

IMPACT OF AN INTRODUCED POPULATION OF *EULEMUR FULVUS* ON A NATIVE
POPULATION OF *LEMUR CATT*A AT BERENTY RESERVE, MADAGASCAR

by

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Abstract

One of the largest protected populations of the Ringtail lemur (*Lemur catta*) lives in Berenty Reserve, a 400ha riverine forest in semi-arid southeastern Madagascar. Nine Brown lemurs (*Eulemur fulvus*) were introduced into Berenty in 1974. When these two species exist in natural sympatry, they overlap little in diet or habitat use. Brown lemurs specialize on closed-canopy forest but Ringtails are semi-terrestrial and use both forest and adjacent scrub habitat. In contrast, preliminary data at Berenty indicated broad interspecific overlap. I tested the hypothesis that the increasing Brown lemur population is having a negative demographic impact on Ringtails at Berenty. I also sought to understand what factors affect Ringtail and Brown lemur population density there. I studied the resource use, population dynamics, and response to drought, of Ringtails and Brown lemurs at Berenty. I compared the diet and habitat use of seven troop-pairs each with one Ringtail and one Brown lemur troop living in overlapping home ranges, and thus sharing access to the same resources. I found that paired Ringtail and Brown lemur troops living in the same habitat type overlapped more in diet than did adjacent troops of the same species. Census data showed that between 1974 and 2000, the numbers of both species increased, and the combined density of the two populations quadrupled. Ringtail numbers have been stable since 1995, while Brown lemur numbers continue to grow. However, juvenile recruitment in Ringtails declined with increasing Brown lemur density in scrub habitat. Juvenile recruitment in Ringtails, but not in Brown lemurs, also declined following droughts. This is likely the result of reduced productivity in the keystone food tree species *Tamarindus indica* after droughts. Despite the high overlap in diet of Brown lemurs and Ringtails at Berenty, I found no evidence that the socially dominant Brown lemur is lowering the demographic performance of the Ringtail. I suggest that water provisioning at Berenty explains this apparent paradox.

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Introduction

It is widely assumed that invasions by non-native species are a major cause of extinction or extirpation of native species (Courchamp *et al.* 2003; Gurevitch and Padilla 2004). Well-documented cases exist of vertebrate species extinctions caused by introduced predators or pathogens, but there are few convincing examples of extinctions or extirpations caused by introduced competitors (Davis 2003). In fact, out of 655 at-risk animal species for which the IUCN Red List cites introduced species as a cause of decline, introduced competitors threatened only 37 species (data from Gurevitch and Padilla 2004). Though extinction and extirpation may be uncommon outcomes, introduced competitors can have severe impacts on numbers or distributions of native species (e.g. Petren and Case 1996; Juliano 1998; Wilcove *et al.* 1998; Byers 2000; Bryce *et al.* 2002).

The risk that an introduced competitor will have a severe impact on a native species may be greater if the recipient system is a habitat fragment, because numbers of the native species and diversity of available resources will be limited (Davis 2003). It may also be greater if the invader is a superior competitor in the dominant local habitat (Juliano 1998; Bryce *et al.* 2002). In addition, an introduced competitor may be more likely to have a severe impact on a native species if the recipient site's ecology has been substantially altered (Petren and Case 1996; Byers 2002). Conversely, the risk of severe impact should be less if the native species has an evolutionary history of coexisting with species similar to the introduced species, under similar ecological conditions (*cf.* introductions to islands, Courchamp *et al.* 2003). This assumption is sometimes used to justify species translocations, reintroductions, and introductions (IUCN 1998). However, populations of non-native species introduced to habitat near to and ecologically similar to their historic ranges, can have unexpected and damaging effects (e.g. Masters *et al.* 2004).

I examined the effects of an introduced population of Brown lemurs (*Eulemur fulvus rufus*) on a native population of Ringtail lemurs (*Lemur catta*) at Berenty Reserve, Madagascar. Conditions facing Ringtail lemurs at Berenty appear to place them at high risk from introduced competitors. Berenty is part of an isolated 350ha fragment of riparian forest in the semi-arid south of Madagascar. It has been altered extensively, including clearing of edge habitat and provision of drinking water for lemurs. Ringtail lemurs are poor competitors adapted to surviving in marginal habitat (Gould *et al.* 1999; Godfrey *et al.* 2004), but are mainly found in

high quality habitat at Berenty. Throughout their southern Madagascar range, Ringtails exist at high density only in high biomass riparian or other closed-canopy dry forest (Sussman *et al.* 2003). High biomass dry forest in southern Madagascar has been extensively cleared, and remains only in isolated fragments (Smith 1997; Sussman *et al.* 2003). The IUCN lists Ringtails as Vulnerable (Ganzhorn *et al.* 2000), but recent habitat surveys suggest this listing should be upgraded (Sussman *et al.* 2003). Of the six protected areas containing wild Ringtails, Berenty holds one of the largest populations.

Unlike Ringtails, the introduced Brown lemurs are strong competitors. Like Ringtails, they eat primarily fruit and leaves supplemented with occasional prey items, and like Ringtails, fruit and leaves from the tree *Tamarindus indica* makes up a substantial part of their diet. In high quality habitat, Brown lemurs reach much higher density than do Ringtails (Sussman 1972) and deplete patches of mutually preferred foods to lower levels, (Ganzhorn 1986). Ringtails and Brown lemurs share great similarities in life history, morphology, seasonal growth patterns, reproductive biology and seasonality, maternal investment, and juvenile development (Sussman 1972; Pereira 1993). Both are group-living and diurnal; Ringtails are territorial while Brown lemurs are not.

