Chapter 1: Introduction

Tree-kangaroos are a specialised subgroup of marsupials belonging to the family Macropodidae, found only in the rainforests of Papua New Guinea and northern Australia (Flannery *et al* 1996, Newell 1998). They are unique in the kangaroo family in that they are arboreal and are believed to have returned to the trees in relatively recent evolutionary times (Groves 1982, Flannery *et al* 1996, Newell 1999a). Eight of the ten known species are found in the rainforests of New Guinea (Flannery 1995, Flannery *et al* 1996, Newell 1999a), while two are unique to Australia's Wet Tropics (Flannery *et al* 1996, Newell 1999a).

All ten species, especially those in Papua New Guinea, warrant serious conservation concern (Betz 2001), with many of them threatened with extinction. Yet, our understanding of the ecology and basic biology of any of the tree-kangaroo species is still rudimentary.

In fact, many Australians did not even know of the existence of tree-kangaroos when surveyed in 2003, with only 36% of Brisbane residents knowing of their existence and 84% not knowing how many species of tree-kangaroo occur in Australia (Tisdell and Wilson 2003). Despite this ignorance, tree-kangaroos are a diverse, unique and fascinating group of animals.

There is presently insufficient information on their ecology to assess the conservation status of the Australian species, *Dendrolagus lumholtzi*. This species is currently classified as rare (Queensland's *Nature Conservation (Wildlife) Regulation* 1994) and is primarily found in privately owned rainforest fragments on the Atherton and Evelyn Tablelands, which are not currently protected from clearing. Therefore, the long-term persistence of *D. lumholtzi* is threatened by land clearing, further habitat fragmentation and mortality from dogs and cars especially when travelling between fragments (Newell 1999b).

Only two other studies of ecology have been undertaken on this species and these were both performed on the same spatially restricted rainforest type and one that is spatially restricted due to clearing. Without further information on their populations and how they utilise their habitat, especially in fragments, their conservation status cannot be reviewed with accuracy.

Our current knowledge of their biology is deficient in areas such as their longevity, age-specific mortality and fecundity, and use of habitat, especially of differing types. It is crucial to the conservation of tree-kangaroos that we establish these fundamental facts before population viability analysis can be conducted with any accuracy.

Population viability analysis (PVA) is a tool that enables us to model and predict future trends for *D. lumholtzi* populations (Lacy 1993). However, PVA's can only be accurate at predicting extinction probabilities of a species if the data they are based on is extensive and reliable (Coulson *et al* 2001). PVA modelling can only be as good as the data and the assumptions input to the model (Lindenmayer *et al* 1993). The best data sets are from long-term ecological studies of at least 10 years, where large amounts of information are known about the biology of the species (Brook *et al* 2000). The World Conservation Union (IUCN) now uses PVA to establish a quantitative classification of endangered species (IUCN 1994), so it is essential that PVA supplies accurate, reliable quantitative predictions of extinction risk (Brook *et al* 1997).

The data required as input for a PVA model are: population densities in different fragments and continuous forest; expected lifespan, age-specific mortality and fecundity; age at maturity and reproductive rates; demographic stochasticity (random fluctuations in birth rate, death rate and sex ratio of a population); movement or dispersal between fragments or populations; genetic processes; and the effects of environmental stochasticity (Lacy 1993).

Without accurate data as input, the results from a PVA can be either over optimistic or under estimate the extinction probability of a population or sub-populations (Brook 2000). If data from small populations or from a few sub-populations are used, then this can also lead to incorrect results (Ludwig 1999). This is because these small populations may have characteristics that enable them to survive when other sub-populations cannot (Ludwig 1999). Therefore, it is essential that as much information as possible about how different sub-populations are operating, especially from differing habitat types and differing sized fragments, before a PVA is undertaken with confidence.

There are two main types of data that is not possible to collect during a PhD due to time limitations: 1) dispersal rates between fragments and 2) the effects of environmental stochasticity. The later is missing from almost all PVA's and the results are limited and possibly misleading without this data. Lastly we need more information about the spatial use by *D. lumholtzi* in other rainforest types as well as continuous forest, as this may vary and affect the population size or carrying capacity of individual fragments.

Although this study was designed to enhance our knowledge of the ecology and conservation status of *Dendrolagus lumholtzi* in order to aid in the future use of a population viability analysis and the requirement for specific information directs the focus of this study, it stops short of actually performing a PVA or constructing a life table for *D. lumholtzi* at this stage. Without data on the effects of environmental stochasticity on *D. lumholtzi,* a PVA could be misleading.

1.0 AIMS OF THE STUDY

The overall aim of this study was to determine the spatial and habitat use by *Dendrolagus lumholtzi* and allow generalisation from the limited scope of previous work, along with establishing an aging technique, to increase our information base to assess the conservation status and population viability of *D. lumholtzi* in the future. Furthermore, diet and the gastrointestinal capacities were examined to look at the relationship of ecology with habitat.

The aims of this study were to:

- Examine the spatial organisation of *D. lumholtzi* in a fragmented landscape (Chapter 4).
- Investigate structural or floristic determinants of spatial use by *D. lumholtzi* (Chapter 5).
- Determine diet in *D. lumholtzi* using microscopic scat analysis (Chapter 6).
- Examine gastrointestinal morphology of *D. lumholtzi* (Chapter 7).
- Develop a practical ageing technique for *D. lumholtzi* (Chapter 8).

Chapter 2: Tree-kangaroo biology and ecology. Literature review.

2.0 AUSTRALIAN TREE-KANGAROOS

The two species of tree-kangaroos found in Australia are the Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi* Collet 1884) and the Bennett's tree-kangaroo (*D. bennettianus* De Vis 1887). Both are considered rare (Queensland's *Nature Conservation (Wildlife) Regulation* 1994) and are the largest of the continent's arboreal mammals (Newell 1999c).

Both species are restricted to the tropical rainforests and adjacent forests of far north Queensland (Newell 1999a, Newell 1999b). Bennett's tree-kangaroos are found north of the Daintree River, while Lumholtz's tree-kangaroos are found south of Daintree to the Cardwell Range (Newell 1998). Several records of sightings of *D. lumholtzi* from the Black Mountain corridor indicate that this species has a continuous distribution across the Atherton and Mt Carbine Tablelands (Tree Kangaroo and Mammal Group 2000, Kanowski *et al* 2001a).

D. lumholtzi are predominantly found at higher altitudes (~ 600-1200m) (Newell 1999a, 1999c, Kanowski *et al* 2001b), while *D. bennettianus* are also found in the lowlands (Martin 1996). It is, however, possible that the two species do occur sympatrically in the Mt Carbine Tableland and Daintree areas (Newell 1999a). There have, in fact, been several claims that Bennett's tree-kangaroos have been seen on the Atherton Tablelands (Tree Kangaroo and Mammal Group 2000). It is believed however, that due to similarities between the two species and the variation in colours of *D. lumholtzi,* these are cases of mistaken identity (Tree Kangaroo and Mammal Group 2000).

Even though Bennett's tree-kangaroos are found within a relatively small area (~ 2000 km^2: Flannery *et al* 1996) of the Wet Tropics, the majority of this area is within a protected 'World Heritage Area' (WHA). Therefore, the conservation status of this species is considered moderately safe, despite its rarity (Newell 1999a). It is also believed that their current distribution may be expanding to lower altitudes due to a decrease in hunting by indigenous Australians in the last 40-50 years (Martin 1992).

The geographical range of Lumholtz's tree-kangaroo covers a larger area (~ 5500 km^2: Flannery *et al* 1996) than its congener, some of which is within protected areas. Kanowski *et al* (2001b) suggest that Flannery *et al's* (1996) estimation of the distribution of *D. lumholtzi* (~5500 km) is an overestimate, as it is based on the area of rainforest encompassing all records of the species, which includes isolated records which may in fact be dispersing individuals. More recent survey results (Tree Kangaroo and Mammal Group 2000, Kanowski *et al* 2001a) suggest that abundant populations of Lumholtz's tree-kangaroos are restricted to elevations above 700-800m on the Atherton Tablelands. Kanowski *et al* (2001b) propose that if the source populations of *D. lumholtzi* are restricted to high elevation rainforests, then the effective range of the species (i.e.: the area encompassing the source population: Caughley *et al* 1988) is likely to be much smaller than earlier estimates, perhaps in the order of 1000 km^2 including both the Atherton and Mt Carbine Tablelands.

However, they appear to maintain their highest densities in forest outside the protected areas, being more commonly found in fragmented forests within an agricultural matrix in a relatively small area on the Atherton and Evelyn Tablelands (Newell 1999a, Kanowski *et al* 2001a). Unfortunately the majority of these fragments are on privately owned land and are not presently protected from clearing (Newell 1998, 1999a, b, c).

Despite the level of clearing and long history of fragmentation on the Atherton and Evelyn Tablelands, *D. lumholtzi* can still be found in isolated patches of rainforest in the area (Newell 1999b). Where fragmentation of rainforest has occurred over large areas on the Tablelands, the remaining patches are very important (Winter 1991). They maintain biodiversity in the area and provide "stepping stones" for rainforest faunal movements between larger areas of forest (Pahl *et al* 1988, Laurance 1990a, Winter 1991) and source populations for nearby fragments (Angelstam and Arnold 1993).

There have been recorded sightings of Lumholtz's tree-kangaroos in the coastal areas of Cairns along the eastern side of the mountain range (Tree Kangaroo and Mammal Group 2000) but these sightings are rare compared to the uplands. Kanowski *et al* (2001a) suggest that the few records of *D.*

lumholtzi from the coastal lowlands may actually represent dispersing individuals. However, it is not clear why *D. lumholtzi*, along with other folivorous marsupials in the Wet Tropics, are rare or absent in the lowlands (Kanowski *et al* 2001b).

The predominantly upland distribution of Lumholtz's tree-kangaroo correlates with several other rainforest endemic arboreal mammals species, such as the Lemuroid Ringtail possum (*Hemibelideus lemuroides*), Green Ringtail possum (*Pseudochirops archeri*), Daintree River Ringtail possum (*Pseudochirops cinereus*) and Herbert River Ringtail possum (*Pseudochirops herbertensis*) (Winter 1997). This distribution has led researchers to speculate that Lumholtz's tree-kangaroos and possibly these other species are physiologically adapted to lower temperatures and therefore upland habitats (Laurance 1990b, Winter 1997). The limited data on the energetics and thermal ecology of tree-kangaroos neither supports nor refutes this proposal (McNab 1988). Other current hypotheses to explain this upland distribution include past hunting of *D. lumholtzi* by Aboriginals in the lowlands (Flannery *et al* 1996, Newell 1999a), habitat destruction in the lowlands (Johnson 1995) and the floristic composition of lowland forests (Laurance 1990b).

Despite their size and appeal, both *D. lumholtzi* and *D. bennettianus* have been relatively poorly studied compared to other mammalian species in Australia (Newell 1999b). This could be because of their rare status, and their cryptic and secretive behaviour within their tropical rainforest habitat (Newell 1999a, 1999b), which makes them very difficult to study.

There have been only three studies of the ecology of the Australian tree-kangaroos to date (Procter-Gray 1985, Martin 1992, Newell 1999a, 1999b, 1999c). Martin (1992) studied the ecology of the Bennett's tree-kangaroo in Shipton's Flat (~ 40km south of Cooktown) in Cape York; Procter-Gray (1984, 1985) investigated aspects of the behaviour and ecology of Lumholtz's tree-kangaroos at Yungaburra on the Atherton Tablelands; and Newell (1999a, b, c) researched the home range and habitat use, and effects of habitat loss on Lumholtz's tree-kangaroos at Yungaburra. However, all of these studies have been undertaken on Type 5b complex notophyll vine forest (Tracey 1982), which is a spatially restricted rainforest type with only <1000ha (2.5%) remaining (Sattler and Williams1999). Furthermore, the study sites for both studies on *D. lumholtzi* (Procter-Gray 1985, Newell 1999b) at Yungaburra where only a few hundred metres apart. The similar localities used so far for studies on *D. lumholtzi* may give a particular or idiosyncratic view of their ecology and habitat use across its range because this rainforest type is no longer representative of the rainforest fragments remaining in the region. Therefore, for a greater understanding of the spatial and habitat use by *D. lumholtzi,* it is crucial that other rainforest types are investigated.

2.1 GENERAL BIOLOGY OF TREE-KANGAROOS

D. lumholtzi is the smallest of the tree-kangaroos (Flannery *et al* 1996), with *D. bennettianus* the second smallest. It is believed that these two species are more primitive in their biology than the Papua New Guinean species, with the tree-kangaroos evolving in Australia and radiating north to Papua New Guinea. *D. lumholtzi* and *D. bennettianus* belong to the "long-footed" group of tree-kangaroos (Flannery *et al* 1996).

Members of this group are sexually size-dimorphic (Flannery *et al* 1996). However, *D. lumholtzi* is the least so (Flannery *et al* 1996). Male *D. lumholtzi* are larger than females (Johnson 1995), with adult males *D. lumholtzi* averaging a body weight of 8.63 kg (7.25 - 9.85 kg), while adult females are smaller and average 7.05 kg (6.60 -7.75 kg) (Newell 1999b). Bennett's tree-kangaroos are larger than Lumholtz's with males weighing 11.5 - 13.7 kg and females 8 - 10.6 kg (Martin and Johnson 1995).

Bennett's and Lumholtz's tree-kangaroos are Australia's biggest arboreal folivores, spending most of their time in the trees (Procter-Gray 1985, Martin 1992, Flannery *et al* 1996). However, they will readily come down to the ground to travel between individual trees or forest fragments, which makes them vulnerable to attack by dogs or dingoes and at risk of being hit by vehicles, especially *D. lumholtzi* (Newell 1999b). Lumholtz's tree-kangaroos have been recorded travelling long distances between forest fragments, particularly sub-adults dispersing into new territories (Newell 1999b, Kanowski *et al* 2001a).

The total number of Lumholtz's tree-kangaroos is unknown. However, there has been an estimate of ten to twenty thousand *D. lumholtzi* in continuous forest (Kanowski 1999) and additional thousands in rainforest fragments on private land on the basis of population densities reported for forest fragments in good habitat areas (Tree Kangaroo and Mammal Group 2000). This may be an over estimation of *D. lumholtzi* abundances as it is presently unclear what represents good habitat for *D. lumholtzi.* Furthermore, these abundances have been estimated using information from a spatially restricted rainforest type. It is also possible that not all habitats support such high densities and there may be vacant areas (Hanski 1994). There is presently insufficient data on the variation of spatial use by *D. lumholtzi* in different rainforest types to accurately estimate their abundances across their range.

2.1.1 Reproductive biology

Tree-kangaroos have the longest gestation period and longest period of maternal care of any marsupial (Dabek 1991, Flannery *et al* 1996). It has been suggested that the tree-kangaroo's long reproductive cycle seems to be more reflective of the group's low metabolic rate (McNab 1988) and may also be reflective of an arboreal lifestyle (Russell 1982, Procter-Gray 1985, Dabek 1991, Johnson and Delean 2003). A long reproductive period and other aspects of reproduction have also been related to the limited energy available from a poor resource base, such as a diet of *Eucalyptus* foliage in koalas (Krockenberger 1996, Krockenberger *et al* 1998, Krockenberger 2003). An extended pouch life and mother-young bond in tree-kangaroos may also be related to better preparation of young for safe movement in trees (Olds and Collins 1973) and for guidance to what foliage to eat by the mother as in sloths (Montgomery and Sunquist 1978). Behavioural observations of captive *D. lumholtzi* suggest females invest significantly in the education of their young to cope with their complex arboreal lifestyle (Johnson and Delean 2003). This long oestrus and gestation period, along with the extended maternal care and hence long interbirth period in tree-kangaroos, supports the conclusion that they have an overall low reproductive potential (Johnson and Delean 2003), as found in most arboreal folivores (Eisenberg 1978).

Unlike most macropods, tree-kangaroos do not exhibit embryonic diapause or post-partum oestrus (Procter-Gray 1985, Heath *et al* 1990, Johnson and Delean 2003). It is believed that oestrus is more likely to occur after the previous young leaves the pouch (Procter-Gray 1985).

The oestrus cycle is in *D. lumholtzi* it is 47-64 days (Johnson and Delean 2003) whereas it is approximately 35 days (34.8 ± 0.6) in red kangaroos (*Macropus rufus*) (Dawson 1995). Most kangaroos have a gestation period of a little over a month, for example 33.2 ± 0.2 days in red kangaroos (*M. rufus*) (Dawson 1995). The gestation period in *D. lumholtzi* is 42-48 days (Johnson and Delean 2003). Post-partum mating has not been observed in *D. lumholtzi* but one female did mate again 22 days after the death of her joey (Johnson and Delean 2003). Another female returned to oestrus 69 days after the permanent emergence of her pouch young (Johnson and Delean 2003).

There appears to be no defined breeding season for Lumholtz's tree-kangaroos (Procter-Gray 1985, Johnson 1995). Procter-Gray (1985) found females to have young at various ages at different times of the year. *D. lumholtzi* studied in captivity also gave birth at all times of the year (Johnson and Delean 2003). Tree-kangaroos are believed to be polygamous with male home ranges overlapping with that of more than one female (Procter-Gray 1985, Martin and Johnson 1995, Newell 1999b).

Mating behaviour is the same as in other macropods, with the male mounting from behind, but occurs either on the ground (Johnson and Delean 2003) or in a tree (pers. obs.). However, a copulatory plug was present after observed matings in captivity (Johnson and Delean 2003).

In captive *D. lumholtzi* juveniles remain in the pouch for 264.8 ± 8.0 days (246-275: Johnson and Delean 2003), with emerged pouch young suckling for a further 87- 240 days (Johnson and Delean 2003). However, it has been reported from observations of *D. lumholtzi* in the wild, that pouch life is 300-350 days post partum (Procter-Gray 1985). Tree-kangaroo joeys can remain with the mother for 2 to 3 years (Procter-Gray 1985, Flannery *et al* 1996, Newell 1998), with female joeys tending to remain with their mother for longer periods of time (Dabek 1994). Births are spaced 12 to 18 months apart, with the shortest period between permanent pouch emergence and a following birth for one female *D. lumholtzi* in captivity of 114 days (Johnson and Delean 2003).

Female Matschies tree-kangaroos reach sexual maturity at three years of age, males at approximately two years (Dabek 1994, Flannery *et al* 1996). Female *D. lumholtzi* in captivity reach maturity at 2.5 years and a single male matured later at 4.6 years (Johnson and Delean 2003). This late maturity in the captive male *D. lumholtzi* could be due to behavioural differences in captivity. Male *D. bennettianus* appear to take at least 3 years to reach sexual maturity and females 2 years (Martin 1992).

2.1.2 Social behaviour

Both Australian species of tree-kangaroos are largely solitary and territorial (Procter-Gray 1985, Martin 1992, Flannery *et al* 1996, Newell 1999b). Social interactions are limited to the relationship between a female and her young, brief interactions between males and females during mating, and occasional fights between males (Procter-Gray 1985, Tree Kangaroo and Mammal Group 2000). Male tree-kangaroos of several species, including *D. lumholtzi* (Newell 1999b, Johnson and Delean 2003) and *D. bennettianus* (Martin 1992), are known to be very aggressive to each other and can induce fatal wounds with their powerful forearms and sharp claws, presumably fighting over access to females (Martin 1992, Flannery *et al* 1996, Newell 1998).

There is little observational data on tree-kangaroo social behaviour in wild New Guinea populations, but the relatively low level of social behaviour seen in Australian tree-kangaroos has been observed in captive studies of two New Guinea species, *D. matschiei* (Hutchins *et al* 1991) and *D. inustus* (Smith 1988). In fact, agonistic interactions have lead to the death of tree-kangaroo pouch young in captivity (Collins 1986, Hutchins *et al* 1991). However, there is other evidence that some of the New Guinea tree-kangaroos maybe more social than Australian species and that sociability may vary between species (Flannery *et al* 1996).

2.1.3 Activity patterns

Tree-kangaroos are believed to be less active than other kangaroos (McNab 1988). Although Lumholtz's tree-kangaroos are thought to be mostly nocturnal, they are active during the day, especially around dawn and dusk (Procter-Gray 1985, Newell 1999b). They are usually found high in the canopy during the day, often in the sun. They are generally lower in the canopy at night, feeding in the mid and understorey (Newell 1998). They will travel during the day from one tree to another or cross open spaces such as roads or paddocks (Tree Kangaroo and Mammal Group 2000).

D. bennettianus is believed to be nocturnal, commencing its feeding rounds roughly two hours after sunset (Martin 1992). However, it has been has suggested that because tree-kangaroo eye-shine is not as bright as possums (Procter-Gray 1990), they may lack the *tapetum lucidum* cell layer in its retinas, which nocturnal mammals use to improve night vision (Flannery *et al* 1996).

In contrast, most New Guinea species are crepuscular or diurnal (Fischer and Austad 1992, Flannery *et al* 1996). It has been suggested that nocturnal activity in tree-kangaroos could be a response to hunting pressure, as *D. goodfellowi buergersi* and *D. matschiei* have been found to be nocturnal near human populations (Flannery *et al* 1996, Betz *et al* unpublished data a).

Procter-Gray and Ganslosser (1986) found that *D. lumholtzi* spend 61% of their time asleep/resting, and even when awake were active (feeding, moving, grooming, interacting socially) only 10% of the time. This lack of activity is possibly due to the greater digestive demands of a folivorous diet (i.e. low nutritional value, high levels of plant defences, etc) (McNab 1978, 1988). The same pattern of extended inactivity, of up to 80% of the time, to allow digestion is seen in some other arboreal folivores such as koalas (Smith 1979, Mitchell 1990), Howler monkeys (*Aloutta* spp.) (Crockett and Eisenberg 1987) and the sloth (Montgomery and Sunquist 1978). *D. lumholtzi* have short feeding bouts (2-20mins) spaced with long periods of inactivity (0.5 – 4 hours) throughout the day (Procter-Gray 1985), similar to that seen in koalas (Smith 1979).

New Guinean tree-kangaroos are less active during rainy periods (Flannery and

Seri 1990, Fischer and Austad 1992), however activity in *D. lumholtzi* seems less affected by precipitation (Laurance 1990b).

2.2 SPATIAL ORGANISATION - home range or territories

The spatial patterns in which individual animals distribute their activities have been extensively studied on the assumption that they reveal important aspects of behaviour and ecology (Ford 1983). These spatial patterns are variously termed home ranges, territories or space use patterns (Burt 1943, Ford 1983). However, Burt (1943) distinguishes between home range and territory, stating that a territory is a defended area and an animal may not defend its entire home range all of the time. In some species this defence involves fierce fighting between competitors, while in others there is a more subtle recognition by competitors of one another's "keep-out" signals (eg. scent) (Begon *et al* 1986). It is possible that female tree-kangaroos avoid each other in the wild by scent marking or by using another "keep-out" signal, as they have been observed to be aggressive towards each other only in captivity (Smith 1988, Hutchins *et al* 1991, Johnson and Delean 2003). Some tree-kangaroo species have been observed to scent mark using paracloacal glands, and both male and female *D. lumholtzi* possess these glands (pers. obs.) and may use them to scent mark (Newell 1999b).

A popular definition of home range is the one put forward by Burt (1943) as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range".

Considerable effort has been spent in developing techniques for characterising the size and shape of these areas (Harestad and Bunnell 1979, Anderson 1982, Ford 1983). The most basic method is the construction of a complex polygon enclosing all location points and defining the bounded area as the "size of the home range" (Stickel 1954, Ford 1983). These so-called minimum convex polygons, however, are heavily influenced by outlying locations. This can include areas that are not being used at all by the animal (Harris *et al* 1990).

