got worms-nematodes in faeces. Various bald patches on inside of arms and legs. Possible juvenile.
L.edwardsi	3	Recaught LL3, no longer juvenile, genitalia mature and heavier than previously. Still no white tip to tail.

Table App2b: *Avahi occidentalis*

SPECIES (AV)	INDIVIDUAL	DATE CAUGHT	SEX	MASS (g)	TOTAL LENGTH (mm)	TRUNK (mm)	TAIL (mm)	EAR (mm) left	EAR (mm) right	TARSUS (mm) left	TARSUS (mm) right
A.occidentalis	6	19.6.92	f	758	630		370			75	
A.occidentalis	5	21.6.92	m	807	570		300			80	
A.occidentalis	1	27.9.92	m	808	585	180	355	26	27	53	51
A.occidentalis	2	29.9.92	f	468	560	140	320	24	26	46	42
A.occidentalis	3	29.9.92	m	708	570	160	345	21	22	42	44
A.occidentalis	0.5	4.10.92	m	#	220	43	102	11	10	18	20
A.occidentalis	4	12.10.92	f	698	575	170	310	24	19	46	47
SUM				4247.00	3710.00	693.00	2102.00	106.00	104.00	360.00	204.00
MEAN				707.83	530.00	138.60	300.29	21.20	20.80	51.43	40.80
VAR				16000.17	19208.33	3074.80	8275.57	35.70	46.70	439.95	146.70
SD				126.49	138.59	55.45	90.97	5.97	6.83	20.98	12.11

SPECIES (AV)	INDIVIDUAL	TIBIA (mm) left	TIBIA (mm) right	FEMUR (mm) left	FEMUR (mm) right	HAND (mm) left	HAND (mm) right	FORE ARM (mm) left	FORE ARM (mm) right	HUMERUS (mm) left	HUMERUS (mm) right
A.occidentalis	6	120		125		70		75		60	
A.occidentalis	5	115		125		65		80		50	
A.occidentalis	1	125	120	127	130	24	26	85	80	70	71
A.occidentalis	2	96	98	101	102	24	22	70	76	56	61
A.occidentalis	3	110	110	111	110	24	24	80	81	72	73
A.occidentalis	0.5	40	41	38	38	11	11	27	26	24	26
A.occidentalis	4	10	10	11.5	12	26	24	76	75	63	62
SUM		616.00	379.00	638.50	392.00	244.00	107.00	493.00	338.00	395.00	293.00
MEAN		88.00	75.80	91.21	78.40	34.86	21.40	70.43	67.60	56.43	58.60
VAR		2009.67	2289.20	2206.15	2564.80	524.11	35.80	388.95	547.30	262.62	360.30
SD		44.83	47.85	46.97	50.64	22.89	5.98	19.72	23.39	16.21	18.98

SPECIES (AV)	INDIVIDUAL	NOTES
A.occidentalis	6	1 of 3 animals in the south of quadrat. Darted, grooved clitoris protrusion.
A.occidentalis	5	Two scent glands under chin. Darted, part of three as AV6.
A.occidentalis	1	Same family as AV2, south of quadrat
A.occidentalis	2	Same family as AV1 south of the quadrat, think this is daughter of previous year.
A.occidentalis	3	Male pair of AV4 in north of quadrat
A.occidentalis	0.5	Dead baby about two weeks of age (observation of north family), no obvious cause of death.
A.occidentalis	4	Female that lost the baby and pair of AV3. Healthy.

Appendix 3: Home range size and nightly distance travelled

(LL:Lepilemur edwardsi, AV: Avahi occidentalis)

Animal	**Date**	**Area of range m2**	**Travel distance m**
LL1	3.6.92	2478.3	395.6
LL1	10.6.92	9912.5	590.7
LL1	15.6.92	6406.1	355.4
LL1	18.11.92	2883.7	472
LL1	20.11.92	3291.9	500.1
LL1		**17021.9**	
mean		**4994.5**	**462.76**
LL2	2.4.93	11003.3	754.9
LL2	15.4.93	6963.6	396.8
LL2	7.6.93	7404.1	393
LL2	9.6.93	5320.9	424.8
LL2		**11825.7**	
mean		**7673.0**	**492.4**
LL3	9.7.92	2965. 5	196
LL3	11.7.92	2869.3	329.3
LL3	26.7.92	1103	41.7
LL3	25.11.92	4811	509.4
LL3	4.12.92	2479.8	234
LL3	23.1.93	1639.9	192
LL3	9.9.93	5809.4	273.2
LL3	11.9.93	5015	532.2
LL3	13.9.93	3434.8	188.3
LL392		**4703.8**	
LL393		**6668.2**	
mean		**4120.6**	**296.4**
LL4	1.7.92	2902.2	216.7
LL4	3.7.92	944.6	182.1
LL4	7.7.92	4539.2	493.6
LL4	30.7.92	2634.3	73.6
LL4	2.8.92	1080.2	347.5
LL4	11.11.92	3608.7	255 2
LL4	3.1.93	3287.4	237.7
LL4		**8088.5**	
mean		**3030.0**	**281.5**
AV1	12.10.92	17345 9	2780.7
AV1	27.11.92	24722.8	604.5
AV1	1.12.92	23351.4	1859.7
AV1	23.6.93	23035.3	2444.5
AV1	28.6.93	25460.2	1605.2
AV1		**24207.8**	
mean		**22783.1**	**1858.9**
AV2	28.9.92	18795.7	1392.9
AV2	1.10.92	15773.0	1386.0
AV2	9.11.92	21923.5	1509.8
AV2		**22364.0**	
mean		**18848.2**	**1447.9**
AV3	5.10.92	2616.9	180.1
AV3	8.10.92	5070.9	577.8
AV3	5.4.93	8715.5	694.0
AV3	9.4.93	7336.1	1357.6
AV3	22.4.93	7053.5	880.0
AV3	21.6.93	8588.7	1254.5
AV3		**11466.7**	
mean		**6563.6**	**824.0**
AV4	16.10.92	6353.9	858.3
AV4	19.10.92	6659.8	653.3
AV4	16.11.92	3767.4	371.3
AV4	26.6.93	5307.2	737.8
AV4		**7637.8**	
mean		**5522.1**	**655.2**

Appendix 4: Frequencies of locomotor modes and support use

Locomotion Frequencies

Locomotor mode	*Lepilemur edwardsi (%)*	*Avahi occidentalis (%)*
leap	55.1	66.2
climb	30.3	17.6
walk	7.5	6.3
foliage cross	3.8	1.7
cantilever	0.1	0.8
frog hop	1.8	1.6
kangaroo hop	0.2	0.6
other	0.5	0.8
run	0.6	2
ladder climb	0.1	2.4

Orientation of first support

Support orientation	*Lepilemur edwardsi (%)*	*Avahi occidentalis (%)*
vertical	42.5	36.4
angled	29.7	24.8
oblique	9.9	18.8
horizontal	4.3	9
fork	10.7	8.6
foliage	2.9	2.4

Orientation of second support

Support orientation	*Lepilemur edwardsi (%)*	*Avahi occidentalis (%)*
vertical	48.1	45.1
angled	30.3	25.6
oblique	8.7	17.1
horizontal	4.1	7.6
fork	5.8	3.2
foliage	3	1.4

Metres per kilometre

Locomotor mode	*Lepilemur edwardsi (%)*	*Avahi occidentalis (%)*
leap	667	800
climb	244	103
walk	52.2	41
foliage cross	11	6
cantilever	1.2	4
frog hop	14	10.6
kangaroo hop	1.1	3.4
other	3	4
run	7.2	17
ladder climb	0.2	11