The Brown lemur introduction, however, may not place the Berenty Ringtail population at risk. Brown lemurs and Ringtails are naturally sympatric in part of their natural ranges, about 300km northwest of Berenty (Sussman 1972). Brown lemurs' range extends from dry forest north into tropical rainforest, while Ringtails' extends south into arid habitat (Sussman 1972). Brown lemurs are not endangered, and were released at Berenty by accident. Yet if their natural range were to become uninhabitable, Berenty would be a logical introduction site. Berenty is similar in resource availability, composition and seasonality, to forests in which the species are naturally sympatric, and has the same species of predators and other sympatric primates (Sussman 1972; Pinkus unpublished data). *T. indica*, a preferred food for both species in natural sympatry, is abundant at Berenty. In naturally sympatric populations of Ringtails and Brown lemurs, Sussman (1972) found little interspecific overlap in habitat use or diet, and rarely observed interspecific interaction of any sort. He described Brown lemurs as highly arboreal diet specialists, who ate primarily mature leaves and fruit from *T. indica*, seldom ventured outside of closed canopy forest, and spent less than 3% of their time on the ground. Ringtails, in contrast, were semi-terrestrial, ate a much greater variety of plant species, and were found at all levels of the forest canopy, most frequently below 15m high and on the ground (Sussman 1972). Like Brown lemurs, Ringtails inhabited closed canopy forest, but most of their territories included

large areas of transition forest and scrub at the forest edge (Sussman 1972). Ringtails outside of sympatry with Brown lemurs act much as Sussman (1972) observed in sympatry (Sauther 1991; Yamashita 2002). Brown lemurs outside of sympatry with Ringtails exist in both dry forest and rainforest, and exhibit a variety of ecologies, none as specialised as in natural sympatry (*e.g.* Overdorff 1991; Scholz and Kappeler 2004).

Sussman (1972) did the **only** study of Ringtails and Brown lemurs in natural sympatry, though Ganzhorn (1985, 1986) studied Ringtails and Brown lemurs housed together in large enclosures at Duke Primate Center. Long-term research on the allopatric Ringtail population at Beza Mahafaly Special Reserve in southwestern Madagascar (*e.g.* Gould *et al.* 1999; Yamashita 2002; Gould *et al.* 2003) provides an important comparison to Berenty. Beza Mahafaly has similar vegetation to Berenty (Sussman 1972; Sussman and Rakotozafy 1994) and similar fauna, but has neither Brown lemurs nor water provisioning. Simmen *et al.* (2003) studied sympatric Brown lemurs and Ringtails in food-provisioned habitat at Berenty. I have not used their results for comparison because the dynamics of food-provisioned Ringtails at Berenty are beyond the scope of this study.

Since their introduction to Berenty in 1974, Brown lemurs have increased exponentially, forming a population that acts very unlike Brown lemurs in natural sympatry with Ringtails. They have colonised all parts of the Reserve, even the edge habitat normally monopolised by Ringtails. Their diet and use of canopy levels at Berenty overlap almost completely with that of Ringtails. Interspecific aggression over food is common. Despite the introduction of Brown lemurs, numbers of Ringtails in high quality habitat at Berenty have recently almost doubled, though they were apparently stable from at least 1972 until 1985. The recent Ringtail population growth suggests a lack of impact from the Brown lemur introduction. However, a population's size may remain stable or even increase as environmental conditions worsen, then decline abruptly (Abrams 2002). Thus, the growth of Brown lemur numbers at Berenty may threaten the long-term stability of Berenty's Ringtail population (*e.g.* Jolly *et al.* 1982; Jolly *et al.* 2002). Information about the impact of the Brown lemur introduction, and its incorporation into our understanding of Ringtail demography at Berenty, is needed to inform a management plan for Berenty's Ringtail population. I provide some of this information in this thesis.

Regulations at Berenty, and the vulnerable status of the Ringtail population, preclude manipulative experiments. Instead, I used natural and human-induced environmental variability at Berenty to examine the effects of Brown lemurs on resources limiting Ringtails. I considered three kinds of limiting resources: presence of closed-canopy forest, water availability, and

availability of *T. indica* fruit, the key dry season food for both lemur species. Closed-canopy forest at Berenty decreases with distance from the Mandrare River. Water availability varies among seasons, with distance ~~from~~ the river, and is affected by water provisioning. *T. indica* fruit availability varies with distance from the river, and fluctuates in response to droughts. Droughts affect both food and water availability in the drought year, and may affect food availability in subsequent years (Ganzhorn *et al.* 2003).

My specific goals are to test the hypothesis that the Brown lemur population is having a negative demographic impact on Ringtails at Berenty, and to understand what factors affect Ringtail and Brown lemur population density there. To do so, I studied the population dynamics, resource use, and response to drought of Ringtails and Brown lemurs at Berenty.

I show here that there are two significant differences between the ecology and demography of Ringtails and Brown lemurs at Berenty as compared to natural sympatry. First, interspecific differences in diet and habitat use are much less at Berenty. Second, relative population densities at Berenty are biased towards Ringtails in rich habitat, and Brown lemurs in marginal habitat. Taken together these results suggest a strong potential impact of Brown lemurs on Ringtails at Berenty; surprisingly, I found no evidence of such an impact. Based on these results and previous studies I suggest water provisioning at Berenty may explain this apparent paradox. Accordingly, the management of water provisioning at Berenty may have a crucial effect on co-existence of Brown lemurs and Ringtails there.

Methods

Study Site

Site Location

Berenty is a 200ha privately owned wildlife reserve in deciduous gallery forest. It lies in semi-arid southeastern Madagascar, 25° 02' S, 46° 15' E. The region is subdesert, but the raised water table around rivers supports narrow bands of gallery forest. Berenty, and an adjacent parcel of degraded, partially cleared forest, form a 350ha habitat island bounded on one side by the Mandrare River and on three sides by sisal plantations. These boundaries effectively prevent immigration or emigration by lemurs. The nearest occupied Ringtail lemur habitat is approximately 40km distant.

The data used in this study were collected in Malaza, a 97ha parcel of gallery forest located at the centre of Berenty. Malaza abuts a tourist development to the west, the Mandrare River to the east, 40ha of closed canopy forest to the north, and 210ha of degraded open-canopy forest and subdesert to the south. Ringtail and Brown lemurs *are* present in all forest parcels. Ringtail, but not Brown, lemurs range throughout the tourist development. Ringtail and Brown lemurs in Malaza are habituated to human presence and can be approached within 2-5 meters without noticeably altering their behaviour.