More recently, techniques have been developed which take into account the fact that different regions within a home range are used with different levels of intensity (Dixon and Chapman 1980, Ford 1983). The harmonic mean method gives a probability of use from the number of locations and presents contours of different levels of use around the areas of highest use (Harris *et al* 1990). Therefore, it presents information on how an animal is using its home range, such as centres of activity, not just the overall size (Harris *et al* 1990). The centre of activity, or core area, is the term given to the area or point of greatest activity (Dixon and Chapman 1980).

It is essential when comparing home range size from different studies that the same technique is used for the analysis as different techniques (Croft 1989, Troy and Coulson 1993) and different software packages will show varying results for the same data (Gallerani Lawson & Rodgers 1997), as they use different algorithms for the calculations (Harris *et al* 1990). Additionally, many studies fail to consider the independence of consecutive fixes or to test for asymptotic response in cumulative area estimates (Troy and Coulson 1993), which is essential for determining if enough fixes have been made to accurately characterise the home range.

2.2.1 Resources and home ranges

There are a number of factors that may influence an animal's use of its home range area. These include social organisation (Croft 1989), the amount of available resources such as food and shelter (Burt 1943) or the number of available females (Lindstedt *et al* 1986), population densities (Ostfield and Canham 1995, Vincent *et al* 1995), differing habitat types (Mitchell 1990) and habitat quality (Melzer 1995).

Therefore, a full understanding of home range use requires information about the ecology and social organisation of the species, and the productivity of the habitat in which it lives (Croft 1989). The range of an animal may be set by the availability of suitable habitat or the lack of dispersal to suitable areas outside this range (Pople 1989). For example, sub-adults may be forced to live in suboptimal habitat because more dominant individuals exclude them from preferred areas (Lindstedt *et al* 1986). Furthermore, sub-adults may need more nutrients for growth, and therefore would require larger home ranges or areas of better habitat quality. Thus, behaviour and social organisation play an important role in determining home range sizes within a species (Lindstedt *et al* 1986).

Among territorial animals the size of the home range is thought to reflect the amount of resources, such as food, water and shelter that the territory holder needs (Burt 1943, Martin 1992). In fact, the availability of resources has been attributed to the variation in spatial use for many animals (McNab 1963, Milton and May 1976, Fisher 2000, Palacios and Rodriguez 2001).

The variation in home range areas of both koalas and several species of possums may be attributed to the number of available individuals within preferred tree species or number of den sites, etc (How 1978, Hindell and Lee 1987, 1988, 1990, Mitchell 1990, Melzer 1995).

Procter-Gray (1985) suggests that the size of the female tree-kangaroo's home range may be determined by the amount of food needed by the female and her dependent. A female's home range size must meet her higher energy requirements, especially if she has a dependant young during and after lactation (Lindstedt *et al* 1986). Therefore, considering energetics alone, females should have larger home ranges than males (Lindstedt *et al* 1986). The size of a male's home range may be determined, not by food requirements, but by the advantage of maintaining contact with several females in order to mate when they come into oestrus (Procter-Gray 1985, Lindstedt *et al* 1986, Martin 1992) therefore having to range farther (Lindstedt *et al* 1986). This is consistent with many other studies of social organisation in mammals where the consensus has been that the behaviour of males is adapted to that of females and related to mating activity (Clutton-Brock 1989, Mitchell 1990, Komers and Brotherton 1997). That is, females usually set the agenda and males do whatever is necessary to gain access to them (Clutton-Brock 1989, Martin 1992, Komers and Brotherton 1997).

Furthermore, an inverse relationship between home range size and population density occurs in some species, especially those with exclusive home ranges, due to competition for resources or due to social interactions (Ostfield and Canham 1995, Vincent *et al* 1995). It is possible that *D. lumholtzi* home range sizes may be influenced by the population size within the fragment (i.e. they are density dependent). It has been found that koalas will use smaller areas in high population densities (Mitchell 1990, Melzer 1995), as will colobus monkeys and howler monkeys (Milton and May 1976). But whether these home range sizes are small due to high populations densities, or whether population density is high due to small home range sizes is unclear.

There are many examples of variation in home range size and densities in koalas (*Phascolarctos cinereus*) from differing habitats (Eberhard 1972, Gall 1980, Martin 1985, Hindell 1984, White and Kunst 1990, White 1999, Ellis *et al* 2002). Studies show that at favourable sites in sclerophyll forest their home range is 1.18 ± 0.7 ha for females and 1.70 ± 1.0 ha for males (Mitchell 1990). In comparison, in parts of the Brigalow country in central Queensland, which is considered poorer or more marginal habitat for the species, individual home ranges for females can reach 102 ha (mean 39.2 ha) and males can exceed 190 ha (mean 86.5 ha) (Melzer 1995).

2.2.1.1 Tree-kangaroos and home ranges

Tree-kangaroos are one of the few macropods that defend or hold exclusive home ranges or territories and the sizes of these vary between species and between individuals (Procter-Gray 1985, Martin 1992, Newell 1999b), and are thought to be due to differences in the habitat type and quality (Newell 1999b). Martin (1996) believes that it may reflect the vigour and status of the occupants as two of his study males of similar body mass had quite different home range areas. He suggests that the male with the larger area was far more vigorous or dominant than the other (Martin 1996).

D. lumholtzi are not only territorial but they also appear to be strongly attached to their home ranges. Individual tree-kangaroos remained within their home ranges even after their forested habitat had been clear-felled, eventually succumbing to starvation, and predation by dogs or disease (Newell 1999c).

Using the minimum convex polygon method, Procter-Gray (1985) found that adult female *D. lumholtzi* established non-overlapping home ranges that averaged 1.8 ± 0.4 ha (1.2 - 2.6 ha, *n* = 3). In contrast, a male home range, 4.4 ha (*n* = 1), included large overlaps with that of several females while not overlapping with other males (Procter-Gray 1985).

Newell's animals (1999b) showed the same spatial arrangement in his study site, which was only a few hundred metres from Procter-Gray's site (1985), with female home range of 0.689 ha (90% harmonic mean, n = 6) (0.6-2.1 ha - minimum convex polygon) and males at 1.952 ha (n = 5)(1.0-3.4 ha - minimum convex polygon). These compare well with those of Procter-Gray's study (1985), despite differences in structural composition of the vegetation at the two sites, the older age class at Procter-Gray's site, and the size of the total forest block (~300 ha vs. 20 ha). Newell (1999b) estimated a density of 1.4 - 1.5 adult Lumholtz's tree-kangaroos per hectare, excluding pouch young and juveniles at-heel with their mother. This equates to a biomass of Lumholtz's tree-kangaroos of approximately 11.37 kg ha^{-1} (Newell 1999b). Newell (1999b) suggests that this is a substantial biomass considering the young successional age class of the forest studied.

Bennett's tree-kangaroos also show a similar spatial arrangement, with males actively defending their range (Martin 1992) of 19.4 to 29.8 ha (*n* = 3). Adult females also occupy discrete ranges of 5.5 to 9.8 ha (*n* = 2) (Martin 1992). Overall density has been estimated to be approximately 0.3 animals/ha (Martin 1992). These home ranges are much larger than those estimated for Lumholtz's tree-kangaroos (Procter-Gray 1985, Newell 1999b) even though Martin's study (1992) was conducted on the same forest type (Type 5b -Tracey 1982) 175 km north of the Atherton Tablelands. However, these sites differed in the height, structural characteristics and floristics of the canopy species, with Martin's (1982) site having larger trees that were more widely spaced with a more open understorey than that of Newell's (1999b) and Procter-Gray's (1985) sites.

Attempts to determine home ranges of New Guinean species have met with little success with the exception of a single measurement of approximately 25 ha for a *D. matschiei* of unrecorded sex (Flannery *et al* 1996, Procter-Gray 1990).

More recent studies, using distance sampling with scat pellet counts, Betz *et al* (unpublished data b) found average densities of Matschie's tree-kangaroos (*Dendrolagus matschiei*) of approximately one animal per hectare (0.9-1.0 animal/ha). Betz *et al* (unpublished data b) suggest that this density is similar to that found with the Australian tree-kangaroo species, however it is between Bennett's tree-kangaroos (0.3/ha: Martin 1992) and Lumholtz's tree-kangaroos (1.5/ha: Newell 1999b). The method that they used to estimate abundance was a point-transect method called DISTANCE sampling, using scat counts. Unfortunately this method has its flaws, as it is dependant upon the knowledge of the number of scats produced per animal per day in the wild, and this could be inaccurate when estimated from animals in captivity, as was done by Betz *et al* (unpublished data b). Animals in wild may defaecate up to two times as much as in captivity due to dietary differences and activity levels (Johnson *et al* 1987, Hume 1999). For example, captive koalas (Cork *et al* 1983) consumed approximately half the amount of leaves as that of free ranging koalas (Krockenberger 2003). Therefore, the density estimate of Betz *et al* (unpublished data b) for *D. matschiei* may be highly overestimated - approximately twofold.

Using the single reading above of 25ha (Flannery *et al* 1996, Proctor-Gray 1990) suggests that *D. matschiei* may have home ranges similar to those of *D. bennettianus.*

The home range sizes of *D. lumholtzi* are not only small compared to other tree-kangaroos (Procter-Gray 1985, Flannery *et al* 1996, Newell 1999b) but are small compared to some other macropods and other arboreal folivores of comparable body size. For example Bridled nailtail wallabies (3-8kg) (*Onchogalea fraenata*) home range sizes are much larger than *D. lumholtzi*, at 65.6 ± 13.3 ha for males and 23.3 ± 2.9 ha for females (Fisher 2000). Similarly for *Thylogale thetis,* with males (7kg) at 14.8 ha, and females (3.8kg) at 9.1 ha (Johnson 1980a). Also, in the rock wallabies, the closest relatives to tree-kangaroos, home range sizes are 11.9ha (in both females; 4.3kg and males:

4.7kg) in *Petrogale assimilis* (Horsup 1994) and from 10.5ha (females: 6.3kg) to 25.9ha (males: 7.9kg) in *P. penicillata* (Scholtz 1980, Short 1980). However, rainforest pademelons *Thylogale stigmatica*, have comparable home ranges to *D. lumholtzi*, with males 3.6 ha (5.1kg) and females 3.5 ha (4.1 kg) (Vernes *et al* 1995). Also Sloths (5.5 - 6.7kg) (Chiarello 1998, Montgomery and Sunquist 1978) have similar home range sizes to *D. lumholtzi* (0.5 - 5.9ha), although there is considerable variation. Furthermore, home range sizes in koalas vary between 1 - 190ha depending on the habitat (Mitchell 1990, Melzer 1995).

This spatial arrangement is probably typical of Lumholtz's tree-kangaroos throughout its range. However, the size of the home range required by Lumholtz's tree-kangaroos may vary considerably between different habitats (Tree Kangaroo and Mammal Group 2000, Kanowski *et al* 2001a) as it does in koalas (Mitchell 1990, Melzer 1995) and other arboreal folivores (Milton and May 1976, How 1978, Kerle 1998, Fisher 2000, Palacios and Rodriguez 2001). In fact, the forest fragments near Yungaburra where these studies occurred appear to support high densities of tree-kangaroos (Newell 1999a, 1999b). Newell (1999b) suggests that while the high biomass and small home areas may be correlated with each other, whether they are both related to the quality of the habitat at the site requires further investigation. It has been suggested that individual tree-kangaroos are likely to require much larger home ranges elsewhere, especially in fragments on less fertile soils or in continuous forest (Kanowski *et al* 2001a). The larger home ranges found in *D. bennettianus* (Martin 1992) and *D. matschiei* (Flannery *et al* 1996, Betz *et al* unpublished data b) were all from continuous forest, not in fragments as were the studies on *D. lumholtzi*.

In conclusion, it is presently unclear whether *D. lumholtzi* home range sizes vary on different habitat types, on differing soil types, in different sized fragments or in continuous forest due to densities or if there is some other factor influencing home range size.

2.2.2 Home range and body size

Home range size correlates positively with body size in mammals (Milton and May 1976, Harestad and Bunnell 1979, Lindstedt *et al* 1986, Troy and Coulson

1993) although body size does not fully explain the variation observed (Croft 1989). Other factors such as habitat, social organisation and ecology may interact to determine home range area (Croft 1989, Troy and Coulson 1993). For example, variation in home range between three macropod species of similar size; *Wallabia bicolor, Macropus rufogriseus* and *Macropus parryi*, could not be explained by body size (Troy and Coulson 1993) and these species occupy different niches. This is supported by the fact that in many studies of home range use in arboreal folivores, there is a great deal of variation in home range sizes within species as well as between species (See Table 4.2). Furthermore, there is variation in home range sizes even within a species within a study site, such as in male koalas from central Queensland whose home range sizes varied from 5.4ha to 296.0ha (Ellis *et al* 2002).

Bennett's tree-kangaroos are approximately 1.5 times the size of Lumholtz's tree-kangaroos (8 kgs vs. 13 kgs) and in general their habits appear quite similar, however they have a much larger home range than Lumholtz's tree-kangaroos (Martin 1992, Newell 1999b). Martin (1992) suggests that there was a linear relationship between body size and the size of the territory occupied by adult male Bennett's tree-kangaroos and that this was related to their relative vigour. However, there was a small sample size of only 3 males in the study (Martin 1992). Furthermore, female range sizes do not seem to be determined by body size in *D. bennettianus* (Martin 1992).

Alternatively, sparsely distributed resources may not be the factor influencing their use of space, but predator or hunting pressure may force females to space themselves out through the forest (Martin 1992).

Newell (1999b) suggested that a study be undertaken in different habitat types to answer the question of whether home-range sizes and densities recorded by Newell (1999b) and by Procter-Gray (1995), are representative of Lumholtz's tree-kangaroos throughout their range.

2.3 HABITAT SELECTION AND HABITAT UTILISATION BY TREE-KANGAROOS

2.3.1 Habitat selection

It is often assumed that a species will select resources that are best able to meet its life requirements, and that high quality resources will be selected more frequently than low quality ones (Manly *et al* 2002). Therefore, resources used should be compared to those available in order to reach valid conclusions concerning resource selection (Manly *et al* 2002). When resources are used disproportionately to their availability, use is said to be selective (Manly *et al* 2002).

Resource selection occurs in a hierarchical fashion from the geographic range of a species, to individual home range within an area (second-order selection), to use of general features within the home range (third-order selection), to the selection of food items or particular elements within the general features (fourth-order selection) (Johnson 1980b, Manly *et al* 2002). There is no single correct level to study and multiscale studies of resource selection have become increasingly common (Manly *et al* 2002).

Habitat selection is undertaken initially when an animal selects a 'home range'. This may of course be in either optimal, sub-optimal or marginal habitat and may be influenced by the body size, sex, age or vigour of the individual (Martin 1996). Territoriality may also influence the position of an animal's home range with respect to the overall study area, but should not invalidate a within-home-range comparison of utilised with available habitat (Aebischer *et al* 1993).

2.3.2 Habitat quality

Habitat patches may differ from each other with respect to their suitability for a given species, their durability (or persistence) and resilience over time (Kozakiewicz 1995). If all life requirements of the species are fully identified, habitat types within a mosaic could be classified as optimal, suboptimal, marginal or non-inhabitable (Kozakiewicz 1995). However, even suboptimal habitats may provide areas of useable habitat to enable the normal social behaviour of populations and to prevent overcrowding of optimal areas (Munks *et al* 1996).

Defining a measure of suitability of habitats is very important. Usually, reproductive success of the species is considered to be a good measure of habitat suitability (Krebs 1985). Habitat suitability can be affected by many factors, such as food and water supply, shelter, mates, nesting sites and predators (Pople 1989, Kozakiewicz 1995). It might be expected that habitat suitability should be reflected by population density. However, many authors have argued strongly that habitat quality cannot be assessed through population density alone (e.g. Van Horne 1983), particularly in heterogeneous landscapes (Kozakiewicz 1995).

Home range size is one indicator of habitat quality (Tufto *et al* 1996). Minimum home range size is a function of habitat productivity and resource distribution as well as individual energy requirements (Harestad and Bunnell 1979, Fisher 2000). In many mammalian herbivores, home range size decreases with increasing food availability (Hulbert *et al* 1996), and herbivores may move their activity centre towards food sources opportunistically (Johnson 1987). Pople (1989) suggests that in macropods, some individuals within a population may use different habitats in different seasons and even at different times of the day. Other members of the same population may or may not show the same habitat associations, known as habitat segregation as seen in red-necked wallabies (*Macropus rufogriseus*) (Johnson 1987), and red deer (*Cervus elaphus*) (Conradt *et al* 1999, 2003), where males and females differ in their habitat use. Additionally, the majority of macropod species have distinct feeding and resting areas (Pople 1989, Vernes *et al* 1995).

Although there have been a few studies on their home range and habitat use, there is only limited information available on the habitat requirements for *D lumholtzi* (Procter-Gray 1985, Newell 1999b). This is partially due to the fact that all three studies on tree-kangaroos in Australia have been undertaken on a single habitat type, Type 5b complex notophyll vine forest (Tracey 1982). Moreover, this habitat type is extraordinarily restricted in extent due to past clearing, with less than 2.5% of the original area remaining (Sattler and Williams 1999). There were however variations in habitat between the studies. Newell's study site (1999b) was of a younger successional age class than

Procter-Gray's (1985). Even within the same forest type Bennett's tree-kangaroos have a much larger home range than Lumholtz's tree-kangaroos (Procter-Gray 1985, Martin 1992, Newell 1999b), although these sites also varied in their structural and floristic characteristics, and this may go some of the way to explain these differences.

Newell (1999b) suggested that habitat quality might have an effect on *D. lumholtzi* densities and home range sizes. The influence of habitat quality on habitat use needs to be explored on a within-site scale, as well as comparing habitat use between sites across a region (Newell 1999b). We need to explore if habitat differences, such as structural or floristic characters, influence variation in home range sizes and intensity of use within their home ranges, especially within a site with varying habitats available to *D. lumholtzi*.

From the little that is known about their distribution, it has been suggested that Lumholtz's tree-kangaroos are present in higher densities in rainforests on fertile soils (such as Type 5b), as found in other arboreal folivores (Braithwaite *et al* 1983, Lunney 1987, Braithwaite 1996), rather than the forest types associated with lower-nutrient granite or rhyolite soils (Newell 1998, 1999a, Kanowski 1999). Kanowski (1999) and Kanowski *et al* (2001b) add that the relative abundance of *D. lumholtzi* on fertile soils appears to be a response to the nutritional quality of the foliage. Soil fertility may have a strong subsequent influence upon both leaf nutrition and palatability of leaf material, and is also likely to relate to the degree of sclerophylly and presence of allelochemicals (Coley 1983, Newell 1999b). Braithwaite *et al* (1983) found that soil fertility was linked to arboreal marsupial density through forest floristics and leaf chemistry. In addition arboreal marsupial abundance tends to increase with increasing altitude (Kanowski 1999, Kanowski *et al* 2001b).

Alternatively, Newell (1998) suggests that *D. lumholtzi* density may relate to the floristics or to the age of the forest since clearing. Lumholtz's tree-kangaroos may show a preference for regrowth as opposed to mature forests (Laurance and Laurance 1996, Newell 1999a), and may be able to maintain smaller home ranges within regrowth forests with a relatively nutritious or palatable food resource compared with other rainforest communities (Newell 1999b). It has been suggested that *Dendrolagus matschiei*, a New Guinea tree-kangaroo, shows a preference for new growth or early successional tree species (Dabek pers comm.). Foliage from regrowth forest may have a higher nutrient quality (Cates and Orions 1975, Coley 1983, Ganzhorn 1995), or lower levels of defences against herbivory (Janzen 1978, Cork and Foley 1997). Early successional plant species are significantly more palatable to a generalist herbivore than later successional and climax plants, possibly due to the smaller investment in defensive substances of the former (Cates and Orions 1975). Procter-Gray (1984) found *D. lumholtzi* preferred primary forest plant species. However, it should be noted that primary rainforest species were the dominant species on her study site.

Fragmentation may also enhance habitat quality by increasing the number of nutritious pioneer plant species (Dooley and Bowers 1998). If it is true that Lumholtz's tree-kangaroos prefer regrowth or successional plant species then this may explain high densities in small regrowth fragments such as those reported by Newell (1999b) and Procter-Gray (1985).

In support, Laurance and Laurance (1996) also suggested that Lumholtz's tree-kangaroos might be expected to increase in numbers in moderately disturbed forest due to the dietary use of both primary and secondary rainforest plants. This is supported to some degree by studies of other tropical arboreal folivores, with increased observations of some species of lemurs in standing forest following low-level logging disturbance of a Malagasy tropical dry deciduous forest (Ganzhorn 1995). Ganzhorn's study (1995) provided evidence that an increase in sighting frequency may be related to increases in leaf quality and fruit production as a result of increased sunlight to other parts of the canopy. An improvement in food quality, along with the loss of habitat was likely to have altered the species' home-range utilisation to accommodate a greater density of animals in the standing forest in the short term. The abundances of arboreal folivores in south India (considered 'generalists' with relatively small home ranges), the large brown flying squirrel (*Petaurista petaurista*) and the Travancore flying squirrel (*Petinomys fuscocapillus*), also increased with decreasing area and increasing disturbance level (Umapathy and Kumar 2000).

There is, however, the question of whether Lumholtz's tree-kangaroos are simply easier to observe in disturbed forest as opposed to mature forest and hence give an impression of higher densities. Laurance and Laurance (1996) observed Lumholtz's tree-kangaroos with spotlights mainly on the edge or along tracks. They are extremely difficult to detect in thick mature rainforest. Whether Lumholtz's tree-kangaroos are simply easier to spot along the edges of fragments or whether they actually maintain higher abundances in fragmented forests, or are an 'edge' species is not clear (Newell 1999a).

Edges might also provide high-quality habitat because of diminished costs of territoriality (Bowers *et al* 1996) resulting from fewer borders to defend (Stamps *et al* 1987) as well as possibly supplying proximity to nutritious new plant growth. Newell (1999a, 1999b) found that when radio-tracking *D. lumholtzi* with home-ranges abutting forest edges, they were only visible by spotlighting on the edge less than 10% of the time; the remaining time was spent away from the edge and therefore usually undetectable. Not surprisingly, Newell (1999a) found that animals with home ranges away from the edge were rarely seen.

Tree density was found to be the best predictor of the occurrence of folivorous primates such as the Nilgiri langur in forest fragments (Umapathy and Kumar 2000). It is the availability of a variety of plant species that is important to the Nilgiri langur to avoid the build up of different secondary compounds beyond their tolerance levels (Umapathy and Kumar 2000).

2.3.3 Habitat fragmentation

Pahl *et al* (1988) suggest that species which tend to survive in small patches of habitat appear to have good dispersal ability, small home ranges, generalised habitat requirements, and depend on food resources which are not temporally or spatially distributed. They add that Lumholtz's tree-kangaroos may have diet and dispersal abilities that enable them to persist in fragmented and disturbed forests.

Lumholtz's tree-kangaroos have been reported to be in significantly lower abundances in small rainforest fragments and corridors and absent in fragments <20 ha (Laurance 1989, 1990a). However, other studies considered the species to be in low abundances irrespective of forest area, forest type (Laurance 1996, Pahl *et al* 1988), or the degree of isolation of the rainforest fragment (Laurance 1996), although results from a multiple regression model did suggest that the species may prefer isolated fragments with a large variation in canopy height (Laurance 1996). Additionally, the relative frequencies of observations of Lumholtz's tree-kangaroos at sites seven years after selective logging activities occurred were different at their reference sites (Laurance and Laurance 1996). These conflicting results suggest that more research is required to clearly establish the effects of disturbance and fragmentation of habitat on populations of Lumholtz's tree-kangaroos.

2.4 FEEDING ECOLOGY

Lumholtz's tree-kangaroos are believed to be generalist folivores that feed on a wide variety of rainforest leaves (Procter-Gray 1984, 1985, Newell 1999a). However, in areas bordering rainforests animals will often enter paddocks, orchards and gardens to feed on cultivated crops such as maize, pumpkins, mandarins and avocados (Newell 1998, Tree Kangaroo and Mammal Group 2000). In their survey Kanowski *et al* (2001a) also obtained numerous records of *D. lumholtzi* from eucalypt forest, as far as 10km from the nearest large rainforest patch. However, they suggest that these records almost certainly represent dispersing animals, as *D. lumholtzi* is believed to be unable to survive on eucalypt foliage. These records could also represent misidentification of *D. lumholtzi,* or inaccuracies of reported localities.

Dendrolagus lumholtzi have been observed utilising at least 130 species of plants from 45 families (Procter-Gray 1984, Newell 1999b,TKMG unpublished data). Unfortunately not all of these are feeding observations, as *D. lumholtzi* are shy and cryptic and feeding observations are difficult (Newell 1998, 1999b).

Procter-Gray (1984) recorded 75 observations of *D. lumholtzi* feeding most of which were on mature leaves of 33 species with only 1.3% on non-leaf parts. *Euroschinus falcata, Elaeagnus triflora* and *Maclura cochinchinensis* leaves made up 36% of the diet (Procter-Gray 1984).

Newell (1998, 1999b) found *D. lumholtzi* utilised 39 species of trees and vines. Of these four of the dominant tree species in his study site made up 51% of his observations, Blackbean or Morton Bay Chestnut (*Castanospermum australe*), Candlenut (*Aleurites moluccana*), Grey Bollywood (*Neolitsea dealbata*) and *Mallotus philippensis*, which were all dominant across the study site. He found that *D. lumholtzi* used a small number of trees frequently and a larger suite of trees much less regularly (Newell 1999b) as do other arboreal folivores, such as ringtail possums (*Pseudocheirus peregrinus*) (Lawler *et al* 1998) and koalas (*Phascolarctos cinereus*) (Hindell and Lee 1987, 1988, 1990, Moore and Foley 2000). Newell (1999b) also found that individual *D. lumholtzi* had favourite individual trees within their home ranges that they used repeatedly. This was also found in some New Guinea tree-kangaroo species (Betz *et al* unpublished data a), and in *D. bennettianus*, where they had favourite daytime roost trees (Martin 1992).

Many of the plant species that Lumholtz's tree-kangaroos were associated with were the same at both study sites (Procter-Gray 1984, 1985, Newell 1999b), and similar in many respects to those recorded for Bennett's tree-kangaroos (Martin 1992). This is not surprising as they were all on the same rainforest type, with Newell's (1999b) and Procter-Gray's (1985) sites only a few hundred metres apart. However, *D. lumholtzi* at Newell's (1999b) site did not use some species that were used regularly at Procter-Gray's (1985) site, such as *Euroschinus falcata*, although the species is present at both sites.

The marked variation between *D. lumholtzi* individuals in the tree species that they used suggests that, at least to some degree, Lumholtz's tree-kangaroos are both catholic and opportunistic in the tree species that they utilise (Newell 1999b). Bennett's tree-kangaroos (Flannery *et al* 1996, Martin 1992), koalas (Hindell and Lee 1987, 1988, 1990, Moore and Foley 2000) and the three-toed sloth (*Bradypus variegatus*) (Montgomery and Sunquist 1978), another tropical arboreal folivore, also displayed individual variation in the tree species utilised.

In many instances, Lumholtz's tree-kangaroos were also associated with vine species. One particular species, *Maclura cochinchinensis*, was commonly associated with sightings of tree-kangaroos, and was a regular food item at both Procter-Gray's (1985) and Newell's (1999b) study sites.

Dendrolagus bennettianus appears to favour similar species as *D. lumholtzi*, but its diet appears to include more fruit, with the fruits of Australian olive (*Olea paniculata*) and various fig species (Moraceae) being favoured (Martin 1992, Flannery *et al* 1996).

Although the knowledge of the feeding ecology of the New Guinea tree-kangaroos is poor, some species seem to be more frugivorous than *D. lumholtzi* (Flannery *et al* 1996, Betz *et al* unpublished data a), also favouring figs. *D. mbaiso* however, appears to be a near obligate folivore.

Some tree-kangaroo species, including *D. matschiei, D. goodfellowi, D. inustus finschi* and *D. lumholtzi*, have been observed to be somewhat carnivorous in captivity, eating eggs, chicken meat and the occasional animal or bird that wanders into the enclosure (Flannery *et al* 1996, Johnson *et al* 2002). However, this behaviour has not been observed in the wild (Betz 2001). Johnson *et al* (2002) has suggested that this behaviour may be due to nutritional deficiencies or boredom in captivity.

Additionally, *D. lumholtzi* have been observed eating plants known to be toxic or at least unpalatable to introduced stock (Newell 1998) such as lantana (*Lantana camara*) or wild tobacco (*Solanum mauritianum*) (Procter-Gray 1984, Newell 1999b, TKMG unpublished data, pers. obs.).

Whether *D. lumholtzi* only eat some species sparingly, or use different tree or vine species in certain sequences to avoid or counteract some of the toxic effects of the chemicals is still unclear (Newell 1998). Mature tropical forest leaves are high in secondary defensive compounds (Coley 1983). Plant defences can also vary both between species as well as within a species (Cork and Foley 1991, 1997, Lawler *et al* 1998). In order to distribute the toxin load, Lumholtz's tree-kangaroo might be expected to follow the dietary strategies of other arboreal folivores such as Howler monkeys (*Aloutta* spp.) (Glander 1977, 1978, Milton 1978), and the Nilgiri langur (Umapathy and Kumar 2000), eating small portions from a wide variety of food plants. Tree-kangaroos in New

Guinea have also been reported to exhibit this behaviour, not only eating a wide variety of food plants but also avoiding consuming large amounts of any one species (Betz *et al* unpublished data a). Eucalypt folivores, such as ringtail possums and koalas also eat a variety of different species (Lawler *et al* 1998, Moore and Foley 2000) and discriminate between individual trees within a taxonomic species (Hindell and Lee 1987, 1988, 1990, Pahl 1987, Lawler *et al* 1998). It is believed that these choices are driven by the variation in nutrients and plant chemicals between foliage of different trees and between different leaf classes (Moore and Foley 2000). The variations in the diet of the howler monkeys have been related to the protein and soluble sugars available in the different food species (Hladik 1978) and both howler monkeys (Glander 1978, Milton 1978) and red spider monkeys (Hladik 1978) eat more young leaves for their high protein content and petioles for their high mineral content. *D. lumholtzi* have also been observed eating new leaves and the petioles of some species (pers. obs.).

Leaf eating monkeys have also been observed eating soil rich in clay (Hladik 1978), and it is believed that this may act as an absorbent for the tannins present in some rainforest leaves (Hladik 1978). Captive and hand raised *D. lumholtzi* have been observed eating basalt soil which is also rich in clay (Johnson and Delean 2003, pers. obs.) but whether they do so in the wild is unknown.

In summary, *D. lumholtzi* have been found to utilise a wide variety of floral species and show individual preferences for tree species, behaviour similar to other folivores such as koalas (Hindell and Lee 1987, 1988, 1990) and leaf eating monkeys (Glander 1977, 1978, Hladik 1978, Milton 1978, Umapathy and Kumar 2000). The reasons for individual choices are unclear. It is possible that they are choosing particular species for foliage characters such as plant defences as do koalas (Moore and Foley 2000) or for other foliage characters. The determination of foliage characters affecting tree choice is beyond the scope of this study, but certainly requires further investigation.

2.5 ADAPTATIONS TO HERBIVOROUS DIET BY ARBOREAL FOLIVORES

The digestion of plants is a challenge to herbivorous animals as materials contained within the cell walls of plants (where a large proportion of the energy contained in plant tissues) are difficult to digest (Bauchop 1978, Eisenberg 1978). The proteins and carbohydrates of plant cellular contents are available to all animals, while the cellulose and hemicellulose carbohydrates of the cell wall are available only to those animals that possess the specific microorganisms that can degrade these substances in their digestive tract (Bauchop 1978, Eisenberg 1978, Van Soest 1982). Therefore, the ability of animals to utilise cellulose, hemicellulose and pectin as food depends on the capacity of the gastrointestinal organisms to degrade them and the ability of the herbivore host to utilise these microorganisms and their products (Bauchop 1978, Eisenberg 1978, Van Soest 1982). Hence, the utilisation of leaves and stems as a relatively complete source of energy requires considerable morphological specialisation in dentition and gut morphology (Eisenberg 1978).

2.5.1 Teeth

Mastication is the first major process in digestion. This preparation of food by teeth affects the capability of the gut for microbial or enzymatic digestion, and hence digestibility (Sanson 1989).

The tree-kangaroo's folivorous, browsing diet has led to modifications in their tooth morphology (Sanson 1978, 1989). Tree-kangaroo dentition is similar to that of koalas. They have a flat tooth row, where all of the molars occlude at once and comprising of one large premolar and four molars (Sanson 1980), of which the molars have completely erupted by the time the animal has reach approximately 18 months to 2 years of age, similar to koalas (Martin 1981, Martin *et al* 1999). The premolars are enlarged, sharp (for shearing thick stems), and more complex than other macropods, having more cusps and cutting edges, and thus also suited for puncturing and shredding leaves (Sanson 1989). The forest-dwelling wallabies and tree-kangaroos have simpler molars than their grazing relatives (Sanson 1980, 1989). The molars of tree-kangaroos are low crowned and have sharp ridges suitable for further dissecting leaves (Flannery *et al* 1996, Sanson 1989).

Ride (1978) recognised a relationship between the reduction in size of the premolar and increased specialisation for grazing. This reduction in premolar size is believed to also allow molar progression in the grazing macropods (Sanson 1989), a process that does not occur in tree-kangaroos (Sanson 1980, Flannery *et al* 1996). Molar progression is an adaptation to compensate for tooth wear as grass contains abrasive silica that is generally absent from foliage of trees (Sanson 1989). Tree-kangaroos and other browsing species have larger premolars than the grazing macropods (Sanson 1980, 1989). Large premolars are believed to act as a buttress preventing the forward drift of molars (Sanson 1989, Hume 1999).

Like other macropods, tree-kangaroos do have a limited number of deciduous teeth (Flannery *et al* 1996) and a peculiar form of tooth replacement. As an animal matures, the permanent sectorial premolar (P3) ejects both a deciduous blade-like premolar (P1) and a molar-shaped tooth (P2) (Flannery *et al* 1996).

As in koalas, plant material is sheared rather than crushed between the sharp cusps of the upper and lower teeth during mastication (Cork and Sanson 1990). This is found in other herbivores faced with high fibre diets, where they employ more cutting than crushing in mastication (Cork and Sanson 1990). This type of mastication ruptures the cells and releases the cell contents. Additionally the cell walls are reduced to many fragments producing high surface areas for more effective fermentation by the microbes in the gut (Cork and Sanson 1990).

2.5.2 Gastrointestinal morphology

The digestive physiology of folivores influences the range of foods available to them (Hume 1982, 1999). Herbivorous mammals have modified digestive tracts with either a foregut or hindgut adapted to the digestion of the structural carbohydrates of plants (Richardson 1980). In the marsupials, the Vombatidae (wombat), Phascolarctidae (koala) and the Phlangeridae (possums) are all hindgut fermenters with a modified caecum and large intestine for microbial fermentation, whereas the Macropodinae (kangaroos and wallabies) and Potoroinae (rat kangaroos) are all foregut fermenters with modified stomachs for fermentation of plant material (Richardson 1980).

Early workers classed macropods as either ruminants or ruminant-like animals (Richardson 1980) because of their modified stomachs. However, foregut fermentation has evolved independently in several mammal groups including ruminants, sloths, leaf-eating colobid monkeys and macropod marsupials (Bauchop 1978).

It is believed that macropods evolved from ancestors that lived in the forest canopy up until the mid Miocene (Flannery 1989). These early macropod ancestors then evolved to inhabit the floor of the temperate forest, which covered Australia at the time (Dawson 1989). Macropod ancestors are believed to have had simple dentition and gut morphology (Freudenberger *et al* 1989). The small omnivorous Musky Rat-kangaroo (*Hypsiprymnodon moschatus*) is considered a modern example of this body form and life style (Dawson 1989, Freudenberger *et al* 1989). The Musky Rat-kangaroo has a simple stomach that is partly compartmentalised (Hume 1982, 1999), and is intermediate between the simple stomachs of the possums and the complex forms of the kangaroos and wallabies (Dawson 1989). Limited fermentation may have occurred in the hindgut, particularly the caecum, as it still does in most foregut fermenters (Freudenberger *et al* 1989).

It is believed that the complex foregut of other macropodids developed at a later stage along with a symbiotic relationship with microbes that allowed the digestion of plant cell walls (Freudenberger *et al* 1989). This development allowed macropods to exploit the many different nutritional niches that appeared as continental Australia became increasingly arid in the late Miocene and early Pliocene, resulting in a divergence of the morphological and physiological adaptations in macropods (Freudenberger *et al* 1989). This diversity ranges from the small Potoroids (0.5 - 3kg) which seek diets rich in nutrients such as plant roots, fungi and invertebrates, to the large grazing kangaroos (up to 85kg) which exploit poor quality but abundant grasslands (Freudenberger *et al* 1989). The diversity of diet and quality of food sources are reflected in gut morphology. Potoroids have a large sacciform forestomach, whereas the large grazing Macropodids tend to have the most reduced sacciform but most expanded tubiform forestomach (Hume 1999, Freudenberger *et al* 1989) with a trend toward increasing relative size of the tubiform forestomach with increasing body size (Freudenberger *et al* 1989) and grazing. It has been suggested that a tubular forestomach, along with the low energy requirements of marsupials, allow macropods to subsist on poorer quality forage than ruminants of similar size (Hume 1984).

For mammals to survive as arboreal folivores, living in the forest canopy with access to the full range of foliage, fruits and seeds, it is suggested that they must weigh less than 15kg (Grand 1978, Eisenberg, 1978, Cork 1996). However, animals with smaller body sizes are likely to encounter difficulties in meeting their nutritional requirements from leaves alone (McNab 1978, Foley and Cork 1992, Cork 1996). Small mammals need to acquire more energy each day relative to their body weight than do larger mammals because as a mammal’s body size decreases, its energy requirements per unit body mass increase without a comparable increase in gut capacity (Parra 1978, Demment and Van Soest 1985, Foley and Cork 1992). For mammals eating high-fibre diets, like leaves, energy requirements can be met by one of two strategies: a “retention-maximising” strategy of delaying passage of food through the gut to maximise digestion by facilitating microbial fermentation of plant cell walls; or, an “intake-maximising” strategy of passing food through the gut as rapidly as possible to maximise the quantity of food processed (Cork 1996). The rate of yield of energy form the retention-maximising strategy is essentially the product of the average daily fermentation rate (determined by the composition of the diet and is independent of body size) and capacity of the digestive system (which scales with body size; Parra 1978, Demment and Van Soest 1985, Cork 1996).

In addition to allowing the utilisation of structural plant materials, a microbial fermenting gut presents a number of advantages which have been well recognised in the ruminants. In addition to bacterial cells, the fermentation products include short-chain volatile fatty acids (VFA’s), can both be utilised by the animal. Furthermore, gut microbes are capable of utilising non-protein nitrogen for growth, converting it to high quality protein the animal can use (Bauchop 1978). That is, there is evidence that urea can be recycled via the large gut (Thornton *et al* 1970) and that this urea can be converted, via ammonia, to microbial protein. This high-quality protein can be a valuable supplement to low-protein diets (Bauchop 1978).

Moreover, tropical browse contains a wide range of potentially toxic plant allelochemicals (Janzen 1978, Coley 1983, Waterman *et al* 1988), which can also affect the utilisation of both cell walls and cell contents (Hume 1989). Some gut microbes are capable of metabolising toxic plant compounds (Barry and Blaney 1987) and there is evidence that tannin-protein complexes can be broken down by microbial action (Milton 1978, Foley and Hume 1987). Additionally, ruminants that feed on browse have been shown to produce salivary proteins rich in proline, which complexes with tannins protecting other proteins from these plant allelochemicals, leaving them available for digestion (Robbins *et al* 1987, Hume 1989). It has been proposed that a symbiosis with detoxifying microbial populations may have been a critical adaptation for the exploitation of browse (Freudenberger *et al* 1989).

Dasilva (1992) postulated that forestomach fermentation allows colobine monkeys to detoxify fruits, leaves and seeds containing a range of potentially toxic ingredients, including cyanide and strychnine, before the toxins are absorbed.

2.5.2.1 The gastrointestinal morphology of tree-kangaroos

Tree-kangaroos returned to the trees when other members of the family were moving out to the grasslands (Flannery et al 1996). They have a gut morphology that appears to fit intermediately between the Potoroids and larger Macropodids, with a large sacciform forestomach and a relatively smaller tubiform forestomach (Hume 1982, 1999). This is similar to other browsing species of the forest, such as pademelons (*Thylogale* spp.), and other foregut fermenting arboreal folivores such as the colobine monkeys and sloths (Ohwaki *et al* 1974, Montgomery and Sunquist 1978, Bauchop 1978, Stevens and Hume 1995).

This sacciform morphology maximises retention of digesta for fermentation (Freudenberger *et al* 1989). On the other hand, a more tubiform morphology, such as in the large grazing kangaroos, leads to a less than maximal retention of digesta for fermentation (Hume 1989) with a greater flow rate, allowing a greater amount of plant material to be processed faster.

One way to compensate for limitations imposed by small body size is to reduce metabolic rate, and tree-kangaroos are reported to have lower metabolic rates than most other marsupials (McNab 1988). *D. matschiei's* metabolic rate is significantly lower (84%), than the value expected for like-sized marsupials, and only 55% of the value for a like-sized placental mammal (McNab 1988, Flannery *et al* 1996). In contrast to most mammals, *D. matschiei* can maintain a constant core temperature while lowering its metabolic rate as ambient temperatures drop. A number of other arboreal folivores, such as the red panda (*Ailurus fulgens*), show a similar metabolic pattern (McNab 1988).

It is not known if tree-kangaroo basal metabolism varies from species to species, but it has been suggested that lowland species would not face very low temperatures and hence would not need to conserve energy through a reduced metabolic rate to the same degree as montane species such as *D. matschiei* (McNab 1988, Flannery *et al* 1996).

Although there have been many studies in the gut morphology, capacity, physiology and digesta flow in macropods (Langer 1980, Langer *et al* 1980, Richardson 1980, Dellow and Hume 1982, Freudenberger *et al* 1989, Freudenberger 1992, Lentle *et al* 1998a, 2003a) and a few early descriptions of *D. lumholtzi* gastrointestinal morphology (Owen 1852, Hume 1982, 1999), little quantitative work has been done on tree-kangaroos.

Tree-kangaroos are foregut fermenting arboreal folivores and are believed to have similar gut morphology to other browsing kangaroos and to other arboreal foregut fermenting folivores. However, we do not presently know how specialised their gastrointestinal morphology is related to their arboreal lifestyle and high-fibre foliage diet. We would expect that they would have larger stomach capacities than grazing macropods for maximised retention of digesta.

2.6 AGE DETERMINATION IN TREE-KANGAROOS

The ability to determine age of individuals is an essential part of any study of the population dynamics of a species (Caughley 1977, Inns 1982). This information can then be used to construct life-tables for the estimation of age-specific mortality (Inns 1982) and may also be important in explaining the distribution of individuals of differing age in habitat of varying quality (Martin 1996).

Mammals can be aged by a variety of techniques, one at least of which is usually applicable to any species being studied (Caughley 1977, Inns 1982). Clues to age are provided by tooth eruption sequences (Sharman *et al* 1964, Driessen and Hocking 1996), tooth wear (Winter 1980, Martin 1981, Blanshard 1990, Gordon 1991, Martin *et al* 1999, Logan and Sanson 2002, Lentle *et al* 1998b, 2003a, 2003c), molar progression (Kirkpatrick 1964, Dawson 1995, Lentle *et al* 2003b, 2003c), size frequency classes, body size (Poole *et al* 1982, Gordon 1991, Johnson and Delean 2003), degree of epiphyseal fusion, lens weight, annual growth rings on claws or horns and in teeth and bones (Laws 1952, Kingsmill 1962, Klevezal and Kleinenberg 1967, Pekelharing 1970, Gasaway *et al* 1978, McCullough and Beier 1986, Cool *et al* 1994, Azorit *et al* 2002a, 2002b), and the number of placental or ovarian scars carried by females (Caughley 1977).

In macropodids, ages of pouch young have generally been estimated from body measurements (Shield and Woolley 1961, Sadlier 1963, Sharman *et al* 1964, Murphy and Smith 1970, Maynes 1972, Poole *et al* 1982, Poole *et al* 1985, Inns 1982, Blanshard 1990, Johnson and Vernes 1994, Johnson and Delean 2003). In older animals either the sequential eruption of the molars (Sharman *et al* 1964, Ealey 1967, Maynes 1972, Driessen and Hocking 1996) or the forward progression of the molar row along the jaw has been used (Kirkpatrick 1964, 1965, Hughes 1965, Sharman *et al* 1964, Dubzinski *et al* 1977, Dawson 1995, Lentle *et al* 2003c).

In addition, tooth eruption and the wear of the first and second upper molars have been used successfully as an age indicator in the ringtail possum *Pseudochirus peregrinus laniginosus* (Gould) (Thompson and Owen 1964) and in the brush-tailed possum, *Trichosurus vulpecula* (Kerr) (Winter 1980).

However, many of these techniques have their limitations. Body measurements, for example, are no longer useful for aging macropods once they are over 1 year old (Inns 1982, Johnson and Delean 2003). Furthermore, it is only possible to establish ages of macropods in the field using molar eruption sequence up to the eruption of the fourth molar, which occurs between 5 and 6 years of age (Inns 1982). After this age an animal cannot be aged using this technique. Despite this, Sharman *et al* (1964), Ealey (1967), Shield (1968) and Inns (1982) concluded that the sequence of molar eruption provides a useful means of determining the ages of macropods in the field. Variations in the timing of tooth eruption stages have also been observed in mule deer, *Odocoileus hemionus* (Robinette *et al* 1957) and Himalayan thar, *Hemitragus jemlahicus* (Caughley 1965).

An alternative to tooth eruption and replacement for ageing is to examine tooth wear. This technique has been widely and successfully used as an age indicator in koalas (Martin 1981, Gordon 1991, Logan and Sanson 2002). Unlike macropods, koalas do not have a deciduous dentition, nor do they show molar progression (Martin 1981, Lanyon and Sanson 1986a, Gordon 1991). The cheek teeth of the koala, comprising of a premolar and four molars (Lanyon and Sanson 1986a), have completely erupted by the time the animal reaches 18 months of age (Martin 1981, Martin *et al* 1999) and is similar to that found in tree-kangaroos (Groves, 1982, Flannery *et al* 1996). After this age there are no new teeth, just continual wear of the biting and grinding surfaces (the occlusal) of the existing teeth (Gordon 1991, Lanyon and Sanson 1986a, 1986b, Martin *et al* 1999). This wear continues until the enamel of the cutting ridges and pyramidal cusps is worn away completely (Martin *et al* 1999). The underlying dentine is then exposed and the characteristic wear patterns that appear can be used to assign age classes or indices of age to animals (Martin 1981, Gordon 1991, Lanyon and Sanson 1986b, Martin *et al* 1999, Logan and Sanson 2002).

It has been suggested, however, that tooth wear as an age indicator has two main sources of error: one being the variation of wear between individuals both within and between populations due to diet; the other is misreading of tooth wear classes by the observer (Winter 1980). The first would be dependant upon the size of the study area and the variation of the diet of the individuals (Winter 1980, Gordon 1991). The second error would be reduced by having one observer taking all of the readings (Winter 1980).