Native Lemur Species, Predators and Competitors

Five sympatric native prosimians are found at Berenty. There are two diurnal group-living species: Ringtail lemurs and white sifakas (*Propithecus verreauxi verreauxi*), and three nocturnal species: common mouse lemurs (*Microtus murinus*), dwarf lemurs (*Cheirogalius major*), and sportive lemurs (*Lepilemur mustelinus*). Potential predators of lemurs include the raptors *Polyboroides madagascariensis* and *Buteo madagascariensis*, feral cats and dogs, and the boa constrictors *Acrantophis madagascariensis* and *Sanzinia dumerilii*. Predation does not seem to be a significant source of mortality for Ringtails or Brown lemurs. The rufous fruit bat (*Pteropus rufus*) is a potential food competitor of Ringtail lemurs.

Introduced Lemur Species

On January 25th 1975, M. Jean de Heaulme introduced eight juvenile red-fronted Brown lemurs (*Eulemur fulvus rufus*) to Berenty. Their provenance was Analabe Reserve, a deciduous dry forest 300km northwest of Berenty (M. Jean de Heaulme, interview, September 1998; see also Jolly *et al.* 1982). In addition up to 9 collared lemurs (*Eulemur collaris*), probably

originating in the Anohahela region east of Berenty, have been introduced periodically since the 1960's (O'Connor 1987; M. Jean de Heaulme personal communication Alison Jolly personal comment). An increasing number of apparent hybrids between *E. collaris* and *E. fulvus rufus* were observed from the late 1980's. Molecular genetic analysis showed that a third of 88 animals sampled were hybrids, and suggested that the actual proportion was even higher (Jekielek 2002). Because of the presumed hybrid nature of the Berenty Brown lemur population, I will use the term "Brown lemur" to mean any of *Eulemur fulvus rufus*, *E. collaris*, or *E. f. rufus* \times *E. collaris*.

Forest Condition

Hunting, logging and grazing by livestock have been effectively prevented within Malaza since 1936, though some hunting may have occurred between 1978 and 1979 (Jolly *et al.* 2002). The forest's structure, and plant species diversity and composition, is typical of gallery forests in the area. Few non-native species are present in the forest interior, with the notable exception of *Cissus quadrangularis*, an invasive creeper. Over the last 20 years, Berenty has become one of the most visited tourist destinations in Madagascar. Most disturbances in Malaza are the direct or indirect result of tourism. Wide trails, and water troughs, filled sporadically during the dry season, are present throughout the forest. The distances between Malaza's water troughs range from approximately 150m in Gallery Forest to 500-1000m in Scrub Forest. Food provisioning with bananas has occurred in the tourist area outside Malaza since 1985 but does not affect troops inside the forest (Jolly pers. com.; personal observation).

Climate and the Lemur Life Cycle

Berenty has a low, but highly variable annual rainfall (545 ± 192 mm/yr) and a 7-8 month dry season beginning in March (O'Connor 1987). Ringtail and Brown lemurs have seasonal and highly synchronous reproduction. At Berenty, late gestation, birth, and most mortality of juvenile Ringtail and Brown lemurs, occur during the late dry season (July to October), when drinking water, young leaves, fruit and flowers are scarce. Most births occur within a one-month period between late August and mid October. The timing of the birth peak varies slightly with species and year (Ringtail lemurs: Koyama *et al.* 2001; Jolly *et al.* 2002). Infants are weaned during the wet season (November to February), when resources are more abundant.

Dispersal

I have assumed that dispersal plays a negligible role in explaining population growth rate or the ratio of juveniles to adult females. At Berenty, Ringtail lemur troops and their offshoots tend to occupy the same home range over long periods (Jolly and Pride 1999). While fewer

years of data are available for Brown lemur troops, they seem to show similar home range stability. In both species, females are philopatric, and adult males transfer regularly among troops (Wimmer and Kappeler 2002; Sauther *et al.* 1999). Thus, while there is considerable turnover of males among troops, dispersal leads to little overall change in the number of males or troops within a region. Since most females remain in their natal troops, dispersal is also unlikely to explain differences in the ratio of juveniles to adult females. Because Malaza is contiguous with other occupied lemur habitat, the occasional troop may move into or out of Malaza. This source of error is small (< 5%); only approximately 10 animals per year appear or disappear.

Habitat Types

Malaza's vegetation grades from closed canopy forest near the river to subdesert as soil moisture decreases. Previous researchers have divided this vegetation gradient into two (e.g. Jolly *et al.* 2002) to eight (Howarth *et al.* 1986) habitat regions. I distinguished Scrub and Gallery habitats. I used a qualitative survey of plant associations, a quantitative survey of canopy cover, and 24 50 x 2m vegetation transects (transect method after Sussman and Rakotozafy 1994) to delineate these habitat type boundaries on a 25m² grid map. This habitat classification system is consistent with other demographic studies of Ringtail lemurs at Berenty (e.g. Jolly and Pride 1999; Jolly *et al.* 2002), which classify forest-dwelling Ringtail lemur troops' home ranges as either Scrub or Gallery. Delineating habitat boundaries rather than individual home ranges allowed me to account for the differing spatial arrangement of Brown and Ringtail lemurs' home ranges.

Gallery Forest stretches from the riverbank to 200m-300m inland. It has a closed canopy approximately 20m in height and dominated by *Tamarindus indica*, *Acacia royumae*, *Celtis philipensis*, and *Neotina isoneura*, and an understory of *Rinorea greveana*, saplings of canopy species, and lianas. As distance from the river increases, the distance between canopy-level trees increases. By 200-300m from the riverbank, Gallery Forest gives way to more open Transitional Scrub Forest. Here the canopy is more open (< 50% cover) and is approximately 15m in height, with similar species composition to Gallery Forest. The understory contains a mixture of gallery forest species and tangles of xerophytic thorny vines and bushes. By 400-600m from the river, Scrub Forest has little canopy (< 2% cover) and few trees over 15m in height. It contains small patches of the same canopy species as in the Gallery Forest, and large thickets of thorny or succulent xerophytes, dominated by *Azima tetracantha*, *Caparis spp.*, and *Euphorbia spp.* Scrub Forest grades into subdesert by 800-1100m from the river within the reserve, or into agricultural fields outside the reserve.