Estimations of age are subject to error (Caughley 1977), with some being worse than others. Indices that change by annual quanta give the most accurate estimates, particularly for adult animals, but they are not foolproof (Caughley 1977). Morphological characters that change continuously with age have a variability that automatically results in some aging errors. Tooth eruption is a good example because it is frequently used to age mammals.

2.6.1 Tooth cementum annuli

Since the early 1930's, the lines observed in growing tissues have been used to estimate the age of vertebrates (Azorit *et al* 2002b). Klevezal and Kleinenberg (1967) give a comprehensive review of the age-related stratification in tissues of teeth and bones.

The tooth annulation method, using either dentine or cementum annuli, is the most accurate means of age determination for mammal species (Thomas 1977) and has been used to age many different species (Laws 1952, Klevezal and Kleinenberg 1967, Gasaway *et al* 1978, Fancy 1980, McCullough and Beier 1986, Cool *et al* 1994, Azorit *et al* 2002a, 2002b), including marsupials (Pekelharing 1970, Clout 1982). In fact, tooth cementum annuli are currently the most widely used method for mammal aging (Fancy 1980, Azorit *et al* 2002a) and has been correlated successfully with known age (Laws 1952).

Although early attempts with marsupials were unsuccessful (Kingsmill 1962, Catt 1979, Inns 1982), recent improvements to the preparation and staining methods have resulted in an accurate and frequently used technique to age or to develop an age index for many marsupial species (Fancy 1980, Azorit *et al* 2002a).

Earlier studies, particularly those of marine mammals, used growth layers in dentine (Fancy 1980). However, dentine is deposited within the tooth and is spatially limited in its growth. Furthermore, it ceases in most mammals soon after the animal reaches maturity (Fancy 1980). In mammals that have limited growth of their teeth dentine does not show clear annual lines (Klevezal and Kleinenberg 1967).

Cementum layers, however, are more commonly used with terrestrial mammals (Fancy 1980). The root of the tooth is covered with cement, the thickness of which increases with time (Klevezal and Kleinenberg 1967). The cement is a mineralised fibrous organic substance, which unlike dentin contains cellular elements, the cementocytes (or bone corpuscles). The thickening of the cement results from the formation of new layers by the periodontium surrounding the root of the tooth in such a manner that the cement layers formed earlier are situated closer to the boundary between the dentin and cement, and the layers formed later are closer to the outer surface of the cement (Klevezal and Kleinenberg 1967).

In various species, the total thickness of cement and the breadth of the annual layers vary considerably as a result of differences in the size and character of the mechanical load exerted on the teeth. One indicator of this load is the rate of wear on the teeth. In many species, the intensive wear of the crown of the tooth is accompanied by the formation of broad layers of cement on the root (Klevezal and Kleinenberg 1967).

There are a wide variety of methods for the preparation of teeth for investigation of cementum annuli in different species (Azorit *et al* 2002a, 2002b) and these have been reviewed by Fancy (1980). It is important to first determine the best tooth to use, and which method for decalcification and staining will give the best results for each species being studied (Fancy 1980, Azorit *et al* 2002a). Decalcification times also vary within a species, with old and very young teeth taking less time to decalcify, possibly due to less calcium (Fancy 1980, Azorit *et al* 2002b).

2.6.2 Ageing in tree-kangaroos

Tree-kangaroos do not have molar progression, and tooth eruption and body measurements are only suitable for young animals, therefore, these techniques are limited in their use for ageing *D. lumholtzi*. Tooth wear and tooth cementum annuli are proposed as techniques for age determination in *D. lumholtzi*. The resulting tooth wear index could then be used to age other tree-kangaroo species, such as the more threatened species of New Guinea. Furthermore, the ability to age tree-kangaroos is essential if we are to perform population analyses such as population viability analysis, which would allow us to review their conservation status and determine future management guidelines.

2.7 SUMMARY

Seven of the ten species of tree-kangaroos from Papua New Guinea and Australia are listed as threatened or near threatened with extinction, with the remaining three species (in Papua new Guinea) listed as having insufficient data for risk assessment (IUCN 2004). Yet, our understanding of the ecology and basic biology of any of the tree-kangaroo species is still rudimentary.

Our current knowledge on the ecology of *D. lumholtzi* is based upon only a few previous studies of their home range, habitat use and behaviour. Unfortunately these studies, although valuable, were both performed on the same spatially restricted rainforest type (Procter-Gray 1985, Newell 1999b). Consequently, we currently have an incomplete understanding of spatial and habitat use by *D. lumholtzi* in different habitats.

Before we can evaluate the conservation status and population viability of *D. lumholtzi*, or any of the tree-kangaroo species with any accuracy, it is essential that we acquire more extensive data on their biology and ecology. The type of information that is necessary for any population analyses are: population densities in different fragments and continuous forest; expected lifespan, age-specific mortality and fecundity; age at maturity and reproductive rates; demographic stochasticity (random fluctuations in birth rate, death rate and sex ratio of a population); movement or dispersal between fragments or populations; genetic processes; and the effects of environmental stochasticity (Lacy 1993). We presently have little of this information and hence cannot conduct these analyses without the possibility of misleading results.

D. lumholtzi are primarily found in privately owned rainforest fragments on the Atherton and Evelyn Tablelands, which are not currently protected from clearing. These patches of rainforest are highly fragmented surrounded by a matrix of agricultural land. Therefore, habitat loss and fragmentation, dogs and cars threaten the long-term survival of *D. lumholtzi*.

From the earlier studies we know that *Dendrolagus lumholtzi* are solitary, territorial with descrete home ranges and have strong site fidelity (Procter-Gray 1985, Newell 1999b). It is currently unclear if habitat type or quality, floristic species composition, soil type, population densities or carrying capacities of fragments influence their home range sizes, whether home range size is correlated with body weight, and whether home range sizes would vary in continuous forest as opposed to fragments. There have been many proposals put forward about how they utilise their habitat such as that they prefer regrowth or successional habitat, prefer a variation in canopy height, and that they prefer the edge of the forest, to mention a few.

Dendrolagus lumholtzi are foregut fermenting arboreal folivores that consume a wide variety of rainforest species and are believed to be broad generalists. Although there have been a few early descriptions of *D. lumholtzi* diet (Procter-Gray 1984, 1985, Newell 1999b) and gastrointestinal morphology (Owen 1852, Hume 1982, 1999), little quantitative work or comparisons to other kangaroos and arboreal folivores has been done. An understanding of their gastrointestinal morphology and capacities will assist in our understanding of how they deal with their highly folivorous diet. Furthermore, a more comprehensive knowledge of their diet will enhance our understanding of how they utilize their habitat.

At present we cannot accurately age tree-kangaroos and the ability to age them using tooth wear will greater improve our ability to construct life tables and perform population viability analysis. This information can also be utilised by other researchers studying the more endangered species of tree-kangaroos in Papua New Guinea. In fact, any information acquired on the ecology of the Australian species will assist in the studies of the Papua New Guinea species, which are much more difficult to study due to the remoteness and difficult terrain in which they live.

Chapter 3: Study Site

3.0 STUDY SITE

This study was undertaken on a 50ha rainforest fragment at Jaggan (~800m above sea level, 17°23’51”S 145°36’16”E), 5km from Malanda on the Atherton Tablelands in far north Queensland (Figure 3.1). This area is part of the Wet Tropics bioregion (Sattler and Williams1999) in which some rain falls in most months of the year, but is highest between December and May (January average 1143.8mm), and averages 1670mm per annum (Malanda Post Office: Cairns Office of the Bureau of Meteorology, 2nd October 2003). The mean maximum daily temperature for the area is 26° C and the mean minimum daily temperature is 14.5° C, with the hottest period between October and April and the coldest between June and September.

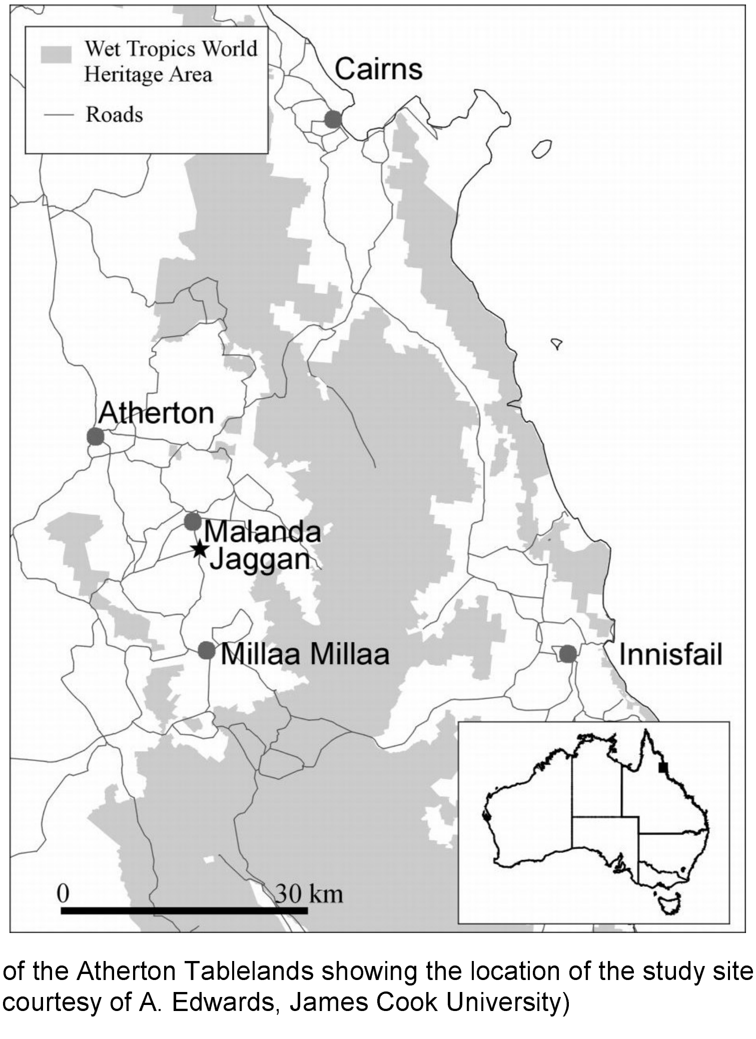


Figure 3.1 Map of the Atherton Tablelands showing the location of the study site at Jaggan near Malanda. (Map courtesy of A. Edwards, James Cook University)

Prior to European settlement, rainforest (particularly types 5a, 5b and 1b - Tracey 1982) covered much of the Tablelands (Winter *et al* 1987, Newell 1999a). Type 5b rainforest is a particular community that supported large stands of Queensland Red Cedar (*Toona ciliata*), which was a prized timber (Newell 1998, 1999a). This attracted the ‘cedar-getters’ to the tablelands in the 1860’s, first leading to selective logging, then to almost complete clearance for agriculture by the 1920’s (Frawley 1983, Winter *et al* 1987, Graham *et al* 1995). By 1980 over 76,000 ha of rainforest had been removed (Winter *et al* 1987), leaving only small scattered fragments of remnant and regrowth rainforest ranging from 1 to 600 ha (eg. Figure 3.2) (Laurance 1991, Newell 1998). There is less than 2.5% (<1000 ha) of Type 5b (complex notophyll vine forest; Tracey 1982) rainforest remaining today (Sattler and Williams1999). All previous studies on tree-kangaroos in Australia have been performed in Type 5b rainforest (Procter-Gray 1985, Martin 1992, Newell 1999b). Type 1b, Complex mesophyll vine forest (Tracey 1982) is also an endangered community with less than 10% of its original area remaining, however it is now more widespread than 5b rainforest.

The rich basalt soil where the majority of the rainforests were growing is still sought after today and clearing continues for cropping and grazing land, as well as timber. Therefore, *D. lumholtzi* are still considered threatened with habitat clearing and fragmentation.

The study site is a 65ha property comprising approximately 50ha of Type 1b rainforest (Tracey 1982: type RE7.8.2 Sattler and Williams 1999) fragment of complex mesophyll vine forest on basalt soil, set in a mosaic of agricultural land (Figures 3.2 and 3.3). It is separated from the neighbouring fragment (~ 40ha) only by the narrow Ithica River, with continuous canopy in some areas. There is also a large area of regrowth in the neighbouring property.

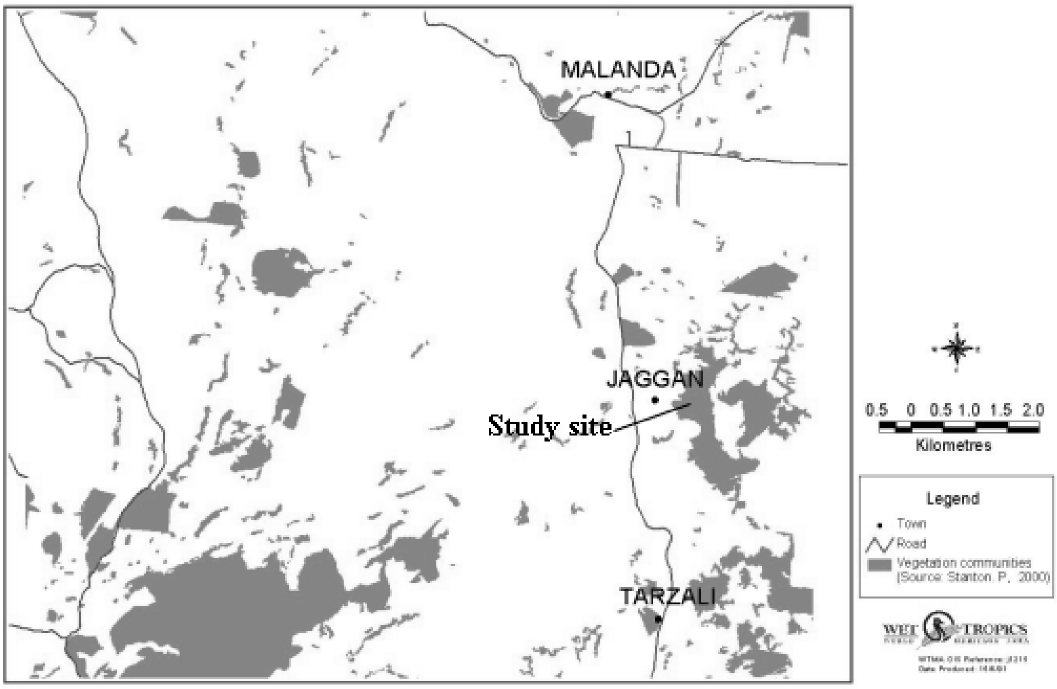


Figure 3.2. Area of the Atherton Tablelands in the region of the study site, showing fragmentation of rainforests remaining in the area. (Map courtesy of Wet Tropics).

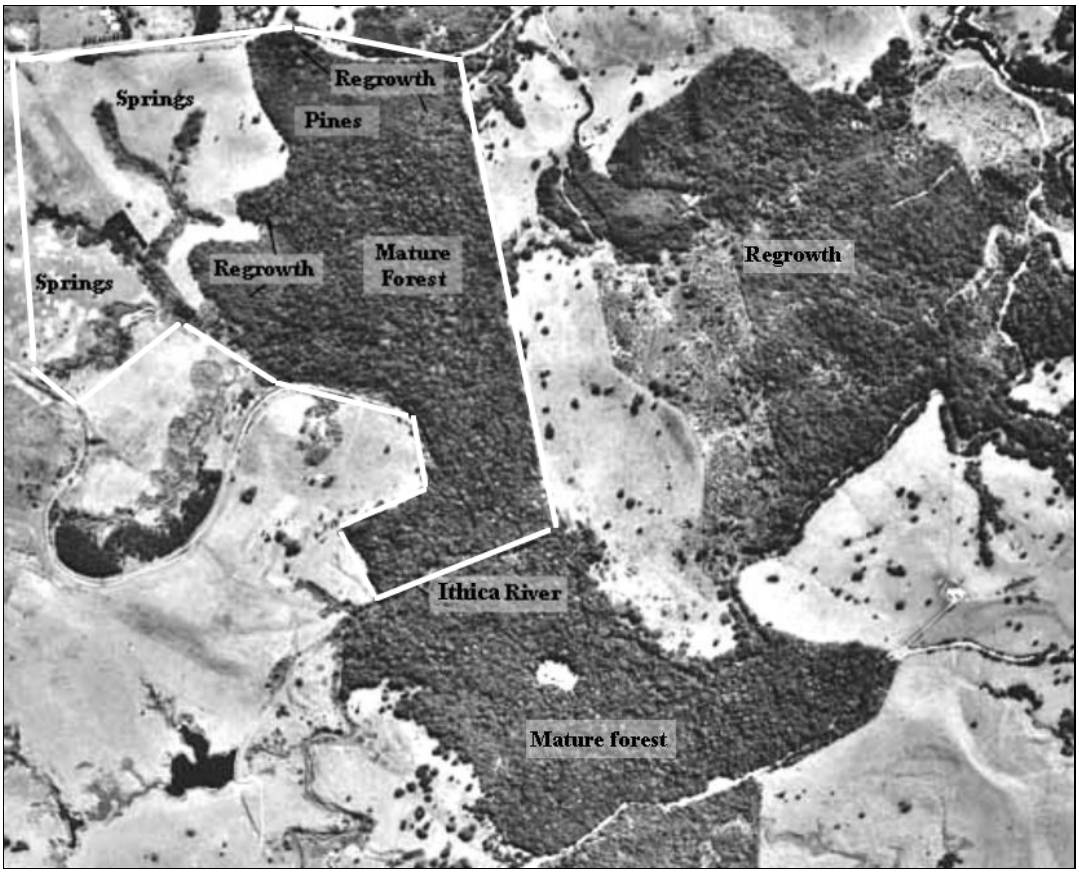


Figure 3.3 Aerial photo of study site and neighbouring fragment, separated by the Ithica River. Study area marked out in white. Also shown are the areas of regrowth, mature forest, pine forest and springs within the study site and area of regrowth to right of study site. (Photo - Queensland Department of Natural Resources).

The fragment itself is a complex mix of forest. It contains a large proportion of mature forest, sections of regrowth at the edge and also areas of riparian vegetation along the springs in the gullies (Figure 3.3). It also contains a section of pine trees, with an understorey of pioneer rainforest species (Figure 3.3). This site proved to be suitable for investigating habitat utilisation by *D. lumholtzi* as it is a complex mix of different habitats, all of which are being utilised by *D. lumholtzi.*

- **Mature forest**

A large proportion of the study site is mature Type 1b rainforest that was only selectively logged and has not been disturbed for approximately 40 years. Many of the canopy trees in this site are at least 30 - 45m tall. There is very little understorey, except for some seedlings and Lawyer cane or Wait-a-while vine that winds up into the canopy.

- **Regrowth**

There are three main areas of regrowth (totalling ~ 14ha) growing next to the mature forest (Figure 3.3). These areas have been allowed to grow back after clearing and are thought to be approximately 20 years of age. The canopy height in the regrowth varies from 10 - 25m, but can be up to 30m particularly in the gullies where there are creeks or springs. There is a large degree of understorey of seedlings and vines, and in some areas where there is lower canopy and more light reaching the floor, the weed *Lantana camara*. The dominant species in the regrowth are late successional species, such as *Guioa lasioneura* and *Alphitonia petriei*. There are also a large number of mature *Litsea leefeana*, which are secondary rainforest species. Some of the other late successional species in these areas are: *Flindersia brayleyana, Glochidion hylandii* and *Neolitsea dealbata.*

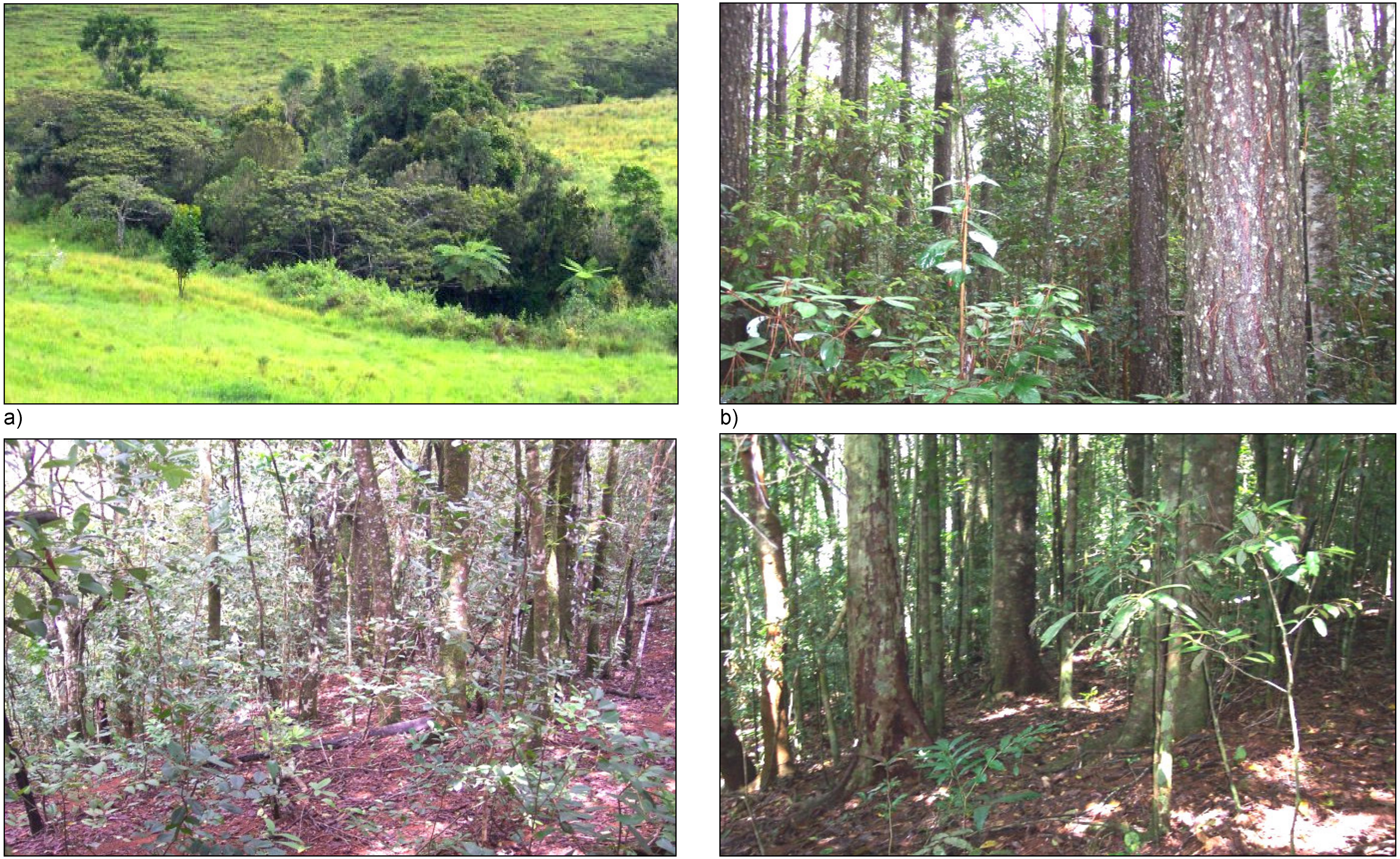
- **Riparian habitat surrounding the springs**

There are several springs in the gullies within the property and neighbouring property, which maintain running water all year round. These springs contain riparian habitat dominated by early secondary species such as *Alphitonia petriei* and *Guioa lasioneura*, and also contains a large amount of weeds such as

Lantana camara. They do, however, contain the occasional large mature rainforest canopy species such as *Ficus crassipes, Flindersia spp* and *Caldcluvia australiensis* up to 20m in height. There are also a number of tree ferns (*Cyathea cooperi).* Overall the canopy is discontinuous with areas of only weed cover between clumps of trees and vines. There is some connectivity between the riparian habitat and the mature forest (Figure 3.3).

- **Pine forest**

The pine forest plantation (*Pinus caribaea*) was planted approximately 25 years ago. It now consists of a large number of pioneer rainforest species in the understorey, as well as some emergent species such as *Alphitonia petriei* amongst the pine trees, reaching approximately 25 - 30m in height. There are also a large number of Stinging trees *Dendrocnide cordifolia* and *Lantana camara* in the understorey.



a) b) c) d)

Figure 3.4. The four different habitats in study site: a) riparian vegetation surrounding one of the springs, b) pine forest, c) regrowth, d) mature forest.

Chapter 4: Spatial organisation of Lumholtz's tree-kangaroo in a rainforest fragment on the Atherton Tablelands.

4.0 INTRODUCTION

Understanding the use of space, and how this relates to habitat is important to the conservation and management of rare species.

While not currently considered endangered, Lumholtz's tree-kangaroos are classified as rare under Queensland's *Nature Conservation (Wildlife) Regulation* (1994). Although the distribution of *D. lumholtzi* is believed to be from Mt Carbine Tableland to the Cardwell Range (Flannery *et al* 1996, Newell 1999b), they are most commonly found in fragmented rainforests that feature fertile soils on the Atherton and Evelyn Tablelands, where their long-term persistence is threatened by land clearing and mortality from dogs and vehicles (Newell 1999b, 1999c). The increasing fragmentation and loss of suitable habitat is likely to lead to a further significant decline in their numbers, forcing a reclassification of the species amid increasing concern for its future (Newell 1999a). Therefore, to ensure the conservation and management of remnant populations of *D. lumholtzi*, it is important to understand their spatial use of habitat.

Lumholtz's tree-kangaroos can be quite abundant in regrowth and fragmented rainforest, especially those on fertile soil types, although we do not yet understand why (Newell 1998, 1999a, 1999b, Kanowski *et al* 2001a). Whether this is due to high habitat quality, a preference for early successional species, or a tendency to build up unnaturally high numbers in these fragments due to surrounding disturbance events is not totally understood.

Moreover, there is no information with which to assess the long-term viability of small populations in fragments, or whether they regularly range between fragments. Consequently, it is crucial that research be conducted to find out more about the habitat requirements of *D. lumholtzi* in order to ensure its long-term conservation (Newell 1998).

Although there have been some studies on the home ranges and habitat utilisation of Lumholtz's tree-kangaroos (Procter-Gray 1984, 1985, Newell 1999a, 1999b) as well as their responses to habitat loss (Newell 1999c) and fragmentation (Pahl *et al* 1988, Laurance 1989, 1990, 1996, 1997, Laurance and Laurance 1996, 1999), our understanding of their population dynamics, ecology and basic biology is still rudimentary (Newell 1999a).

Both Bennett's tree-kangaroos and Lumholtz's tree-kangaroos are largely solitary and territorial (Procter-Gray 1985, Martin 1996, Newell 1999b). Social interactions are limited to the relationship between a female and her young, brief interactions between males and females for mating purposes, and occasional territorial disputes between males (Procter-Gray 1985, Newell 1999b). Tree-kangaroos are one of the few macropods that defend a home range or territory, the sizes of which vary between species and individuals (Procter-Gray 1985, Martin 1992, Newell 1999b). Home range size has been suggested to reflect the vigour and status of the occupants (Martin 1992, 1996) and possibly the habitat type and quality (Newell 1999b), but the relationship is not yet totally understood. Body weight has also been shown to have a positive relationship with home range sizes in many animals (McNab 1963, Milton and May 1976).

The few previous studies done on this species determined home range in an extremely spatially restricted rainforest type (Complex Notophyll Vine Forest, CNVF on basalt substrate; Type 5b: Tracey 1982; Procter-Gray 1985, Newell 1999b). Interestingly, ranging behaviour of Bennett's tree-kangaroos is also only known from this rainforest type (Martin 1992). CNVF previously covered the Atherton Tableland north and west of the township of Malanda. However, there are now only a few fragments remaining, comprising < 1000 ha in total extent, thus CNVF is considered an endangered community (Sattler and Williams 1999). Consequently, it is unlikely to provide a good representation of the use of space by *D. lumholtzi* across its range.

In addition, both studies of *D. lumholtzi* on the Atherton tablelands were undertaken only a few hundred metres apart (Proctor-Gray 1985, Newell 1999b). These studies found that individual Lumholtz's tree-kangaroos used small home range areas within their fragmented rainforest habitat. Male home range sizes were significantly larger than those of females, did not overlap with other males, but did overlap with several females. Female home ranges did not overlap with other females.

This present study of ranging behaviour is the first performed in a different and more widespread rainforest type (Complex Mesophyll Vine Forest on basalt; Type 1b: Tracey 1982), allowing consideration of habitat-related variability in movements and spatial requirements of *D. lumholtzi,* and providing information that is relevant to a much greater area of *D. lumholtzi's* range.

4.1 METHODS

4.1.1 Animal capture and location

Eight animals (3 males and 5 females) were captured between January 2001 and November 2001 using a tranquiliser dart gun (Black Wolf; Tranquilarms) and 0.5ml mini-darts containing a tranquiliser (Zolazepam and Tiletamine 50:50, 60mg per individual in 0.2 ml; Zoletil 100, Virbac (Australia) Pty Ltd.). Tree-kangaroos proved difficult animals to find and collars were therefore fitted opportunistically. Additionally, animals were only darted if they were lower than 10m high in the canopy for the safety of the animal. Five to ten minutes after successful darting tree kangaroos lost their hold on the branch and fell into a large net set directly below them. No animals were injured during capture.

After capture the animals were restrained in a hessian bag and given an intra-muscular injection of diazepam (Pamlin, Parnell Laboratories (Aust) Pty Ltd, 1mg/kg) to provide a smoother recovery from the tranquiliser. Each animal was weighed, sexed, measured and radio-collared using a two-stage transmitter with 18 month battery life contained in a double-ended aluminium housing and attached to a food grade flexible plastic collar (Figure 4.1: Microlite 2-stage transmitter weighing 90gm; Titley Electronics Pty Ltd.). Collars were sewn closed at the appropriate size with waxed cotton to allow eventual breakage.

Measurements recorded were body length (mm) (from crest of head to base of tail), head length (mm), head width (mm), tail length (mm), hind foot length (mm), hind foot width (mm), forearm length (mm) (from elbow to wrist), hind leg length (mm) (from knee to ankle), testis length and width (mm) and ear length and width (mm).

Each animal also had a PIT (Passive Induced Transponder; Destron Fearing Corporation 1997 - Life Chip Animal Electronics I.D. Systems, NSW) tag implanted subcutaneously and suprascapularly and ear tagged to allow identification if the collar was lost. Transmitters were marked with individually colour coded reflective tape to aid in identification at night. Animals were kept for three hours for recovery before being released at the capture site.

Each animal was located using a Regal 2000 Telemetry receiver and a Yagi antenna (Titley Electronics Pty Ltd.). Location attempts were made twice a day for the first few days after capture and then at varying times of day or night, on a daily basis until several animals were being tracked at one time, then every two days or weekly until the collar came off. If the focal animal moved before sighting the fix was not used in the analysis. The position was determined by GPS (Garmin 12CX, Garmin Corporation) with accuracy better than ±10m. Generally, only locations where animals were visually confirmed were recorded. Locations were visually confirmed in >96% of cases. In the remainder the location was determined by triangulation to within 10m. After location was determined, date, time, height in canopy, tree species, and presence of other tree-kangaroos were recorded.

Figure 4.1. a) Sedated *D. lumholtzi* being measured and radio collared after capture. b) *D. lumholtzi* in hessian bag being weighed. c) Animal being checked before release. d) Tracking animals. e) *D. lumholtzi* with radio collar being tracked. Note how difficult it is to see the second animal (to the left).

4.1.2 Analysis of home range

It is difficult to compare home range sizes from different studies because different techniques are often used to analyse home range areas (see Croft 1989, Troy and Coulson 1993) and different software packages have been shown to give varying results for the same data (Gallerani Lawson & Rodgers 1997). For this present study, home ranges were calculated with the Harmonic mean method (Dixon and Chapman 1980) and Minimum Convex Polygons using the computer software Ranges V (Kenward and Hodder 1995) to allow comparisons with the studies of Procter-Gray (1985) and Newell (1999b).

Calculating home range sizes from 20-99% harmonic mean, and estimating the proportional change for each 5% increment allowed determination of the core range or centre of activity for the animals. Core range was defined as the isopleth where the proportional increase in range size was minimised (Johnson 1991) when locations are incrementally added (Figure 4.2). In addition, 90% was calculated as a comparison to Newell's (1999b) study. Minimum convex polygons were also calculated for each animal as Proctor-Gray (1985) had used this technique.

For accurate estimation of home range size there must be a sufficient number of locations in the area used by an animal such that new locations do not increase the range size (Harris *et al* 1990). Harris *et al* (1990) suggested that 30 or 40 locations would be adequate in most cases.

To determine the number of observations required to define home range sizes, the cumulative home range area was calculated for randomly selected subsets of locations from each animal and plotted against the number of locations, according to the procedure of Harris *et al* (1990). These were inspected visually to estimate the minimum number of sightings required to determine home range sizes (Figure 4.3). In this study there was variation in the number of fixes obtained for each animal because some animals proved difficult to locate and it was also difficult to keep collars on some animals.

One female tree-kangaroo (Simone) was rescued after being hit by a car, radio-collared and relocated to the study site, during this study and she was included in the investigation of home range use. However, as she was initially settling into the new locale, her first ten locations (5 days) after release were not included in the analysis. After this time, Simone remained in a certain area of the forest and did not make large movements as she had during the first five days.

Statistical analyses were performed using Statistica (Softstats Incorporated 1993). The differences between male and female home ranges from this study and Newell's study (1999b) were tested using Student's t-tests. Homogeneity of variance was tested using F-tests. The relationships between body size and home range size from this and Newell's (1999b) study were investigated with Pearson's product moment correlation analysis.

4.1.3 Activity and daily movements

Observations were made on the activity of *D. lumholtzi* during radio tracking, such as whether the animal was eating or sleeping. In addition, if locations were made more than once a day, movements during this time were recorded and the distance travelled calculated using Ranges V (Kenward and Hodder 1995).

4.2 RESULTS

4.2.1 Core areas and number of sightings

The animals in this study had two core areas of activity within their home range, at the 55% harmonic mean and at the 75% harmonic mean levels (Figure 4.2). These levels, 55% and 75%, were used (along with 90% HM) to calculate home range sizes.

The minimum number of sightings required allowing accurate home range sizes averaged 41 ± 5.5 (se). The home range area of each animal reached a plateau at or before the number of locations collected (eg Figure 4.3).

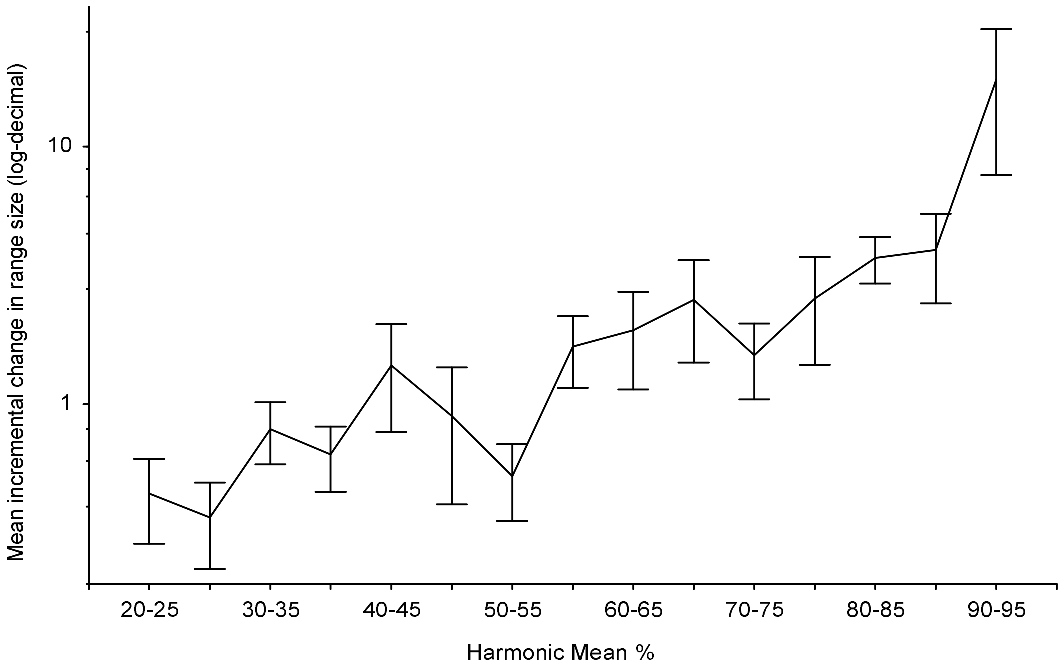


Figure 4.2. Core areas for *D. lumholtzi* from this study (mean ± se) were estimated by analysing the proportional incremental increases (log-decimal) in home range for 20-90% HM.

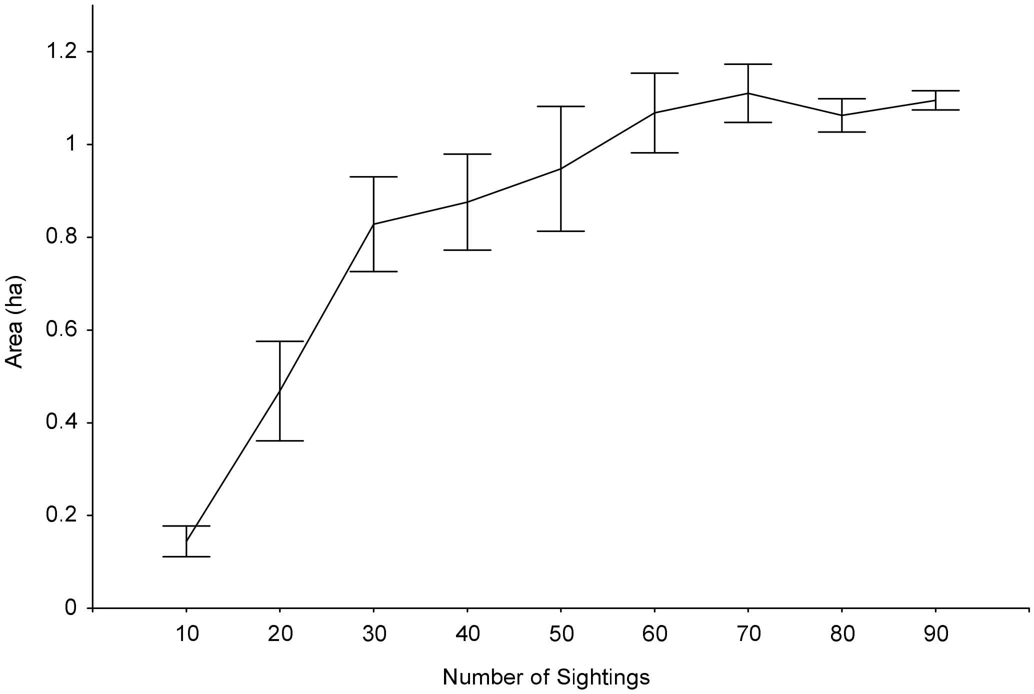


Figure 4.3. Number of sightings required at 90% harmonic mean (mean ± se) to accurately estimate one male's (Colin) home range. For this animal an asymptote was reached at around 70 sightings.

4.2.2 Home range sizes

In this study the average home range size for male *D. lumholtzi* in 1b rainforest was 2.09 ± 0.68ha (90% HM, range 1.08 – 3.38ha, *n* = 3, Figure 4.1). Female *D. lumholtzi* had an average home range (90% harmonic mean) of 2.14 ± 0.8ha, with a large amount of variation (range 0.11 – 4.85ha, *n*=5).

There were no spatial overlaps in range between adult females, or adult males in this study (Figure 4.4), but the 3 males did overlap with females.

There was no significant difference between the size of male home ranges in this study and those found in 5b forest (Newell 1999b, *t* = 0.36, *df* = 6, *P* = 0.74; Table 4.1). Neither were there statistically significant differences between the home ranges of females in this study (2.14ha) and Newell's (1999b: 0.7ha) (*t* = 1.75, *df* = 4, *P* = 0.16; T-test with unequal variances, Table 4.1) even though the average value for female home range size (2.14ha) was larger than Newell's females (1999b: 0.7ha). This was due to the greater variance in female home ranges in this study (*f* = 17.97, *df* = 9, *P*= 0.004).

Unlike Newell's (1999b) results, the female and male home ranges (90% harmonic mean) in this study were not significantly different (*t* = -0.04, *df* = 6, *P* = 0.97, Table 4.1).

Newell (1999b) found that the home range sizes using minimum convex polygons (females: 0.58 - 2.11ha; males: 1.96 - 3.42ha) were similar to those of Procter-Gray's (1985) animals (females: 1.2 - 2.6ha; male: 4.4ha). The male home ranges in this study were also similar with no significant difference to Newell's (1999b: *t* = -0.40, *df* = 6, *P* = 0.7; table 1). However, using this measure of range also, females in this study were more variable than in Newell's (1999b) study (0.2 – 15.8ha, this study vs. 0.6 – 2.1ha, Newell 1999b, *f* = 125.3, *df* = 9, *P* = <0.001).

Table 4.1. Home range (ha) of *D. lumholtzi* in 1b forest with comparison to Newell's (1999b) 5b animals using 55%, 75% and 90% harmonic means (HM) and Minimum Convex Polygons (MCP). Values = Mean ± SE, *n* = number of animals. Values for 55% and 75% HM for 5b are not known.

	55% HM Area (ha)	75% HM Area (ha)	90% HM Area (ha)	MCP
1b Male range (*n* = 3)	0.24 - 1.15	0.59 - 2.19	1.08 - 3.38	1.72 - 4.17
1b Male mean ± SE	0.73 ± 0.26	1.35 ± 0.46	2.09 ± 0.68	3.06 ± 0.72
5b males - range (*n* = 5)			1.38 - 2.99	1.01 - 3.42
5b males - mean ± SE			1.95 ± 0.29	2.80 ± 0.29
1b Female range (*n* = 5)	0.01 - 1.21	0.03 - 2.76	0.11 – 4.90	0.20 - 15.81
1b Female mean ± SE	0.55 ± 0.22	1.41 ± 0.54	2.14 ± 0.80	5.31 ± 2.84
5b females - range (*n* = 6)			0.34 - 1.53	0.58 - 2.11
5b females - mean ± SE			0.69 ± 0.17	1.06 ± 0.23

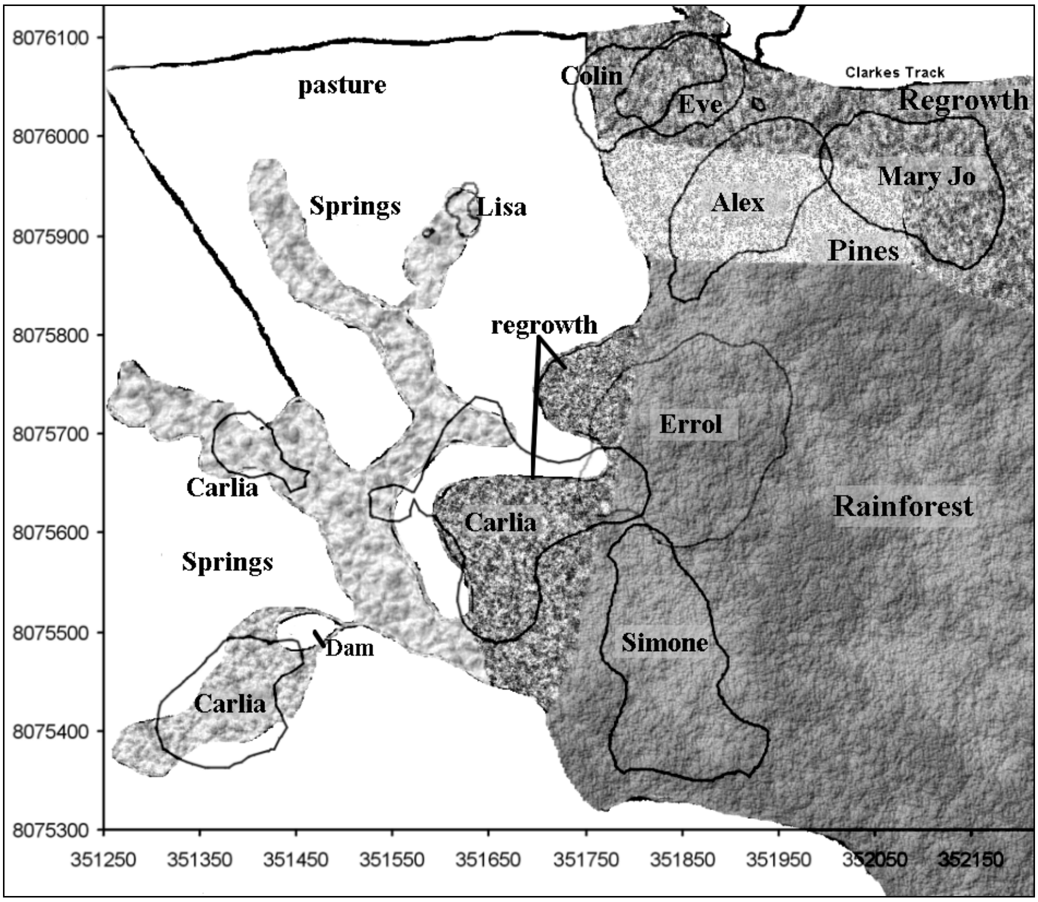


Figure 4.4. Study site showing home ranges of all 8 animals at 90% harmonic mean.

4.2.3 Body weight and home range size

There was no difference between the masses of radio-tracked adult male and female *D. lumholtzi* in this study (t = 0.19, df = 5, P = 0.86) with male averaging 6.6 ± 0.48kg (6.0 – 7.55kg, n = 3) and females 6.77 ± 0.69kg (4.83 – 7.82kg, n = 4).

There were no significant correlations between body weight and home range size in either males or females in this study.

Furthermore, there was still no relationship when males from both 5b and 1b forest were combined for the analyses (r = 0.19, P = 0.63, n = 8; Newell 1999b, this study) or when both males and females from both studies were combined (r = -0.007, P = 0.98, n = 18).

The females of both *D. lumholtzi* and *D. bennettianus* showed no significant correlations between home range size and body weight when data from all three studies were combined (Martin 1992 n =2, Newell 1999b n = 6, this study n = 5).

4.2.4 Activity and daily movements

Unlike earlier observations (Proctor-Gray 1985; Newell 1999a 1999b) where animals have been reported to be mostly nocturnal, the animals in this study were observed to be active, eating and moving within their home range during the day.

Daily movements were variable. One male (Colin) was recorded moving when radio-tracked twice in one day (morning and afternoon) on five occasions, averaging 110.8m ± 21 (se), with one movement of 136m in one hour. Another male (Errol) was recorded moving during the day on three occasions, averaging 84.7m ± 13.1 (se), including a movement of 109m in a four-hour period on one occasion.

Females were not observed moving great distances like males during the day, except for foraging in early morning and later afternoon. One female (Lisa) and her offspring, inhabiting the riparian habitat surrounding the spring, moved regularly each morning and afternoon from one side of the home range to the other, on one occasion moving 43m within 3 hours.

4.3 DISCUSSION

4.3.1 Comparison of home range sizes and densities

It has been suggested that Complex Notophyll Vine Forest (Type 5b: Tracey 1982) fragments appear to support unusually high densities of tree-kangaroos (Newell 1999a, 1999b), while individual tree-kangaroos are likely to require much larger home ranges elsewhere, especially in rainforest fragments with less fertile soils (Kanowski *et al* 2001a, 2001b).