These forest types form a roughly linear gradient of decreasing availability of preferred food species, water, and access to tree cover; there is a corresponding decrease in lemur population density and an increase in home range size for Ringtail (Budnitz and Dainis 1975; Jolly and Pride 1999) and Brown lemurs. Jolly *et al.* (2002) define a further habitat type at the forest edge, "Tourist", an area of cleared forest with buildings including accommodation, a restaurant and a museum. This area, developed since 1985, has intensive food provisioning, permanent standing water during the dry season, and many introduced tree species that are heavily utilized for food by some Ringtail troops in the dry season (Rasamimanana and Rafidinarivo 1993). Ringtail lemurs live at high density in Tourist habitat. These troops range and forage primarily in Tourist habitat but sleep in Gallery, and feed there briefly each day (Jolly *et al.* 2002). There are no resident Brown lemurs in Tourist habitat, though troops occasionally forage there. I have not included Tourist area troops in my demographic analyses.

Continuity of Research

The demography and ecology of Ringtail lemurs in Malaza have been studied repeatedly since the 1960's (*e.g.* Jolly 1966; Jolly 1972; Budnitz and Dainis 1975; Sussman 1972; Budnitz 1978; Jolly *et al.* 1982; Howarth *et al.* 1986; O'Connor 1987; Jolly *et al.* 1993; Rasamimanana and Rafidinarivo 1993; Jolly and Pride 1999; Mertl-Millhollen 2000; Mertl-Millhollen *et al.* 2003; Simmen *et al.* 2003; reviewed in: Mertl-Millhollen *et al.* 1979; Koyama *et al.* 2001; Jolly *et al.* 2002). Researchers have developed and passed on intimate familiarity with the identities and home range locations of all Ringtail lemur troops. The demography and ecology of Brown lemurs in Malaza have also been studied, but less intensively, since their introduction (Jolly *et al.* 1982; O'Connor 1987; Davidson 1991 unpublished; Jekielek 2002; Simmen *et al.* 2003).

Diet Overlap and Activity Patterns

Sampling Design

To compare Ringtail and Brown lemur diet, activity patterns and micro-habitat use, I observed 7 troop-pairs, each composed of one troop of Brown lemurs and one troop of Ringtails of similar size (within 2 adult animals) and with nearly or completely overlapping home ranges, and therefore access to similar resources. Four troop-pairs in Gallery Forest and 3 pairs in Scrub Forest were each sampled for one 12-hour "follow" per troop. Ringtails have similar foraging and ranging patterns on different days, with changes reflecting food plant phenology rather than erratic ranging (Alison Jolly, pers. comm.). I assume that one 11-12 hour sample reflects a given troop's foraging and ranging patterns at a given stage of food plant phenology. To control for

changing resource availability, paired troops were followed within two days of each other (range: 1-4 days). Most follows lasted from 0600-1800h; a few began later when particular troops were hard to find, but always before 0715h. Data were collected between 9/05 and 9/20, 2000.

Personnel

Follows were done by teams of 5-8 observers (minimum 2 observers for every 3 lemurs). All observers had previously observed lemur behaviour using similar data collection methods. At least one of two observers, Alison Jolly and myself, supervised all data collection in order to assure standard interpretation of data categories. R. Ratsirarson from Tsimbazaza Botanical Museum in Antananarivo identified all plant species.

Data Collection

During follows, 5-minute scan samples (Martin and Bateson 1993) were used to record activity patterns and resource use. The total duration of data collection for one scan varied from 30-90 seconds. At each scan, we recorded the major activity of the troop (feed, travel between patches, move within a patch, rest, sun, interspecific encounter) and the location of the majority of the troop. "Major" was defined as the greatest number of animals doing the same activity or in the same location. For each patch being fed in by a troop member we recorded species and size of the patch, plant part being fed on (young leaf, mature leaf, old leaf, unripe fruit, ripe fruit, flower, insect, drink, other), majority height of troop members in the patch, number of animals visible, number feeding, and total number known to be in the patch.

Definition of "Patch"

In this study, I use the word "patch" to refer to a discrete food source fed in by a lemur. A patch could be a tree, a bush, a swarm of caterpillars on a dead log, a clump of herbs on the ground, etc. A patch is equivalent to one plant of a given species if it is a tree or bush, the diameter of the patch is then its canopy diameter, estimated by eye. For patches in ground vegetation, a patch is a group of plants, dead leaves, insects, etc. in which a lemur can feed continuously. For these patches and for patches of lianas, patch diameter is the greatest width of the patch from edge to edge, estimated by eye.

Data Analysis

For each follow, I summed the number of scans in which each activity was recorded and expressed them as a proportion of the total number of scans recorded that day. To analyse the feeding data, I summed the number of animals recorded on each scan feeding on a particular resource type, resource part, or height, and expressed it as a proportion of the total number of animals recorded feeding on any patch that day. Most resource types were trees, shrubs, lianas

or forbs identified to species level. Two resource types represent more than one food species: "Litter" refers to dry plant matter found in the leaf litter, and "Insect" refers to any invertebrate eaten before it could be identified to species. Four other resource types were: "Phromnia" = glucose-rich secretions of the insect *Phromnia rosea*, "Egg" = bird eggs, "Acacia Worm" = swarms of the larvae of a recognised (though unidentified) butterfly species, "Dirt" = soil without visible plant or animal material in it. "Animal Minute" refers to one animal feeding in one patch during one scan. Feeding data are presented as proportions of total Animal Minutes spent feeding.

I calculated Horn's Index of Overlap (Krebs 1999) to estimate diet overlap between all pair-wise combinations of lemur troops. I compared estimates of overlap between members of the same troop-pair with the mean of the estimated overlap between each member of the troop pair and all other troops in that habitat type. Diet breadth, or degree of diet specialization, can be thought of as the number of resource types making up some minimum proportion of the diet (Krebs 1999). I characterised diet breadth as the number of resource types making up at least 4% of total diet for one lemur species in one habitat. To estimate diet breadth, for each habitat type, I summed the number of Animal Minutes each lemur species spent feeding on a given resource type, and expressed it as a proportion of the total number of Animal Minutes that species spent feeding.