This study has shown that the home ranges of *D. lumholtzi* are similar in both rainforest types (Type 5b, CNVF: Newell 1999b and Type 1b CMVF: this study), both on basalt substrates. However, male and female home ranges were not significantly different in this study, as they were in 5b rainforest type (Newell 1999b). There was, however, a large degree of variation in the female *D. lumholtzi* home range area in Type 1b rainforest, which makes it difficult to compare statistically.

This variation in female home range area is an important finding. As *D. lumholtzi* females have exclusive home ranges, their home range sizes and density are inversely proportional. *D. lumholtzi* are believed to be polygamous (Flannery *et al* 1996), therefore the reproductive potential for the population will be set by the density of females (Begon *et al* 1986).

The home range sizes of *D. bennettianus* are much larger than that found in the spatial studies of *D. lumholtzi* (Newell 1999b, Proctor-Gray 1985), in the same rainforest type and substrate. Furthermore, there was a great deal of variation found in the ranging behaviour of *D. bennettianus*, especially in males (Martin 1992; Table 4.2).

Martin (1982) has suggested that this is likely due to the fact that the study site for *D. bennettianus* was connected to continuous lowland rainforest and not an isolated fragment as with the *D. lumholtzi* studies on 5b forest (Proctor-Gray 1985, Newell 1999b), hence the animals can spread out. He has also suggested the larger home range sizes for *D. bennettianus* may be due to hunting pressure in the past (Martin 1992) with animals spreading themselves out to avoid predators or hunters.

There have been no published studies on spatial use by tree-kangaroos in New Guinea, with the exception of an observation of 25ha for a single *D. matschiei* of unknown sex (Flannery *et al* 1996). However, Betz (2001) estimated the density of *D. matschiei* using DISTANCE sampling analysis of scats and found the species to have densities of 0.9 – 1.0 animals/ha. Betz (2001) suggests that these densities are similar to the densities found in the Australian tree-kangaroos. *D. matschiei* densities fall between the densities of the two Australian tree-kangaroo species (0.3/ha for *D. bennettianus*: Martin 1992, 1.5/ha for *D. lumholtzi*: Newell 1999b). This shows that there is not only variation in home range sizes (or densities if home ranges are exclusive) within species, as seen in this study, but there is also variation between tree-kangaroo species.

This variation has also been found in other arboreal folivores (Table 4.2), such as koalas, possums, leaf eating monkeys (*Colobus,* and *Presbytis*), howler monkeys (*Alouatta* spp) (Milton and May 1976, Estrada 1984) and tree-sloths (*Bradypus* sp) (Montgomery and Sunquist 1978), which also show a great deal of variation in densities and home range sizes both within and between species.

Some species are able to reach very high densities (Table 4.2), due to the fact that arboreal folivores have abundant and concentrated resources available to them, along with their relatively low metabolism and sedentary lifestyle (McNab 1988, Betz *et al* unpublished data a). For example howler monkeys (*Alouatta* spp.) can reach densities of >1 animal /ha (Milton and May 1976, Estrada 1984), red colobus monkeys (*Piliocolubus* spp.) can occur in densities as high as 3 animals/ha (Chapman *et al* 1999), and smaller more solitary folivores like three-toed sloths (*Bradypus* spp.) can reach densities of up to 7 animals/ha (Montgomery and Sunquist 1978, Chiarello 1998).

4.3.2 Body size and home range area

Attempts to describe the variation in home range sizes in animals has led to the argument that home range size should increase linearly with body size (Harestad and Bunnell 1979) and this is certainly true for many mammals (McNab 1963, Milton and May 1976, Harestad and Bunnell 1979, Lindstedt *et al* 1986, Troy and Coulson 1993) including macropods (Fisher and Owens 2000). Croft (1989) suggests that comparable home range areas could be expected for species of similar size, social structure and ecological niche. However, the highly 3-dimensional world of the tree-kangaroo, as with all arboreal folivores, makes it difficult to compare with the traditional body size/home range size relationships. Furthermore, territoriality in tree-kangaroos would mean that a smaller home range is easier to defend than a larger one, so there could be some energy trade-offs between the two.

D. bennettianus are approximately 1.5 times the size of *D. lumholtzi* (8kgs vs. 13kgs) and in general their ecology appears quite similar, however they have a much larger home range than *D. lumholtzi* in the same rainforest type (Martin 1992, Newell 1999b: Table 4.2). Martin (1996) suggests that there was a linear relationship between body size and the size of the territory occupied by adult male *D. bennettianus* and that the difference was due to the relative vigour of individuals. However, it should be noted that samples were relatively small (Martin 1992: $n = 3$).

In contrast, male *D. lumholtzi* did not show any relationship between body mass and range size (Newell 1999b, this study).

Males in Newell's (1999b) study were larger than females. This was not the case in this study, with males and females showing no significant difference in body weight. The results of this study suggest that this species may not be sexually dimorphic (see Appendix 1).

There was no relationship between home range size and body mass in female *D. lumholtzi* either. Therefore, body mass cannot explain the variation in home range size found in female *D. lumholtzi* in this study.

Troy and Coulson (1993) found that variation in home range size between three macropod species of similar size - *Wallabia bicolor, Macropus rufogriseus* and *Macropus parryi* - is not explained by body size. The different niches occupied by these species supports the view that factors such as habitat, social organisation and diet may also influence home range area (Milton and May 1976, Troy and Coulson 1993).

4.3.3 Habitat quality

Inter-specific and intra-specific variation in home range sizes in macropods has usually been attributed to body size, diet and habitat quality or type (Jarman *et al* 1991, Fisher and Owens 2000).

The concept of habitat quality explaining variation in densities or home range size in animals is one favoured by many researchers (Milton and May 1976, Newell 1999b). It has been suggested that home range size is a function of the interaction between habitat productivity and resource distribution and individual energy requirements (Harestad and Bunnell 1979, Fisher 2000).

Variation in home range size in possums has been reported to be related to habitat, specifically to the number of home trees available (How 1978, How and Hillcox 2000). Similarly, variation in Howler monkeys (*Alouatta* spp) has been related to habitat variables and floral species present (Palacios and Rodriguez 2001). There have also been significant relationships found between the distribution of koalas and the structural and floristic characteristics of the vegetation (Hindell and Lee 1987).

Koalas have been found to have very different home range sizes in different habitats, ranging from 1.2 ha in sclerophyll forest to 190 ha in brigalow country, which is considered poorer or more marginal habitat for the species (Mitchell 1990, Melzer 1995). This may also be the case in tree kangaroos but information on other habitat types or different soil types is not yet available.

Newell (1999b) believes that habitat quality has an effect on tree kangaroo densities and home range sizes. This is supported by Kanowski (1999) and Kanowski *et al* (2001b), who believe that the relative abundance of *D. lumholtzi* on fertile soils appears to be a response to the higher nutritional quality of the foliage.

Table 4.2: Comparison of the home range sizes of Lumholtz's tree-kangaroos and other arboreal folivores. HM, Harmonic Mean Method; MCP, Minimum Convex Polygon; MAE, Minimum Area Estimate; DISTANCE, indirect faecal sampling; M = male, F = female; N/A = not available; Home range area is shown as "range" except where mean ± SD or $^{\#}$ mean were available.

Species	Mass (kgs)	Method	Home Range (ha)	Density (no/ha)	Reference
Dendrolagus lumholtzi	4.8 - 7.8	90% HM	1.1 - 3.4 M (2.1 ± 0.7) 0.11 - 5.6 F (2.1 ± 0.8)		This study
		MCP	1.7 - 4.2 M (3.1 ± 0.7) 0.2 - 15.8 F (5.3 ± 2.8)		This study
	6.0 - 7.5	90% HM	1.4 - 3 M 0.3 – 1.5 F	1.5	Newell (1999b)
		MCP	1.0 - 3.4 M 0.6 - 2.1 F		
	7.0 - 9.0	MCP	4.4 M 1.2 – 2.6 F		Proctor-Gray (1985)
D. bennettianus	10.5 - 13.5	95% HM	3.8 - 29.8 M (n = 3) 5.5 - 9.8 F (n = 2)	0.3	Martin (1992)
		MCP	6.4 – 40.0 M 3.7 – 8.3 F		
D. matschiei	9.0[1]	DISTANCE	N/A	0.9 - 1.0	Betz (2001), Betz *et al* (unpub a)
Phascolarctos cinereus (koala)	10.0 F 13.0 M	No of trees	3 - 11.5 trees 1.0 - 2.5 ha	1.0 - 3.0	Eberhard (1972, 1978)
	8.5 -12.0	90% HM	1.7 ± 1.0M 1.2 ± 0.7F	0.7 - 6.2	Mitchell (1990)
		N/A	190 ($^{\#}$ 86.5) M 102 ($^{\#}$39.2) F		Melzer (1995)
		95% Kernel	34.4 ± 11.8 M 15.0 ± 29.4 F		White (1999)
		95% HM	135.6 ± 76.6M 101.4 ± 67.1F		Ellis *et al* (2002)
Pseudocheirus peregrinus (ringtail possum)	07 - 1.0	N/A	$^{\#}$0.4 0.8 M, 0.5 F	10.0	How (1978) Crawley (1973)
			3.0 M, 1.1 F 7.4 M, 5.7 F		Dunnet (1964) How (1972)
Hemibelideus lemuroides (Lemuroid ringtail possum)	0.8 - 1.1	MCP	0.6 ± 0.1		Wilson (2000)
Trichosurus vulpecula (Brushtail possum)		N/A	2.6 ± 0.4 M 4.6 ± 1.7 F	0.4	Sampson (1971)
	2.0 - 2.8	MAE	0.3 - 3.2		Ward (1978)
		MAE 90%	7.4 ± 0.7 M 4.7 ± 0.9	0.4	How (1981)
	1.2 - 4.5	MAE 50%	1.1 ± 0.1 M 0.9 ± 0.7	3.0	Kerle (1998)
	1.8 - 2.6	95% HM MCP	13.7 ± 5.5 11.8 ± 3.4	1.2	Scrivener (2000)
		MAE	0.3 - 4.9 M (2.2 ± 1.3) M 0.1 - 4.3 F (1.3 ± 1.3) F	2.0 - 3.0	How & Hillcox (2000)
Bradypus torquatus (three-toed sloth)	5.7 - 6.7	MCP MAE	2.8 - 5.9 ($^{\#}$4.5) 0.5 - 0.7 ($^{\#}$0.6)	6.0 - 7.0	Chiarello (1998)

[1] D. matschiei weight taken from Flannery *et al* (1996).

Procter-Gray (1985) suggests that the size of the home range of female *D. lumholtzi* may be determined by the amount of food needed by females and their dependents. In eutherian mammals, the ultimate reason for female spatial patterns, and thus mating systems, is often variation in food patchiness or quality (Clutton-Brock 1989, Fisher and Owens 2000). This has also been suggested for spatial requirements in female koalas, where food trees are likely to be the limiting resource for survival and successful rearing of young (Hindell and Lee 1988). Female koalas in Hindell and Lee's (1988) study also showed considerable variation in home range size. This could also explain variation observed in female *D. lumholtzi*.

4.3.4 Hunting or predator pressure

In contrast, Martin (1996) postulated that sparsely distributed resources may not be the factor influencing the use of space in female *D. bennettianus*, but in fact, that it may be the legacy of predator or past hunting pressure that is forcing them to space themselves out through the forest. This has also been postulated for high densities and increased social behaviour in New Guinea tree-kangaroos, where there are more animals in areas where there is little or no hunting pressure (Flannery *et al* 1996, Betz *et al* unpublished data b). There is no evidence that hunting pressure has influenced the distribution and abundance of *D. lumholtzi*.

4.3.5 Females as resources and territoriality

It has been postulated for eutherian mammals that exclusive territories in conjunction with small home range sizes in females allows males to monopolise female territories, promoting the evolution of monogamy (Komers and Brotherton 1997, Fisher and Owens 2000), or polygyny when a single male is able to control a small group of territorial females (Hixon 1987, Fisher and Owens 2000). Female mammals are expected to minimise their home ranges, especially in a heterogeneous habitat, to enable them to forage widely enough for sufficient food but suffer minimum predatory risk or energy expenditure (Fisher and Owens 2000).

This is supported with the idea that male tree-kangaroo home range sizes appear to be related to their age and vigour, and reflecting their status and the number of females with which they are able to maintain contact (Procter-Gray 1985, Martin 1996). This is also consistent with many other studies of social organisation in mammals where the consensus has been that the spatial organisation of males is affected by female space use, as a male's reproductive success is dependent on the number of mates he can find and defend (Clutton-Brock 1989, Komers and Brotherton 1997, Fisher and Owens 2000). That is, females usually set the agenda and males do whatever is necessary to gain access to them (Martin 1996). This has been also found in koalas, where the complex shapes of male home ranges may be a reflection of the males' attempts to overlap the home ranges of several females (Hindell and Lee 1988).

However, males searching competitively for receptive females should not necessarily be larger in body size than females, but they should have larger home range sizes (Fisher and Owens 2000). This is partially consistent with the findings of this study, where there is no significant difference in body mass of *D. lumholtzi* males and females (Appendix 1). However, there was also no significant difference in average home range sizes of males and females in this study.

4.3.6 Population density

It is believed that the abundance and evenly dispersed nature of an arboreal folivore's diet, combined with their typically low metabolic rate and relatively sedentary nature can lead to high population densities (Milton and May 1976, Montgomery and Sunquist 1978, McNab 1988, Chiarello 1998).

Population density can also influence home range size in mammals, especially for species that are territorial (Fisher and Owens 2000) and where females hold exclusive home range areas. This is certainly true in koalas, where population densities can reach very high numbers and the home ranges of individuals decrease with increasing densities (Mitchell 1990). Howler monkeys (*Alouatta* spp), also arboreal folivores, also show an inverse relationship between home range areas and animal densities (Bravo and Sallenave 2003).

It is possible that higher population density was causing the smaller home ranges of females in Newell's study (1999b), as these animals were unable to disperse and hence forced to use smaller areas.

4.3.7 Activity and Movements

Lumholtz's tree-kangaroos have always been reported as being largely nocturnal (Proctor-Gray 1985, Newell 1999b). However, during this study, animals were observed to be quite active during the day as well as at night, especially on cooler days or during the cooler times of the day (morning and afternoon, i.e. crepuscular). Proctor-Gray (1985) also observed this behaviour, although she claimed that they were mostly nocturnal.

Pople (1989) states that many species of macropods show varying degrees of activity through the day, although they are largely nocturnal, with peaks of activity around sunrise and sunset. Nevertheless, some rainforest macropods are mostly diurnal, such as *Hypsiprymnodon moschatus* (Dennis 1997) and some are quite active during the day as well as the night, such as *Thylogale thetis* (Johnson 1980) and *T. stigmatica* (Vernes *et al* 1995).

Diurnal or crepuscular behaviour has also been reported for most tree-kangaroo species in New Guinea (Fischer and Austad 1992, Flannery *et al* 1996, Betz 2001, Betz *et al* unpublished data b). Betz (2001) suggests that tree-kangaroos are not fully adapted for nocturnalism because they lack the *tapetum lucidum* cell layer in their retinas (Flannery *et al* 1996), which nocturnal mammals use to improve night vision. He adds that nocturnal behaviour may be a defensive reaction to hunting pressure (Betz 2001). Three-toed Sloths (*Bradypus torquatus*) were also found to have a predominantly diurnal period of activity with them ranging more during the day than at night (Chiarello 1998). In contrast, *D. bennettianus* were found to be totally nocturnal, sleeping in favoured “roost” trees during the day (Martin 1982).

In this study, *D. lumholtzi* rarely used the same tree and did not “roost” during the day in this study. They were observed browsing and moving across branches periodically during the day. They rested or slept for short periods of about 30 minutes or so, then continued feeding again. This behaviour is typical of arboreal folivores (Montgomery and Sunquist 1978, Smith 1979, Crockett and Eisenberg 1987, Mitchell 1990) and may be an adaptation to their highly folivorous diet, with small and frequent feeding bouts best suited for easy digestion (see Section 7).

Male *D. lumholtzi* were observed moving more often and further than females during the day, on some occasions moving even as far as the other side of their home range. It is possible that this could be associated with territory maintenance, as was found with *D. bennettianus* (Martin 1982). Male koalas also move more often than females, although usually at night (Mitchell 1990). This was also attributed to territory maintenance and female visitation (Mitchell 1990).

4.4 CONCLUSIONS

This study was the first to undertake home range analyses for *D. lumholtzi* on a rainforest type other than Complex Notophyll Vine Forest. It shows that the home ranges of *D. lumholtzi* do not differ significantly between the two rainforest types, but suggests that variation in female spatial use is greater in the Complex Mesophyll Vine Forest.

Population density may be influencing home range sizes in *D. lumholtzi*, especially those of females, with a tendency for decreased home range area with an increase in population size. Although *D. lumholtzi* are territorial, it is plausible that females would relinquish part of their home range to their female offspring if other suitable habitat were unavailable. This could be one explanation for the high numbers of animals in Newell's (1999b) study site.

If female *D. lumholtzi* density or home range size is affecting the home range sizes of males, then understanding the variation in female spatial use is most important, as female will determine carrying capacity and reproductive output of a population (Begon *et al* 1986).

The variation in female spatial use cannot be explained by differences in body weight. In fact, there is no sexual dimorphism found in body mass in the animals in this study. However, resources such as habitat quality or types of trees available may influence this variation, and this is the focus of Chapter 5.

4.5 MANAGEMENT IMPLICATIONS AND FURTHER STUDY

Although replanting and restoration of most rainforest types is now occurring on the Atherton and Evelyn Tablelands, emphasis has been directed towards the conservation and restoration of 5b rainforest fragments. This was largely influenced by reports that *D. lumholtzi* was found in high densities in this forest type, along with other rare species, together with the fact that less than 2.5% of 5b remains.

The results of this study suggest that 1b rainforest fragments are as important as 5b to *D. lumholtzi* and that the conservation and restoration of 1b is as crucial, with less than 10% of this rainforest type now remaining. In fact, as there is more 1b rainforest than 5b, this would suggest that 1b is more important to *D. lumholtzi*.

However, the conservation and restoration of all rainforest fragments on the Tablelands is crucial, as we still do not know if *D. lumholtzi* numbers differ in other rainforest types or in continuous rainforest on the Atherton and Evelyn Tablelands. Additionally, small fragments or stepping-stones of clumps of trees are also vital to assist in safe dispersal of individuals across the agricultural landscape.

Therefore, further studies need to be undertaken into the spatial use of *D. lumholtzi* in other rainforest types including continuous forest.

Chapter 5: Habitat requirements of Lumholtz's tree-kangaroos, *Dendrolagus lumholtzi* in a rainforest fragment.

5.0 INTRODUCTION

It is well accepted that an animal's usage of its environment, especially the kind of food it consumes, the varieties of habitats it occupies and how it uses its home range area or territory, is central to the study of its ecology (Johnson 1980, Manly *et al* 2002). Together this is habitat "selection". There is a hierarchical ordering of selection processes (Johnson 1980, Aebischer *et al* 1993), which is recognised as "the concept of selection order" (Owen 1972, Johnson 1980, Manly *et al* 2002).

The highest level, *first-order selection* is the geographic or physical range of a species. Within that range, the *second-order selection*, determines the home range of an individual or social group. *Third-order selection* pertains to the usage made of various habitat components within the home range. Finally, if third order determines the feeding site then the actual procurement of food items from those available at that site can be termed *fourth-order selection* (Johnson 1980, Manly *et al* 2002). However, the very fact that an animal has its home range where it does, or that it occurs in the study area, is itself indicative that the animal has already made a selection (Johnson 1980).

For example, Wiens (1973) recognised different levels of distributional patterns among birds, and identified geographic range (first order), local site and plot patterns in territories (second order), and patterns of utilisation (third order).

Many studies of habitat selection utilise radio tracking as a source of data (Aebischer *et al* 1993). Common aims are to determine whether a species uses the habitats available to it at random, to rank habitats in order of relative use, to compare use by different groups of animals (eg. males and females), to relate use of variables such as food abundance, or to examine the effects of habitat on movement and home range size (Aebischer *et al* 1993).

The *abundance* of a component is the quantity of that component in the environment. The *availability* of that component is its accessibility to the animal. The *selection* of a component is the process in which the animal actually choses that component (Johnson 1980, Manly *et al* 2002).

Another consideration is that preference is reflected in selection, which can only occur when the component is relatively scarce. A component vital to the consumer may be so abundant that the consumer needs only use small amounts of it to satisfy its requirements (Johnson 1980). Thus, the usage is less than availability, but a conclusion that this component is not important may be false and misleading (Johnson 1980).

Only limited information is currently available on the habitat requirements for *D. lumholtzi* (Procter-Gray 1984, 1985, Newell 1999b), although there have been some studies on the home ranges and habitat utilisation of Lumholtz's tree-kangaroos (Procter-Gray 1984, 1985, Newell 1999a, 1999b) as well as on their responses to habitat loss (Newell 1999c), the effect of fragmentation on arboreal folivores (Pahl *et al* 1988, Laurance 1989, 1990, 1996, 1997, Laurance and Laurance 1996, 1999) and the effect of altitude and geology on arboreal folivores (Kanowski *et al* 2001b). From these studies there have been several explanations of observed distributions of *D. lumholtzi* that relate to third order habitat selection, such as, they are edge specialists (Laurance and Laurance 1996, Kanowski *et al* 2001a), prefer regrowth or successional vegetation (Laurance and Laurance 1996, Newell 1999a, Kanowski 1999); prefer a large variation in canopy height (Laurance 1996) and/or they use some species of trees more than others (Newell 1999b). If it is true that Lumholtz's tree-kangaroos prefer regrowth or successional plant species then this may explain high densities in small regrowth fragments such as those reported by Newell (1999b) and Procter-Gray (1985).

Variation in the individual home range areas and differences in intensity of use of areas within home ranges of a number of species, including other folivores such as koalas (Hindell and Lee 1987, Mitchell 1990, Melzer 1995), possums (How 1978, How and Hillcox 2000), howler monkeys (Palacios and Rodriguez 2001) have been related to variation in habitat. It has been postulated that range size and the intensity of use within a range in *D. lumholtzi* may also be associated with structural or floristic features of the habitat (Newell 1999b, Kanowski *et al* 2001a).

This study investigates these suggestions and others, by examining the use of habitat of *D. lumholtzi* within a fragment with mature, regrowth and riparian habitat, using radio-tracking data.

The main aim of the research was to investigate the patterns of use by *D. lumholtzi* within a rainforest fragment using the levels of use in the home range areas of *D. lumholtzi* and determining whether these characters could be used to predict use in other parts of the landscape. Furthermore, to determine whether D. *lumholtzi* prefers particular tree species and if individuals have different preferences.

The specific questions investigated were:

1. Can large-scale structural and floristic differences in vegetation explain differences in tree-kangaroo habitat usage?
2. Do *D. lumholtzi* prefer regrowth or successional vegetation to mature forest?
3. Do *D. lumholtzi* use the edge of the forest more than expected?
4. Do *D. lumholtzi* prefer areas with high tree species diversity or high tree species density*?*
5. Do *D. lumholtzi* prefer areas with a large variation in canopy height?
6. Do *D. lumholtzi* prefer areas with high vine species abundance?
7. Is there a positive relationship with *D. lumholtzi* intensity of use and dominant tree species?
8. Do *D. lumholtzi* show a preference for certain tree species that are available to them within the forest?
9. Do individual *D. lumholtzi* have different preferences and are these due to tree species present in their home range?