Censuses of Brown and Ringtail Lemurs

Comparability of Censuses

Complete censuses of Ringtail lemurs in Malaza were performed in 1972-3 by Budnitz and Dainis (1975), in 1975 by Merti-Millhollen *et al.* (1979), in 1983-5 by O'Connor (1987), and in 1989-2000 by Jolly *et al.* (2002). In all these censuses, observers walked along trails, and transects between trails, until they had accounted for all known Ringtail troops and identified any unknown troops (Jolly *et al.* 2002). Ringtail lemurs maintain nearly identical home range boundaries over decades, and females are individually recognizable and do not migrate, so known troops are easy to find and identify (Jolly *et al.* 2002). New troops tend to be offshoots of known troops and usually range within or immediately adjacent to the source troop's home range (Jolly and Pride 1999). Malaza's small size, the predictable distribution of Ringtail lemur home ranges, Jolly's decades of familiarity with the population, and the repeated censuses, allowed almost complete censuses.

The first complete censuses of Brown lemurs at Berenty took place in 1985 (O'Connor 1987) and 1991 (Davidson, unpublished data). I assume that the Brown lemur censuses done prior to 1993 are fairly accurate, as numbers of individuals then were fairly small. Between 1993 and 2000, I conducted 5 complete population censuses of Brown lemurs in Malaza. My method was adapted from that used to census Ringtails. However, because ranges of Brown lemur troops overlap more than Ringtail lemur troops, and are less predictable, I added several steps to the census method used for Ringtail lemurs in order to avoid missing or double-counting troops (see below). The following describes the Brown lemur census method only. For a complete description of the method used to census Ringtail lemurs, see Jolly *et al.* 2002.

Timing and Personnel

Brown Lemurs were censused mainly during the late dry season, when troops are most conservative in their range use, migration among troops is infrequent, and juveniles are small enough to be clearly distinguished from 2 year olds and adults. Moderate daytime temperatures, low nighttime temperatures, and low rainfall make animals more active during the day and therefore easier to see and hear than during the wet season. The censuses in 1993-2000 were conducted by myself, assisted by John Walker in all years. Sabine Day, Stuart Hall, Jan Jekielek, Voudjanahary Ranaivosoa, Margaret Solberg, George Williams and Theresa Williamson assisted for one year each.

Accuracy of Census Data

Conditions in Malaza allow accurate and complete Brown lemur censuses. The forest's low height and open mid-story make it easy to see into tree canopies, where Brown lemurs spend the majority of their time. The trail system makes all areas of the forest easily accessible. During the dry season, even troops inhabiting regions of the reserve without trails use the trails every 1-3 days to visit water troughs. The Brown lemur population is well habituated and can be approached closely enough for an observer to distinguish facial characteristics and to dye-mark individuals (see below) without capturing them.

I tested the completeness of my censuses in the following way. After finishing the 1996, 1998 and 2000 censuses I waited for at least two weeks and then spent 2-3 further weeks (120-200 observer hours) recounting known troops and searching for unknown troops. I identified only one unknown troop of seven animals in 1998. During the re-census period, this troop ranged primarily outside my census region, but occasionally ventured a short distance into Malaza to visit a water trough.

Census Procedure

To locate Brown lemur troops, observers used binoculars to scan tree branches and canopies. They also listened for Brown lemur vocalisations, which vary from soft pig-like grunting contact calls to unmistakable and loud retching long calls made by several animals at once. I divided the census region into approximately 4 ha sections, each small enough that an observer walking through the area could scan with binoculars into and under every tree, and walk along every trail transecting it within one hour. Sections were smaller (2-3ha) in areas with denser vegetation. In each census, we searched every section with similar minimum intensity, during the morning and afternoon peaks of lemur activity and the midday rest period. We searched each section until we had reached at least the minimum search intensity, and four consecutive searches had yielded no new troops.

In addition to the walking censuses, observers visited every water trough at least every 2 days and spent at least 3 activity periods on different days watching each trough in the dry and transition regions. I considered the census complete when no new troops had been found in at least a week of daily all-day searches. A complete census took 400 - 600 person-hours.

Data Recorded

When an observer encountered a troop they identified it, recorded its location on a 25m² grid map, and noted the age and sex composition of all visible troop members. The first time a troop was sighted we also described at least one third of troop members using a standard system of terms and facial sketches, and noting distinctive characteristics such as missing limbs or tails, unusual pelage characteristics or eye colour, notched ears or facial scars. Sex was identified by pelage colouration; non-infant male Brown lemurs are gray with orange caps while females are brown with black caps. Age classes were distinguished by the size of the animal's genitalia, and corroborated by its body size and the presence or absence of juvenile facial features. All non-infant animals fell into one of two age classes, juvenile (11 to 15 months old) or adult (23 months or older).

Instances when troops crossed open areas were used to check that all animals were accounted for. I considered a troop count to be complete if the same age and sex composition were recorded during at least 4 consecutive independent sightings. In each census, I verified all troop compositions recorded by another observer, and verified troop location and identity for about 85% of all sightings of known troops. An assistant verified all troop compositions that I recorded.

Dye-Marking

To ensure that no troop was counted twice, we used "Bigen" black hair dye (supplier: Nishimoto Trading Co.) to place unique markings on the pelage of several individuals in every troop. Only juveniles, adult males and non-lactating females were marked. The dye remained visible for 10-16 weeks, several weeks longer than the duration of a census. To apply the dye, we used banana or mango to bait members of a troop to within 1m and then squirted dye onto their bodies with a 5cc syringe. Most animals did not react noticeably to being marked. Some individuals, particularly juveniles, appeared startled by the sensation of the dye; but they returned to normal behaviour within about one minute. The baiting disrupted the troop's behaviour for 30-60 minutes while they searched for leftover fruit.