5.1 METHODS

5.1.1 Sampling vegetation

In January and February 2003, a 50m grid was superimposed over the study site without reference to habitat or topographical features. This resulted in 98 gird intersections within the forest fragment and neighbouring springs across the previously determined home ranges (Section 4.2.2) (Figure 5.1).

Measurements of the vegetation structure and species composition were taken within a 5m radius from each intersection point. Nineteen habitat variables were measured at each of the 98 quadrats (Appendix 2). Aspect (N, S, E, W), slope (deg) of the substrate, canopy height (m), the abundance of epiphytes, total number of species present in understorey (ground), mid-canopy, and canopy, total number of families present in understorey (ground), mid-canopy and canopy, were recorded for each quadrat. Numbers of individuals of plant species were not counted in understorey and mid-canopy, presence or absence only was recorded. Canopy depth (m) was used as a measure of variation in canopy height and was calculated by the difference between the top of the canopy down to where the canopy was discontinued. That is, if branches came all the way to the ground then the canopy depth would be from the top of canopy to the ground (eg. 20 - 0m = 20m), if branches halted at 10m then canopy depth was from top of canopy down to 10m (eg. 20 – 10m = 10m). The occurrence of floral taxa in ground cover, mid-canopy cover and the number of vines were estimated visually on an ordinal scale of 0-3 (0, none; 1, present in low abundance; 2, abundant; 3, highly abundant). Movement, or ease of traversing through a quadrat or the thickness of vegetation, was also visually estimated on an ordinal scale of 1-3 (1 = easily traversed to 3 = hard to traverse).

All species with a DBH >2.5cm were measured, identified on-site by experts (A. Irvine and R. Jensen) and the height (m) was estimated, including vines that had their stems within the 5m quadrat. This was used to estimate the basal area, total number of species measured (diversity) and total number of trees measured (density) for each quadrat. Additionally, the abundance of individual tree species (183 species) was included in the analysis.

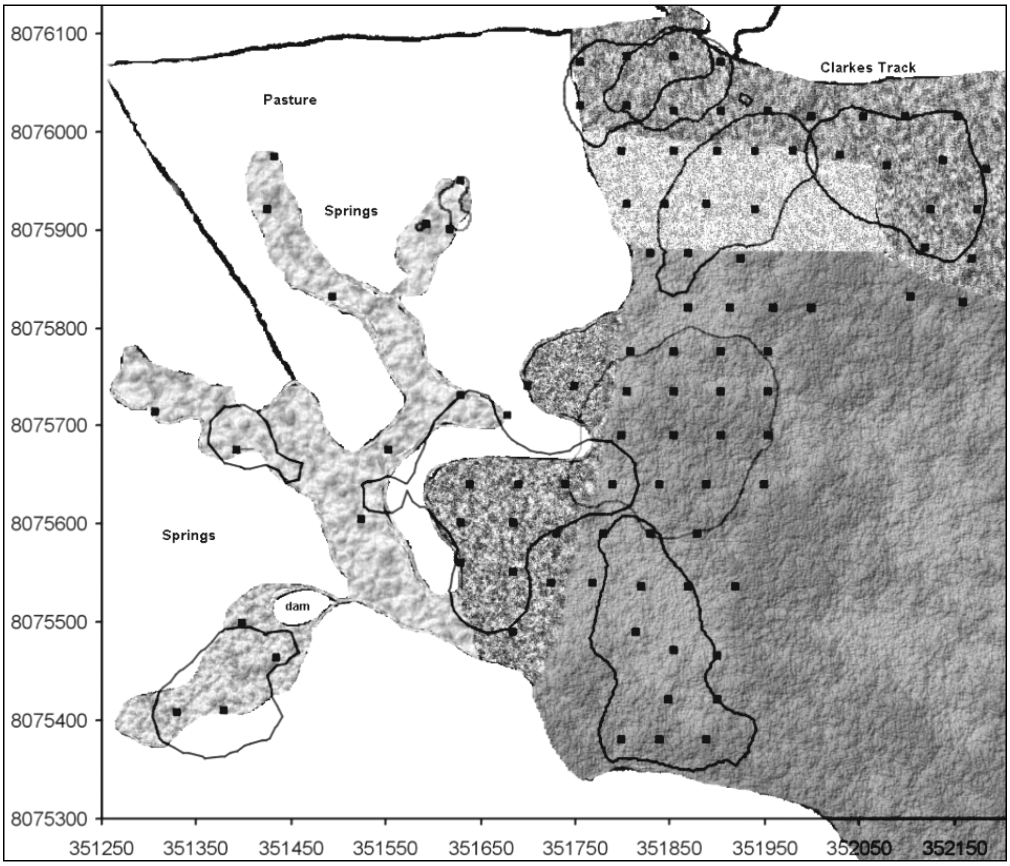


Figure 5.1. Map of study fragment with 50m point transects and an overlay of 90% Harmonic mean measure of each animal's home range. Axes represent Universal grid reference (AGD 66, East and North).

5.1.2 Intensity of use

Two different measures of intensity of use by *D. lumholtzi* were used during this study to investigate patterns of usage in association with vegetation structure and composition: harmonic mean from home range analysis and faecal counts. Harmonic mean was used as a measure for the intensity of use of radio-tracked animals within their home range areas and faecal counts were used to include areas of activity for all animals in the study site.

5.1.2.1 Within Home ranges

The percentage of harmonic mean from home range analysis estimated in previously (see 4.2.2) was used as an index of the intensity of usage by *D. lumholtzi*. Contours of different harmonic means, 55%, 75%, 90% and 95-99% intervals for each animal were generated using the Program Ranges 6 (Kenward *et al* 2003) and positioned over the vegetation grid (Figure 5.2 shows HM contours over the grid). The vegetation sampling quadrats were then categorized according to the harmonic mean (HM%) contour they fell within from high use (55% HM), medium use (75% HM), low use (90% HM), very low use (95% HM) to no use (outside 95% HM).

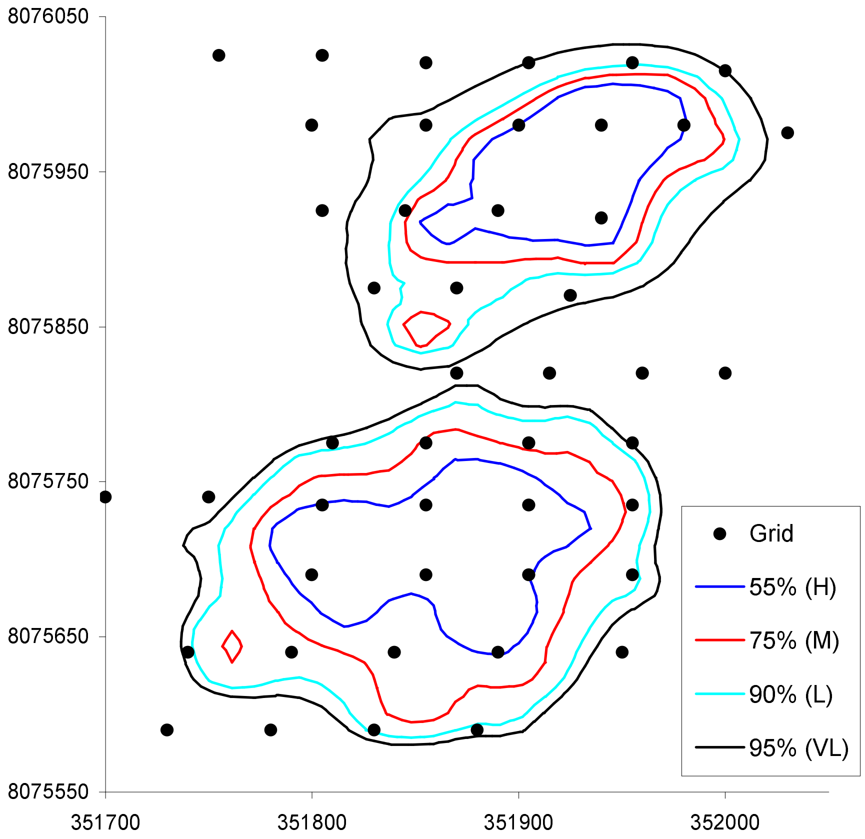


Figure 5.2. Harmonic mean contours over quadrat grid for two males using Ranges 6 (Kenward *et al* 2003). 55% Harmonic mean is the inside contour and represents high use, 75% is the next line out representing medium use, 90% is the next representing low use and 95% is the outside contour representing very low use. All quadrats or plots outside contours were classed as no known use. Axes represent Universal grid reference (AGD 66, East and North).

5.1.2.2 Faecal counts

Scats were collected in 4 x 1m^2 quadrats, 1m north, south, east and west of the centres of each of the 98 vegetation sampling quadrats. The quadrats were cleared of tree-kangaroo faecal pellets in August 2003 and then the accumulated tree-kangaroo faecal pellets were collected one month later. Six vegetation sampling quadrats were not sampled for scats. These were within riparian zones and inaccessible due to dense vegetation.

The rate of tree-kangaroo scat decomposition was determined over the same time period as the faecal pellet collection. Freshly frozen, then defrosted pellets collected from captive tree-kangaroos (fed a diet of local rainforest foliage) were placed in each of the main habitat types within the study site (Section 3.0, Figure 3.3): the pine forest, mature forest and regrowth. Two sets of 30 pellets each were placed within marked 1m^2 areas in each habitat type.

5.1.3 Analysis of D. lumholtzi usage

Associations between the different measures of intensity of use, HM% and the number of scats collected were tested using Spearman’s rank correlations (SPSS V 12.0.1 for Windows).

5.1.4 Analysis of vegetation data

A robust ordination method, nonmetric multidimensional scaling (NMS) using the program PC-ORD (with the Sorensen dissimilarity index and all default options in the Automatic mode) (McCune and Mefford 1999) was used to determine floristic and structural correlates of intensity of use by tree-kangaroos. All of the vegetation floristic and structural data (202 attributes) for the 98 plots were used in this analysis against the intensity of use (home range Harmonic Mean % of use - H, M, L, VL and N) to investigate patterns of use for different plots. Multi-Response Permutation Procedure (MRPP) using PC-ORD (McCune and Mefford 1999) was used to detect differences between clusters of quadrats of similar intensity of use using Sorensen (Bray-Curtis) method (McCune and Mefford 1999). A cluster dendrogram was also generated with PC-ORD (McCune and Mefford 1999) as an alternative to NMS to determine floristic and structural correlates of intensity of use by tree-kangaroos.

Spearman’s rank correlations were used to look at relationships between intensity of use for HM% (categorical) and structural or floristic characters, and Pearson’s correlation coefficient was used for investigating the relationships between the number of scats collected (numerical) and structural or floristic characters using SPSS. Spearman’s rank correlations were also used when comparing the number of scats and any categorical variable. Bonferroni corrections were performed on the analyses and the new alpha level used was 0.003.

Crosstabulation frequencies and correlations (SPSS) were used to investigate the relationships between two categorical variables (eg. vine species present and intensity of use).

5.1.5 Type of forest

Quadrats were categorised into different types of forest; mature, regrowth, springs in regrowth, springs and pine forest, determined by which type each quadrat was situated. These categories were used to look at relationships between the intensity of use (HM% or the number of scats) in each area and types of forest, using crosstabulations and Spearman's rank correlation (SPSS).

5.1.6 Edge versus not edge

To investigate whether *D. lumholtzi* prefer edge to mature forest, the quadrats less than 20m from the edge of the vegetation were classed as "edge" and those not as "interior". For the purposes of this study the definition of "edge" is not the classical definition of "true edge" (usually defined as far as 500m into the rainforest), but further in than an observer could see to test the proposition about observability of *D. lumholtzi* at the edge of the forest.

Crosstabulations and Spearman's rank correlation (SPSS) were used to identify whether "edge" plots were used more than "interior", and Pearson's Chi square (SPSS) was used to test if "edge" was used more than expected.

5.1.7 Tree availability and selection analysis

Randomisation tests were used to compare the abundances of tree species >5cm DBH for all plots to all the tree species utilised by all eight *D. lumholtzi* in the radio tracking study, to test whether *D. lumholtzi* preferred or avoided specific tree species.

There were 449 observations of tree use made during radiolocation of all the tree-kangaroos. To generate an expected distribution of observations if *D. lumholtzi* were using trees randomly, 449 records were randomly selected from all the individual trees recorded in vegetation sampling and the frequency of occurrence of each species recorded. This was repeated 20,000 times.

Observed frequency of tree use was compared directly with the randomised distribution and considered non-random (either preferred or avoided) if they lay outside the central 95% of the distribution.

This procedure was repeated for each individual animal using only the observations of that individual and generating the expected distribution from the vegetation sampling only within the home range of that animal.

5.2 RESULTS

A total of 2786 individual tree and vine species were measured and identified (183 species, 52 families) in the 98 plots. 26 tree species were dominant (>20 individuals) (Table 5.1).

5.2.1 Scat versus harmonic mean as a measure of D. lumholtzi usage.

There was no rain during the scat decomposition trials and sampling in August and September 2003 and scats took up to two months to decay.

There was no correlation between the number of scats and the intensity of home range use (HM) ($P = 0.43$, $r_s = -0.08$).

5.2.2 Patterns in structural and floristics versus tree-kangaroo usage.

Although there is variation across the site in floristic and structural attributes of the vegetation (Stress axis 1 and 2 $P = 0.03$, final stress 2 dimensions = 8.64, final stability = <0.001), this variation is not associated with the pattern of use by *D. lumholtzi* (Figure 5.3). *D. lumholtzi* is using the entire range of variation in vegetation to approximately equivalent extents.

(MRPP results grouped by HM P = 0.78 = *Probability of a smaller or equal delta; T = 0.8; A = -0.005 = more heterogeneity within groups than expected by chance*).

The classification (cluster dendrogram) SPSS also shows that there is no pattern to the levels of intensity of use by *D. lumholtzi* (Appendix 4).

There were no significant correlations between home range use (HM%) and any of the structural characters of the vegetation (Appendix 3). There was, however, positive relationships between HM% and the abundance of some floral species; *Acronychia acidula* (P = 0.05, r_s = 0.2)*, Synima macrophylla* (P = 0.03, r_s = 0.2), and negative relationships with *Cissus penninervis* (P = 0.04, r_s = -0.2)*, Cyathea cooperi* (P = 0.04, r_s = -0.2) and *Sarcotechia lanceolata* (P = 0.05, r_s = -0.2).

There were also positive correlations between the number of scats collected and some species; *Ficus crassipes* (P = 0.000 r = 0.4)*, Flindersia brayleyana* (P = 0.008 r = 0.3), *Neolitsea dealbata* (P = 0.04 r = 0.22) and *Zanthoxylum venificum* (P = 0.000 r = 0.6).

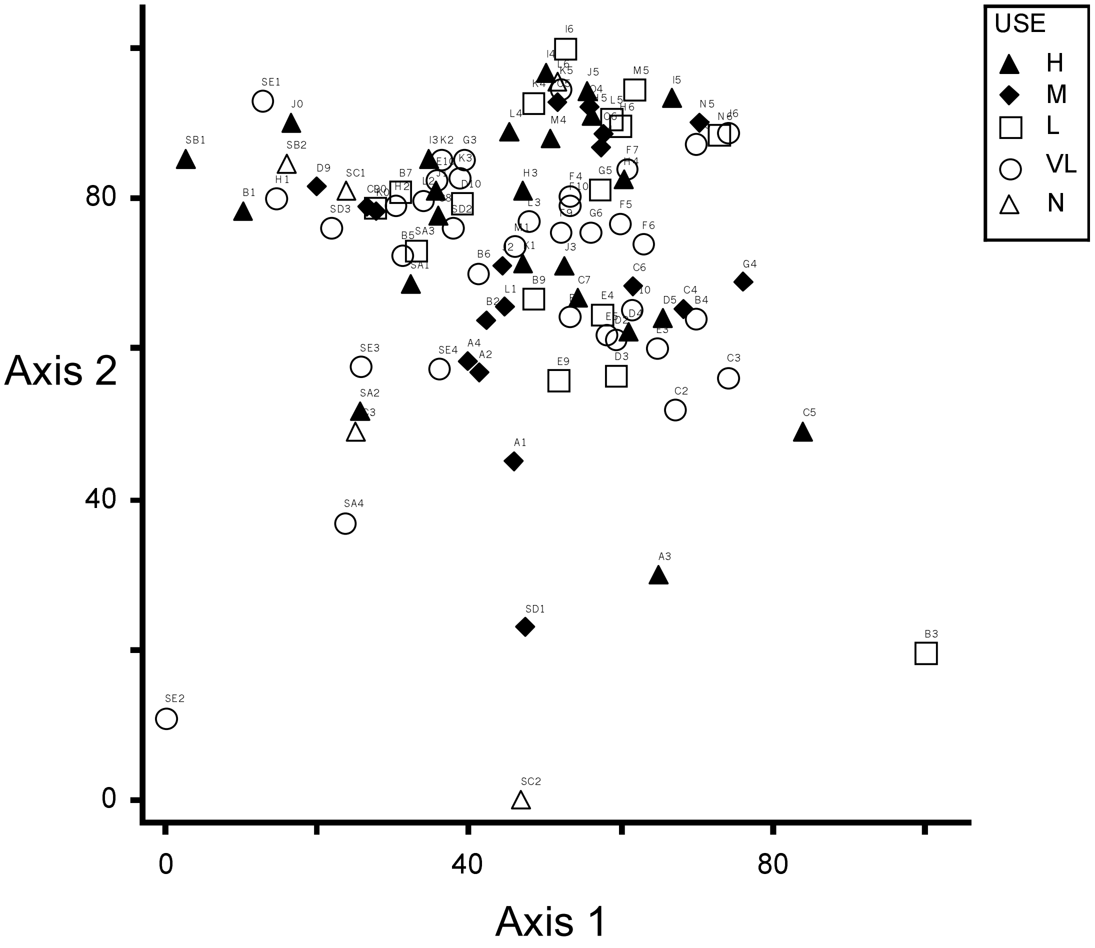


Figure 5.3. Nonmetric Multidimensional Scaling (NMS) of the 202 variables (structural characters and tree species abundances) for the 98 quadrats against intensity of use (HM%) by *D. lumholtzi*. H, high use, M, medium use, L, low use, VL, very low use, N, no known use.

5.2.3 Do D. lumholtzi prefer successional or regrowth to mature forest?

The results show that there is no significant difference between intensity of use (HM%) and the type of habitat: regrowth or mature forest ($P = 0.16$ $r_s = -0.14$).

However, there is a significant relationship between the type of forest and the number of scats ($P = 0.001$, $r = 0.3$), with more scats in the springs ($n = 88$) including regrowth springs ($n = 4$) than the mature forest ($n = 21$), regrowth areas ($n = 28$) and only 1 scat from the pine forest. There were very high numbers of scats ($n = 67$) collected in one spring in which a female (Lisa) and her offspring inhabit a very small home range (0.1ha).

5.2.4 D. lumholtzi prefer "edge"?

D. lumholtzi was not found to be using the "edge" more than "interior" in this study ($P = 0.56$ $r_s = -0.06$), with only 24.5% of the total usage being in the edge quadrats. In fact, only 4 out of the 24 edge quadrats (16.7%) were in high use areas and 54.1% were very low or no use. Furthermore, two of the females ("Mary Jo" and "Simone") did not use the edge at all. Edge quadrats were not used more than expected (Pearson's $\chi^2 = 3.96$, $df = 5$, $P = 0.56$).

This was confirmed with the results from the number of scats at each plot ($P = 0.18$ $r_s = -0.14$, $n = 93$), with 21.5% in edge plots and 78.5% in non-edge. (Pearson's $\chi^2 = 12.48$, $df = 9$, $P = 0.19$).

5.2.5 D. lumholtzi prefer areas with higher species diversity or higher tree density?

There were no significant relationships between intensity of use and tree species diversity ($P= 0.49$ $r_s = -0.07$) or tree density ($P = 0.61$ $r_s = -0.05$).

There was also no significant correlation between intensity of use and number of floristic families ($P = 0.27$ $r_s = -0.11$). Furthermore, there were no significant correlations between the number of scats collected and the number of tree species ($P = 0.51$ $r = -0.07$) (diversity) or the total number of trees (density) ($P = 0.52$ $r = 0.07$).

5.2.6 D. lumholtzi prefer a forest with a large variation in canopy height?

The results show that there was no significant preference for areas with a large variation in canopy height (intensity of use P = 0.57, r_s = -0.06; scats P = 0.58, rs = -0.06).

There was also no significant relationship between canopy height (m) and intensity of use (P = 0.96, r_s = -0.01) or with the number of scats (P = 0.09, r = -0.18).

5.2.7 Vine species present

Although there were a high number of vines in both the high and medium intensity if use areas (40%), there was no significant correlation between *D. lumholtzi* levels of use and the number of vine species present (intensity of use: P = 0.43, r_s = -0.08, scats: P = 0.55, r_s = 0.06).

5.2.8 Dominant tree species

Twenty-six tree species dominated the vegetation sampled, with greater than 20 individuals recorded (Table 5.1). However, there was a significant relationship between only 2 of these dominant species and intensity of use (HM%) (Appendix 3). These were *Acronychia acidula* with a positive correlation (P = 0.047, r_s = 0.2) and *Cyathea cooperi* with a negative correlation (P = 0.04, r_s = -0.2).

There were significant correlations (<0.01) between the number of faecal pellets collected and only two of these dominant species: *Flinderisa brayleyana* (P = 0.01, r = 0.3), and *Neolitsea dealbata* (P = 0.04, r = 0.2).

Table 5.1. Twenty-six dominant tree species from all vegetation sampled.

Species	Abundance (n)	*Species*	Abundance (n)
Acronychia aberrans	22	*Flindersia brayleyana*	31
Acronychia acidula	27	*Franciscodendron laurifolium*	166
Alphitonia petriei	89	*Glochidion hylandii*	40
Beilschmiedia tooram	23	*Guioa lasioneura*	718
Caldcluvia australiensis	40	*Helicia nortoniana*	25
Ceratopetalum succirubrum	22	*Litsea leefeana*	59
Cryptocarya lividula	22	*Lomatia fraxinifolia*	28
Cryptocarya melanocarpa	20	*Melicope jonesii*	22
Cyathea cooperi	21	*Neolitsea dealbata*	216
Dinosperma stipitata	38	*Pinus caribaea*	68
Endiandra leptodendron	67	*Psidium cattleianum*	84
Endiandra wolfei	25	*Rhodamnia sessiliflora*	36
Flindersia bourjortiana	24	*Rhodomyrtus pervagata*	173

5.2.9 Tree use.

There were a total of 449 observations of tree usage in 46 species, whilst radio tracking *D. lumholtzi* during this study (Table 5.2). Only 12 species (2.7%) were observed being eaten.

5.2.10 D. lumholtzi use of tree species available in 1b forest

There were a total of 1350 trees from 108 species in the vegetation sampling quadrats (>5cm DBH) available within the areas of all of the radio-tracked animals.

There were 11 tree species used more than expected (P = <0.05) out of the 46 species used by all of the animals combined; *Alphitonia petriei, Beilschmiedia bancrofti, Beilschmiedia recurva, Cryptocarya angulata, Ficus crassipes, Flindersia pimenteliana, Glochidion hylandii, Litsea leefeana*, *Solanum mauritianum, Syzygium gustavioides, Syzygium johnstonii.* (Table 5.3, Figure 5.4).

Six species were used by animals but did not occur in the quadrats: *Cinnamomum camphora*, *Cinnamomum laubatii, Citronella aromatica, Gillbaea adenopetala, Gmelina fasciculiflora, Perapentadenia mearsii.* It is assumed that these tree species were in low numbers, but because their occurrence was not measured, *D. lumholtzi* preference for these species could not be tested. There were also some species that were observed being used by some individuals that were not present in the quadrats in that particular animal's home range (Table 5.3).