Analysis of Census Data

Rainfall

Monthly rainfall data for the years 1983-1986 and 1987-2000 were collected by M. Charles Rakotmalala and provided to A. Jolly. High rainfall in July 2000 was the result of cloud seeding to assist drought-stressed food crops. To examine the effect of rainfall on lemur survival and recruitment I considered the sum of rainfall over two seasons: "Wet", from October of year N until March of year N+1, corresponding to lactation and weaning of Brown and Ringtail lemurs; and "Dry", from April until September of year N+1, corresponding to mating and gestation. To get total rainfall per "lemur year" N, corresponding to the first year of life of the juvenile cohort censused in October of year N+1, I summed rainfall from one Wet season to the end of the next consecutive Dry season (October year N until September year (N+1)(Jolly *et al* 2002).

I designated each lemur year and Wet or Dry season of rainfall as "drought" or "regular". I defined drought rainfall as less than 60% of the yearly or seasonal mean for 1983-2000, and regular rainfall as 60% or more of the mean. In analyzing the effect of rainfall on lemur demography, I used rainfall from lemur year N, and census data from October of lemur year N+1. To examine lagged effects of drought, I classified the two lemur years following a drought year (*i.e.* census data from October of lemur year N+2 and N+3) as "post-drought" and grouped them for analysis. In one case, 1992, a post-drought year had drought rainfall and was analysed as a drought year. Because demographic data were available for only one year in which there was a Dry season drought without a Wet season drought, I could not distinguish the effect of drought in a particular season. In my analysis, I considered only Wet season drought because

most growth and opportunity for building up energy reserves occur during this season (Jolly *et al.* 2002). To test the hypothesis that lemur demography was affected by the degree of year-to-year variation in rainfall rather than the absolute amount, I repeated the analysis using "change in rainfall", the difference between wet season rainfall in the year preceding the census and in the previous year.

Habitat Classification of Troop Ranges

To examine the relationship between habitat type and lemur demography, I assigned each troop of Brown or Ringtail lemurs to a habitat type. The habitat categories I used reflect dry season home ranges. Dry season home ranges are likely similar to wet season home range for Ringtails (Jolly and Pride 1999). Brown lemurs, however, vary their range use considerably among seasons (Overdorff 1991; J. Davidson pers. comm.). I have assumed that each troop's demography was primarily affected by the habitat type in which I categorised it.

I classified all Brown and Ringtail lemur troops as either Scrub or Gallery or, for Ringtail lemurs only, Tourist, based on the location of their home ranges. I classified the habitats of Brown and Ringtail lemur troops using slightly different methods because of differences in the range data available for each species. To classify Ringtail lemur troops I followed Jolly's habitat classifications (Jolly and Pride 1999; Jolly *et al.* 2002), which she based on the location of a troop's home range and primary feeding and resting sites during opportunistic sightings and 12-hour follows.

I estimated the location of Brown lemur home ranges (N=92) as the smallest area including all grid squares in which the troop was sighted during the census. These data represented an average of 16 individual sightings per troop (range 9-46) including an average of 3 sightings during which each troop was followed throughout an entire activity period (range 1-5). Six troops were followed once only. I excluded them from analyses of habitat-specific survival and recruitment, but included them in analyses of population size and density. I assigned Brown lemur troops to the habitat type they occupied in at least 75% of sightings. If a troop was not sighted in a single habitat type 75% of the time (n=8 troop ranges, out of 92 analysed), I assigned it to the habitat type in which it fed and rested.

I assumed that opportunistic sightings and short follows of Brown lemurs gave a sufficiently accurate estimate of home range location to assign the troop to a habitat type. To test this assumption, I compared estimates of home range locations of four troops based on opportunistic sightings with estimates for the same troops based on eight weekly 12-hour follows in which troop location was recorded every 10 minutes. For an additional seven troops of Brown

lemurs, I compared estimates of home range location based on one 12-hour follow in which troop location was recorded every 5 minutes (Jolly and Pinkus unpublished data). In all cases, home range locations estimate by both methods fell within the same habitat.

An average of two troops of Ringtail lemurs (range 1-3) and three troops of Brown lemurs (range 1-6) per year ranged in Transitional Scrub habitat and were grouped with Scrub troops for analysis. I assumed that the demography of these troops was similar to the Scrub troops with which they were grouped. To check this assumption I explored trends in population growth rate and juvenile recruitment for Transitional Scrub troops. For some non-drought years there is a visual trend towards higher juvenile survival in Transitional Scrub than Scrub troops of both Ringtail and Brown lemurs. There is no clear trend for population growth rate, or for juvenile survival during drought years. Excluding Transitional Scrub troops from the analysis, or analyzing them as a third category, neither changed the direction of population trends nor produced a significant difference in estimates of population growth rate or juvenile survival (t-test, 2-tailed, $p > 0.10$ for all tests).

Juvenile Recruitment

In 1995, 1998 and 2000 I was unable to count the numbers of births in Brown lemurs. I therefore used the ratio of adult females to juveniles within a troop as an index for recruitment of one-year-olds. This ratio is affected by several demographic parameters besides juvenile survival: fecundity, survival of adult females, and rate of dispersal by adult and juvenile females. The ratio's utility as a relative measure of juvenile recruitment depends on these parameters varying similarly among all troops within a habitat type. I assumed that this assumption was met by the troops I studied. There are insufficient demographic data to evaluate this assumption rigorously, but it is consistent with the few data that are available.

Finite Rate of Increase

I calculated the finite rate of increase (Sibley *et al* 2003) of *L. catta* in each habitat as $\lambda = N_{t+1}/N_t$, where N is the number of animals at least 2 years old counted in an October census, and t is the lemur-year of the census. Censuses for *E. fulvus* were not done in consecutive years, so I could not directly calculate λ for *E. fulvus*. I chose not to estimate λ of *E. fulvus* by interpolation because λ is sensitive to small changes in population size. However, I did use interpolation for estimates of *E. fulvus*' density (see below), since density is less sensitive than λ to changes in population size.

Population Density

Using the 25m² grid map of habitat types, I calculated the area of Gallery habitat in Malaza as 0.18km², and the sum of Scrub and Transition habitat as 0.80km². I therefore estimated population density as the number of animals ranging in that habitat type, divided by the area of the habitat type. I extrapolated Brown lemur population size for years in which they were not censused using a simple linear regression of Brown lemur population size over time, from 1975–2000.

Ringtail Census Data

I have analysed data from 94 Ringtail lemur troop counts in Gallery and 86 in Scrub/Transition. Each troop count represents the annual census record for one troop in one year. Jolly *et al.* (2002) describe Ringtail lemur census data, and the relationship of numbers of animals to habitat type and rainfall. I have re-analysed many of these data, but with a different emphasis. I made the following five assumptions and decisions about Ringtail lemur census data. First, many of the same troops were recounted in consecutive years but, because troop identities were often uncertain, I have treated annual censuses as independent. Second, for years in which the sex of 2-year-old adults was not censused, I assumed a 50% sex ratio. Third, I excluded from my analysis all years or habitat types in which not all Ringtail troops were censused, with the following exception. Fourth, I included data from Scrub habitat in 1991, 1992 and 1993 which *may* be undercounts (Jolly pers. comm.) but which indicate a large increase in population size and are useful minimum estimates to show the trend in population growth. Fifth, I excluded from my analysis any biologically unrealistic increases in numbers of particular age classes, on the assumption that these represent counting errors. For example, I excluded data for a troop with two infants in 1991 and five 1-year-olds in 1992. In total, I excluded one year of data for each of five troops under this rule. For years in which troops were counted in August but not found again in October, I used the August count.

Brown Lemur Census Data

I analysed data from 54 Brown lemur troop-counts in Gallery, and 37 in Scrub/Transition. I excluded data from counts of five troops censused in Malaza but that ranged primarily in adjacent forest.

Statistical Analysis

In most cases, I used a significance level of 5% and two-tailed tests. In some cases, however, I comment on trends where sample sizes were low and alpha was > 0.05. I used parametric statistical tests when possible. Where my data did not meet the assumptions of parametric tests, I used the non-parametric equivalent. I used Pearson's product-moment

correlation to analyse the correlation between population size in different species and habitats, and linear regression to analyse the effect of rainfall-amount and troop size on λ and mean juvenile recruitment. One-way Analysis of Variance (ANOVA) was used to analyse differences in annual means of λ and juvenile recruitment among drought, regular and post-drought years. I employed 2-sample t-tests to compare samples of population sizes and measures of juvenile recruitment among time intervals and habitats. Data were described using 95% confidence intervals (C.I.), and coefficients of variation (C.V.), where C.V. = Standard Deviation /Mean.

Results

I characterized the effect of the introduced Brown lemur population on the native Ringtail lemur population in two ways. First, I examined interspecific overlap in resource use (Section A) and second, I considered the effect of growing numbers of Brown lemurs on the population dynamics (Section B) of Ringtail lemurs. I considered separately density-dependent effects (Section C) and the possibility of a density-independent numerical response to annual variation in rainfall (Section D).

A. Interspecific Overlap in Resource Use

Were the Conditions for Interspecific Resource Competition Present?

The growing population of Brown lemurs is expected to have a significant demographic impact on the Ringtails if the two populations share the same limiting resources, and are able to deplete them. Although Ringtails and Brown lemurs in natural sympatry have low overlap in diet and habitat use (*e.g.* Sussman 1972), the situation at Berenty was very different. Pilot studies at Berenty (Davidson unpublished data; Jolly *et al.* unpublished data) suggested a high degree of overlap in diet during September and October, a time of seasonal resource scarcity during which reproducing females face their highest energy demands (Jolly *et al.* 2002; Sauther 1993). Anecdotal observations (personal observation; Naoki Koyama pers. comm.) of interspecific aggression in food patches during these months confirm potential contest competition for the keystone food tree species (*sensu* Sauther 1993) *Tamarindus indica*. I also found that feeding lemurs deplete the availability of fruit and new leaves on *T. indica* (see Discussion). Based on these indications of interspecific resource competition, and because of the contrast with the ecology of naturally sympatric Brown lemurs and Ringtails, I analysed interspecific diet overlap, the use of keystone resources, and the use of vertical and horizontal space.

Diets

I analysed the degree of interspecific diet overlap between Brown lemurs and Ringtails at three levels: food species eaten, part of the food species eaten, and use of keystone resources. I compared the proportion that each diet component made up of a troop's total feeding time. For several reasons, these data should be considered minimum estimates of diet overlap. Simulations have shown that Horn's Index underestimates overlap, particularly when sample sizes are small

or uneven, as they are in these diet data (Krebs 1999). In addition, these diet data may underestimate Brown lemurs' dietary breadth because Brown lemurs feed both by day and by night, and we only collected feeding data during the day. I found that Brown lemurs ate few resource types not eaten by Ringtails (5 spp in Gallery, 4 spp in Scrub), and sampled fewer species in total. It is possible that, had we sampled nighttime feeding, we would have recorded a broader diet for Brown lemurs, resulting in higher estimates of inter-specific diet overlap. Nonetheless, the data presented below show substantial diet overlap.

Overall Diet Breadth and Overlap

Despite Brown lemurs' previous characterization as specialists, and Ringtails' as generalists (Sussman 1972), diet breadth at Berenty did not differ significantly between the two species, though Brown lemurs had a slightly narrower diet, particularly in Scrub (Figures 1A & 1B). Diet breadth in Scrub was 4 spp for Ringtails and 2 spp for Brown lemurs. The pattern reversed in Gallery: 3 spp for Ringtails and 4 spp for Brown lemurs. Four plant species accounted for 84% of the diet of Ringtails in Scrub, 87% for Ringtails in Gallery, 90% of the diet of Brown lemurs in Scrub, and 94% for Brown lemurs in Gallery. Both Ringtails and Brown lemurs ate all of these species. Two of the three plant species fed on most intensively (*Tamarindus indica* and *Celtis philipensis*) were the same for both lemur species in both habitats.