5.2.11 Individual D. lumholtzi use versus tree species available

Most animals showed a preference for both *Alphitonia petriei* (75% or 6 out of 8 of the animals more than expected and 1 out of 8 or 12.5% as expected, 12.5% used but not present in quadrats) and *Litsea leefeana* (50% or 4 out of 8 of the animals more than expected and 3 out of 8 or 37.5% as expected, 1 out of 8 used but not present in quadrats) (Table 5.3).

Flindersia pimenteliana was also selected more than expected by 2 animals. *Guioa lasioneura* and *Flindersia brayleyana* were used by all of the animals as expected.

D. lumholtzi has been observed using *Guioa lasioneura*, a successional to mid climax species, frequently*.* All animals utilised this species in this study, but as it was very common throughout the study area (718 trees of this species out of 98 vegetation quadrats) it was not selected more than expected.

Only one female (Lisa) used *Ficus crassipes* more than expected. In this case it had a vine species, *Cissus hypoglauca,* throughout its canopy. This vine species is a food species for *D. lumholtzi* (personal observations) and was found in the faeces of this animal (see Section 6.2).

There was considerable variation between individuals for species preferences (Table 5.3). That is, 6 out of 8 animals preferred *Alphitonia petriei*, whereas 1 of 8 used this species as expected. *Endiandra wolfei* was preferred by 1 of 8 animals, used as expected by 1 of 8, avoided by 3 of 8, and 1 of 8 did not have access to it and 2 of 8 used this species but was not present in quadrats.

Individual *D. lumholtzi* used an average of 22 ± 0.04% of tree species of the species available to them within their home range areas.

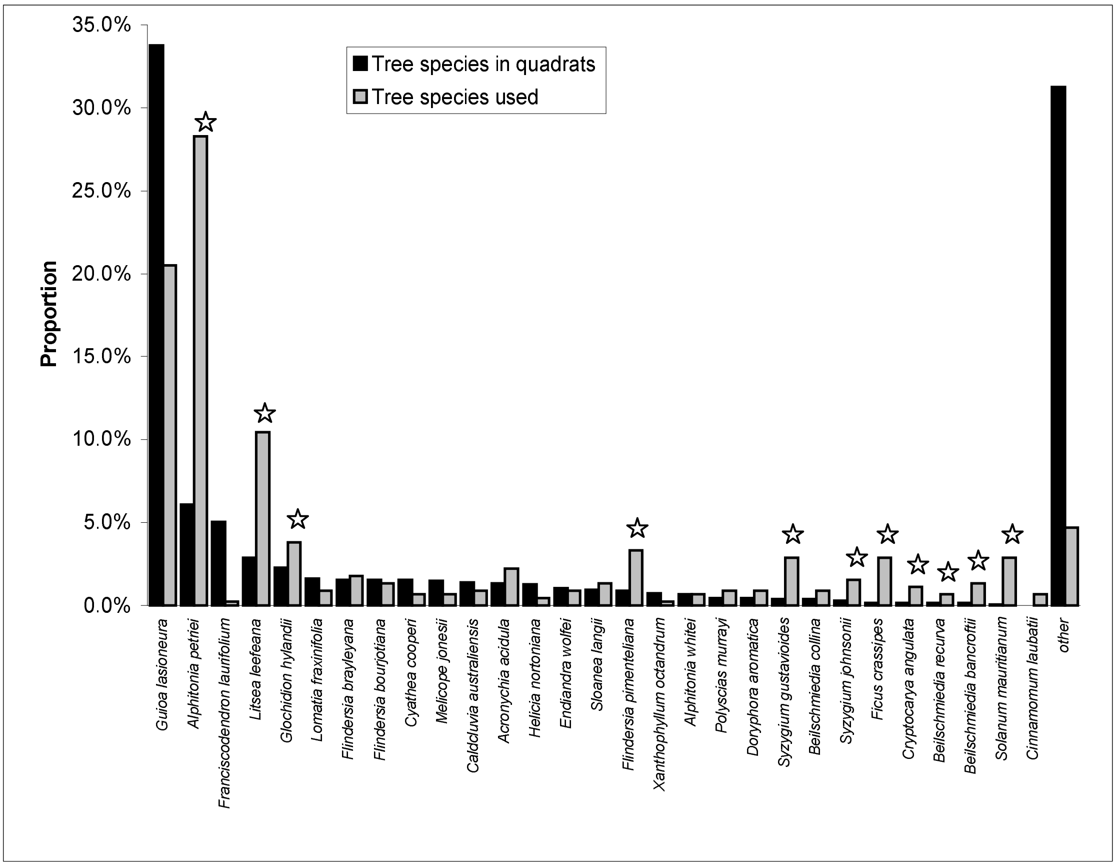


Figure 5.4. Proportion of tree species used and tree species available. Tree species are in order of abundance. All species not used or used less than 0.5% (except significant) are placed in “other”. Stars represent significant use >0.05.

Table 5.2: Use of tree and vine species by *D. lumholtzi* in 1b rainforest.
Number of sightings indicates sightings of animals in trees. Values are proportions of these records. Proportions are calculated separately for trees and vines. # Indicates feeding record. * Indicates a weed species. Bold indicates species utilised in 5b (Procter-Gray 1984, 1985, Newell 1999b).

Tree Species	**Colin**	**Errol**	**Alex**	**Eve**	**Lisa**	**Carlia**	**MaryJo**	**Simone**
No of sightings	**96**	**55**	**37**	**38**	**106**	**28**	**49**	**45**
Acronychia acidula	0.04	0.05		0.05				0.02
Alphitonia petriei #	0.37	0.07	0.59	0.29	0.32	0.29	0.22	0.07
Alphitonia whitei			0.05					0.02
Arytera pauciflora #	0.01							
Beilschmiedia bancrofti		0.02						0.11
Beilschmiedia collina #				0.05				0.04
Beilschmiedia recurva		0.04						0.02
Caldcluvia australiensis						0.11	0.02	
Ceratopetalum succirubrum		0.02						
****Cinnamomum camphora #***	0.02							
Cinnamomum laubatii		0.05						
Citronella aromatica								0.02
Cryptocarya angulata		0.09						
Cryptocarya murrayi				0.05				
Cyathea cooperi #					0.03			
Doryphora aromatica		0.02						0.07
Elaeocarpus largiflorens								0.02
Elaeocarpus ruminatus	0.01							
Endiandra wolfei #	0.01			0.03			0.02	0.02
Erythrina indica	0.01							
Ficus crassipes					0.12			
Flindersia bourjotiana		0.05					0.04	0.02
Flindersia brayleyana		0.02		0.05	0.04		0.02	
Flindersia pimenteliana		0.11	0.05					0.16
Fraciscodendron laurifolium		0.02						
Gillbaea adenopetala		0.02						
Glochidion hylandii #	0.05		0.19				0.10	
Gmelina fasciculiflora		0.02						
Gonothalamus australis		0.02						
Guoia lasioneura #	0.24	0.02	0.03	0.05	0.37	0.39	0.29	0.04
Helicia nortoniana # (fruit)	0.02							
Litsea connersii		0.02						
Litsea leefeana #	0.14	0.13	0.08	0.26	0.01	0.04	0.20	0.04
Lomatia fraxinofolia						0.14		
Melicope johnstonii	0.03							
Opistheolepis heterophylla		0.02						0.02
Perapentadenia mearsii		0.02						
Polycias murrayi							0.08	
Pullea stutzeri								0.02
Sloanea australis ssp parviflora								0.02
Sloanea langii		0.04				0.04		0.07
**Solanum mauritianum #*				0.03	0.11			
Symplocos cochinchinensis ssp gittinsii								0.04
Syzygium gustavioides #		0.13						0.13
Syzygium johnstonii	0.02			0.13				
Xanthophyllum octandra		0.02						
Vine species/No of sightings	**30**	**4**	**0**	**3**	**63**	**1**	**2**	**13**
Austrosteenisia stipularis #		0.25					0.5	0.31
Cissus hypoglauca #	0.6	0.75		0.67	0.21			0.08
Elaeagnus triflora #	0.37			0.33	0.73	1.0		
****Lantana camara #***	0.03				0.06			
Maesa dependens #								0.08
Unidentified vine species							0.5	0.31
Birds nest ferns & basket ferns								0.23

Table 5.3: List of tree species used by *D. lumholtzi* and compared to those available to all 8 animals. Also tree species used by individuals compared to those available within their individual home ranges. E = utilised as expected; ** = 0.01 more than expected; * = 0.05 more than expected, L = Less than expected. BLANK CELLS = not available. Tree species diversity is number of tree species in plots in animal's home range area. Tree species density is number of trees in plots in animal's home range area. Species in bold are significant to all animals combined >0.01. Numbers of trees in parenthesis. UN = used but not in quadrats.

Tree species (no)	ALL	Colin	Alex	Errol	Eve	Carlia	Lisa	Mary Jo	Simone
Tree species density	**1350**	**60**	**301**	**329**	**51**	**418**	**45**	**259**	**197**
Tree species diversity	**108**	**16**	**57**	**86**	**14**	**40**	**10**	**30**	**66**
Acronychia acidula (27)	E	E	L	*	E	L		L	*
Alphitonia petriei (106)	**	**	**	E	*	**	**	**	**
Alphitonia whitiei (16)	E	L	UN	L		L		L	E
Arytera paucilfora (2)	E	E							
Beilschmiedia bancrofti (2)	**			UN					**
Beilschmiedia collini (13)	E			L	UN				**
Beilschmiedia recurva (3)	**			UN					E
Caldcluvia australiensis (40)	E		L			*		E	L
Ceratapetalum succirubrum (22)	E		L	E		L			L
Cryptocarya angulata (3)	**			**					
Cryptocarya murrayi (9)	E		L		UN				
Cyathea cooperi (28)	E		L			L	E	L	
Doryphora aromatica (8)	E			E		L			**
Elaeocarpus largiflorens (1)	E								*
Elaeocarpus ruminatus (2)	E	UN	L						
Endiandra wolfei (25)	E	UN	L	L	UN	L		*	E
Erythrina indica (1)	E	E							
Ficus crassipes (2)	**						**		L
Flindersia bourjotiana (26)	E			E		L		**	E
Flindersia brayleyana (31)	E	L	L	E	E	L	E	E	L
Flindersia pimenteliana (17)	**		UN	**		L			**
Franciscodendron laurifolium (170)	L		L	E		L			L
Glochidion hylandii (48)	*	E	**	L		L	L	*	L
Goniothalamus australis (7)	E			E					
Guioa lasioneura (718)	L	E	E	E	E	E	E	E	E
Helicia nortoniana (25)	E	E	L	L		L		L	L
Litsea connersii (9)	E			E		L			L
Litsea leefeana (63)	**	E	**	**	**	E	UN	**	E
Lomatia fraxinifolia (28)	E			L		**			L
Melicope jonesii (23)	E	E	L	L		L		L	L
Opisthiolepis heterophylla (2)	E		L	E					UN
Polyscias murrayi (6)	E		L	L				**	
Pullea stutzeri (14)	E			L					E
Sloanea australis (11)	E		L	L				L	*
Sloanea langii (16)	E		L	E		E		L	UN
Solanum mauritianum (3)	**				**		UN		
Symplocus cochinchinensis var gittinsii	E					L			**
Syzygium gustavioides (8)	**			**					**
Syzygium johnstonii (7)	**	UN		L	UN				L
Xanthophyllum octandrum (11)	E			E					L

Not in Quadrats

Cinnamomum camphora (0)	
Cinnamomum laubatii (0)	
Citronella aromatica (0)	
Gillbaea adentopetala (0)	
Gmelina fasciculiflora (0)	
Peripentadenia mearsii (0)	

5.3 DISCUSSION

5.3.1 Home range usage

As it did not rain during the period of scat decomposition trials and sampling, it was assumed that re-sampling after one month would ensure that all scats in the quadrats were a maximum of one month old and that none would have decayed in this time.

It was believed, however, that the harmonic mean is a more robust method of measuring usage if available as this gives all possible areas within an animals home range not just the areas where scats were visible.

Macropods are known to defaecate mostly while feeding, therefore areas used for feeding have high numbers of scats and those used for resting have relatively few (Johnson *et al* 1987). If this holds true for *D. lumholtzi* then there will be areas of usage where no scats will be found. During radio tracking (Section 4.1.1) there were many instances where there were no scats beneath the animal, so the absence of scats cannot be logically used to infer the absence of animals. In addition, scats are very difficult to find within the leaf litter of the forest floor, making the precision of this technique dubious.

5.3.2 Structural and floristic characters of habitat versus tree-kangaroo usage

This study shows that we can not use structural characters of the habitat to model *D. lumholtzi* habitat use as there was no association with levels of use and these characters. In support of this, in an ordination of structural and floristic characters of fragments of different habitat types, Laurance and Laurance (1999) also found that abundance of *D. lumholtzi* was not significantly influenced by forest type.

However, Laurance and Laurance (1999) found that Lumholtz's tree-kangaroos were less abundant in primary forest than regrowth forest. In this study *D. lumholtzi* used both regrowth and mature forest and did not show any preference for regrowth over mature forest. However, from personal observations of the time it takes to detect *D. lumholtzi* in tall versus shorter forest, it is clear that *D. lumholtzi* are much more difficult to detect in tall forest, therefore Laurance and Laurance's (1999) result may simply indicate a differential in visibility of *D. lumholtzi* between forest types.

The results of this study did find, however, that there were more scats in the springs including the springs in the regrowth. This suggests that animal activity is higher in the springs and possibly because of the access to water or the fact that the trees have more access to water. It has been suggested that trees growing in riparian zones may be favoured by arboreal folivores because of the availability of foliar moisture and possible higher nutritional quality of the foliage (Munks *et al* 1996). However, the high number of scats in one of the springs (n = 67) could merely reflect the small area of the riparian fragment in which the animals are living ("Lisa" and offspring in 0.1ha home range) and hence a high concentration of scats in one area.

It has also been suggested that *D. lumholtzi* decline in smaller <20 ha fragments (Laurance and Laurance 1999). The female in the spring in this study (Lisa - 0.1ha home range) shows that this is not always the case. This is also supported by several observations of tree-kangaroos in small fragments, with up to 3 females in a 1ha fragment in one example (Tree Kangaroo and Mammal Group 2000).

This study has found that *D. lumholtzi* spent less than 25% of the time at the edge of the forest. This is no more than expected. Furthermore, even though all of the animals did have access to the edge, two of the animals did not use the edge at all. This supports Newell's (1999b) findings where he only found his animals visible by spotlighting at the edge 10% of the time. Many studies are performed along the edge or tracks of forest fragments (Laurance 1989, 1990, 1996, 1997, Laurance and Laurance 1996, 1999, Pahl *et al* 1988). Therefore, the suggestion of *D. lumholtzi* being an edge species may be purely an artefact of them being easier to observe at the edge and humans tending to be an "edge species", sampling from the edge or a track through the forest. Furthermore, *D. lumholtzi* are very difficult to sight even when radio tracking collared individuals in either regrowth or mature forest, especially away from the edge. In addition, spotlighting is not an accurate technique for detecting tree-kangaroos as their eye-shine is not as bright as other folivores (Procter-Gray 1990) and they also tend to look away from the light (Flannery *et al* 1996, pers. obs.), which makes it difficult when relying on eye-shine to spot these animals at night. In fact, it was easier, although still quite difficult, to spot tree-kangaroos during the day.

It has been suggested that *D. lumholtzi* might prefer fragments with a large variation in canopy height (Laurance 1996) and that the height of the canopy may also have an effect on the size of the home range of folivores (Milton and May 1976). However, *D. lumholtzi* did not select areas with a large variation in canopy height nor do they show any relationship with intensity of use and canopy height. Yet again, the relationship Laurance (1996) found with variation in canopy height may also be an artefact of sampling from the edge or in areas of regrowth with a large variation in canopy height, hence making observations of *D. lumholtzi* easier.

There was no relationship between *D. lumholtzi* intensity of use and tree species diversity and density as was found in Nilgiri langur monkeys (Umapathy and Kumar 2000) and as might be expected from a generalist folivore (Newell 1999b, Chiarello 1998). The animals resident at the spring have a smaller home range size to others and they have fewer species or tree densities in their area than the other animals. If tree density or diversity were a contributing factor to their home range size, one would expect these animals to have a larger home range, extending their area to cover connecting springs.

In many instances, *D. lumholtzi* have been associated with vine species when seen in a tree (Procter-Gray 1984, 1985, Newell 1999b) and they have been observed frequently consuming a variety of vine species (Table 5.2, Section 6.2, Tree Kangaroo and Mammal Group unpublished data). However, there was no correlation between vine species and their level of usage in this study. If it was possible to count vine abundance similarly to tree abundance, the vine availability could have been tested for individuals as it was for tree species. This may have then given us a frequency of use that we could have tested for preference. Unfortunately, vine abundance was only measured when the stem of the vine was in the quadrat.

5.3.3 Tree species preferences by D. lumholtzi

D. lumholtzi are considered to be generalist and tautological catholic folivores (Newell 1999b, 1999c) consuming a variety of tree species (Procter-Gray 1984, 1985, Newell 1999b). Many of the plant species that Lumholtz's tree-kangaroos were associated with were the same in both studies (Procter-Gray 1984, 1985, Newell 1999b) and similar in many respects to those recorded for Bennett's tree-kangaroos (Martin 1992). However, there were some species that *D. lumholtzi* utilised at one site and not the other, such as *Euroschinus falcata* (Procter-Gray 1984, 1985, Newell 1999b), although present.

D. lumholtzi used five species common to the study site and 5b rainforest: *Cinnamomum camphora* (weed), *Flindersia brayleyana*, *Litsea leefeana*, *Elaeagnus triflora* (vine) and *Lantana camara* (weed) (Procter-Gray 1984, 1985, Newell 1999b). Obviously, as the forest types are different they do contain different species in each. However, it is interesting that *D. lumholtzi* use those five that are common to both forests when available to the animals. Moreover, they prefer *Litsea leefeana* in both forests. *Flindersia brayleyana* is also used by all of the animals in both forests. Furthermore, *Elaeagnus triflora* and *Lantana camara* are both eaten regularly by *D. lumholtzi* (Procter-Gray 1984, Newell 1999b, pers. obs., TKMG unpublished data).

Even though *D. lumholtzi* are selecting a variety of species, they are not broad generalists as such, as suggested (Newell 1999b) but are only using 22% of the trees available to them with their home range areas. This is similar to that of sloths, which also select less than 20% of the tree species available to them (Chiarello 1998). Koalas also select a small number of tree species available to them (Hindell *et al* 1985, Hindell and Lee 1987, 1988, Ellis *et al* 2002). Chiarello (1998) suggests that diet selectivity in arboreal folivores is probably an adaptation to a particular group of plants in order to cope with a smaller range of feeding deterrents in the plants.

When considered on a whole *D. lumholtzi* do appear to concentrate their use on particular tree species within the forest. However, this assumes that all of the animals have free and equal access to all of these species within their home range areas. In a territorial species such as *D. lumholtzi*, resources in another animal’s territory are not available. Consequently, considering all individuals together would give information on third order selection, if patterns were relatively uniform across individuals. However, as individuals show considerable differences in their preferences it was necessary to investigate them separately to explore fourth order selection for trees within their individual home ranges.

Newell (1999b) also found that there was marked variation between *D. lumholtzi* individuals in the tree species that they used. This study has substantiated Newell’s (1999b) findings that *D. lumholtzi* show individual preferences for tree species, even when some species are available to all animals. Bennett’s tree-kangaroos (Flannery *et al* 1996, Martin 1992), koalas (Hindell *et al* 1985, Hindell and Lee 1987, 1988, Ellis *et al* 2002), ringtail possums (Lawler *et al* 2000), Colobus monkeys (Hladik 1978, McKey 1978), howler monkeys (Glander 1978), the tree-toed sloth (*Bradypus variegatus*) (Montgomery and Sunquist 1978) and the maned sloth (*Bradypus torquatus*) (Chiarello 1998) have also displayed individual variation in the tree species choice and preference for certain trees within a species.

Newell (1999b) also found that individual animals had a number of favourite trees within their home ranges. However, in this study some individual *D. lumholtzi* used a particular tree more than once, but not on a regular basis and hence could not be referred to as “favourite” trees as found by Newell (1999b). Furthermore, *D. lumholtzi* do not use the same tree to roost during the day, as do *D. bennettianus* (Martin 1992) and New Guinea tree-kangaroos (Betz 2001, Betz *et al* unpublished data) and some koalas (Eberhard 1978). In fact, *D. lumholtzi* did not “roost” as such in this study and were quite actively feeding at varies times of the day especially at cooler times. This predominance of using trees only once is consistent with many other arboreal folivores, such as Howler monkeys (Glander 1978) and many koala populations (Mitchell 1990, Ellis *et al* 2002). Ellis *et al* (2002) suggests that repeated tree use might be an artefact of the number of trees available. The only animal in this study that did use trees repeatedly inhabited a small fragment of riparian habitat with few trees available.

Clearly a range of species is chosen by *D. lumholtzi* and animals have individual preferences but the reason for those specific choices are currently unclear and probably multifactorial.

It is possible that tree-kangaroos may not be selecting trees at a taxonomic level, which is the level considered in this study, but for foliage characters. That is, choosing the trees on the basis of palatability, levels of nutrients, the amount of plant defences or some other character of the foliage, similar to the pattern seen in koalas and other arboreal folivores such as folivorous monkeys (Glander 1978, Moore and Foley 2000, Umapathy and Kumar 2000).

We already know that koalas and other eucalypt folivores select for particular plant defences that vary within a species as much as they do between species (Cork and Foley 1991, 1997, Lawler *et al* 1998, Moore and Foley 2000). Nutrient levels also vary between different trees and between different leaf classes (Moore and Foley 2000).

D. lumholtzi were observed eating petioles of at least two species in this study and the young leaves of many species when available (pers. obs.). Howler monkeys are reported to eat more young leaves and petioles than older leaves of some species because these plant parts contain less secondary compounds and are more easily digested (Glander 1978).

5.4 CONCLUSIONS

This study has shown that we cannot use habitat structural characters to model *D. lumholtzi* habitat usage or to determine differences in home range sizes. It has revealed that they may be selecting areas for territorial or social reasons or areas that are not occupied (third level selection) rather than selecting areas for particular habitat characters. They are then selecting particular species available to them within these areas (fourth level selection). Therefore, it may not be habitat type that is the primary determinant of usage or home range size. Furthermore, due to the variation in individual tree preferences, tree species use or diet cannot be used to explain variation in home range sizes in this study.

This study has also cleared up a lot of assumptions made about *D. lumholtzi* habitat use, in that they are not edge specialists, do not show a preference for regrowth to mature forest, are not selecting areas with high species diversity or density, are not using areas with a large number of vines more, and do not prefer areas with a large variation in canopy height.

In addition, it has shown that they are also not “broad” generalist folivores as such, as believed (Newell 1999b) and are only selecting less than a quarter of the species available to them.

However, *D. lumholtzi* are selecting particular species within their home range and there is a lot of individual variation in this choice. This individual preference could be explained by tree choice being, not for tree species but for foliage characters such as plant defences or nutrient content, which vary within species as much as between species.

It is clear that further studies to investigate foliage characters of trees chosen by *D. lumholtzi* are required.

With these conclusions in mind, most of the rainforest fragments remaining on the Atherton Tablelands are potential habitat for *D. lumholtzi*. Therefore, conservation, restoration and replanting of areas of different rainforest types are essential for the long-term conservation of *D. lumholtzi*. Furthermore, corridors and small fragments as stepping-stones for dispersing individuals are also vital. Moreover, the tree species that they showed a preference for in this study, especially those that *D. lumholtzi* utilised in both rainforest types, will provide a foundation for planting lists for revegetation, although a large variety of species would be preferable to account for individual preferences.