In both Scrub and Gallery habitats, Ringtails ate more different food species (Gallery and Scrub = 27 spp) than Brown lemurs (Scrub = 18 spp; Gallery = 15 spp). However, Ringtails ate only small amounts of the species not eaten by Brown lemurs. In consequence, diets were similar across the two species. No food plant species eaten by only one lemur species represented more than 2.5% of the lemur species' diet. As a result, diet breadth, which I calculated as the number of food types making up at least 4% of the diet (Krebs 1999), is similar between Ringtails and Brown lemurs despite the much larger number of resource types sampled by Ringtails. To put these diet breadth data in perspective, given the sample sizes in this study, half of a troop recorded feeding on a resource during one 5-minute scan represents about 0.5% - 1% of that lemur species' diet for that habitat type.

Diet Overlap Across Troop-pairs and Habitats

There was high diet overlap within each troop-pair. The mean value of Horn's Index of Overlap (I_o) was 0.84 (95% C.I. 0.74-0.94, $n=4$ troop-pairs) for troop-pairs in Gallery, and 0.79 (95% C.I. 0.75-0.83, $n=3$ troop-pairs) in Scrub. Troop-pair diet overlap was similar to overlap of either member of the pair with other troops of the opposite species (95% C.I. Gallery 0.73-0.85, $n=4$ troop-pairs; Scrub 0.80-0.88, $n=3$ troop-pairs). Within each habitat type, intra-specific diet

overlap was almost identical to inter-specific diet overlap, and was not significantly different from overlap within troop-pairs (Figure 1C). Seven of eight troops in Gallery, and four of six troops in Scrub, had greater diet overlap with their pair-troop than with other troops of the same species. Comparing across habitats, inter- and intra-specific diet overlap was slightly higher within than between habitats (inter-specific I_0 between habitats: Brown lemurs 0.75; Ringtails 0.71; intra-specific I_0 between habitats: Brown lemurs 0.76; Ringtails 0.72).

What stands out from these results is that diet overlap is greatest between different species of lemur using the same home range. The diets of Brown and Ringtail lemurs are so similar that, even within a habitat type, different species using the same home ranges are more similar than troops of the same species using different home ranges. Species-specific differences in diet appear to have a negligible effect in comparison to the effect of small-scale habitat variation. This variation among habitats may reflect differences in both spatial distribution and abundance of food species, and temporal variation in plant phenology.

Feeding Height

Even with nearly complete diet overlap, competition could be reduced if Brown lemurs and Ringtails fed at different heights. Naturally sympatric populations of Brown lemurs and Ringtails do forage at different average heights, with Ringtails spending more time near the ground and Brown lemurs using the highest canopy levels (Ganzhorn 1985; Sussman 1972), thus depleting different "slices" of shared resources. In contrast, at Berenty there was almost complete overlap in the feeding heights in both Scrub and Gallery (Figures 2A and 2B). The amounts of time spent feeding on the ground, close to the ground, and in the upper canopy were all similar. Though the Ringtails spent 4-6% of their time feeding 2-5m above the ground, a height class barely utilized by Brown lemurs, this result stemmed from the behaviour of only two out of seven Ringtail troops - one in Gallery and one in Scrub. The remaining five Ringtail troops used the 2-5m layer similarly to Brown lemurs.

Use of a Keystone Resource

Another potential mechanism for reducing competition, given a high degree of diet overlap, is for the competing consumer species to feed on different individuals of a given plant species, or on different parts of the same individual. Since there was evidence of direct interspecific competition for keystone resources, I compared Brown lemurs' and Ringtails' use of different plant parts (fruit, leaves, buds *etc.*) and patch sizes of *T. indica*. I present here data for Scrub habitat, in which *T. indica* comprises a much larger portion of both species' diet; the pattern is similar for Gallery.

Although *T. indica* trees have very deep canopies with apparently abundant feeding sites at all strata above 5m in height, there was little difference in the feeding heights chosen by Brown lemurs and Ringtails (Figure 2C). There was also no significant difference in use of the most frequently chosen patch diameters, 10-15m and 15-20m. There is a statistically insignificant trend for Brown lemurs to use patches of 5-10m, and >20m in diameter to a greater extent than Ringtails.

There was high overlap in plant parts utilised (Figure 2C), with no significant difference except for leaf buds, which were only fed on by Ringtails. Since leaf buds are an extremely ephemeral resource, opening into new leaves within two days, and Brown lemurs and Ringtails feed on new leaves to a similar extent, it is likely that this diet difference reflects the day that troops were followed rather than inter-specific diet preferences. In choice of patch diameter and plant part, as with diet as a whole, intra-specific variation equalled or exceeded inter-specific variation. Ripe and unripe *T. indica* fruit are the most frequently eaten items. The relative frequency with which Brown lemurs and Ringtails eat each part varies more within than between species (Figure 2D).

Diurnal Activity Budgets

Feeding at different times of day could reduce contest competition for resources, though the slow rate at which plant parts regenerate makes it unlikely that this mechanism would reduce markedly scramble competition (Ganzhorn and Kappeler 1996). In both Gallery and Scrub habitat, Brown lemurs at Berenty spend a smaller proportion of daylight time feeding than Ringtails (2-sample t-tests, $n=14$ troops, $p < 0.05$), and a greater proportion of time sleeping or resting (2-sample t-tests, $n=14$ troops, $p < 0.05$; Table 1). Brown lemurs at Berenty are frequently observed feeding and moving after dark, so their daylight time spent feeding is likely only a part of their total feeding time. We did not make quantitative observations at night.

In summary, overlap in resource use between Brown lemurs and Ringtails at Berenty was extensive; few obvious mechanisms that might have reduced resource competition were evident. This high degree of overlap at Berenty differs from the marked differences in the ecology of these lemur species in natural sympatry (e.g. Sussman 1972). I predicted, therefore, that the presence of the introduced Brown lemurs at Berenty would have a negative demographic impact on the previously stable native population of Ringtails.

B. Population Dynamics

To analyze the demographic effect of the Brown lemurs on the Ringtails, I described changes in the size and demographic rates of the two populations following the Brown lemur introduction in 1974. Few demographic data are available prior to 1974, and Brown lemurs were uncommon until 1990. I did not expect Brown lemurs to have much demographic impact on Ringtails before 1990, and thus distinguished two time intervals, 1974 to 1989, and 1990 to 2000.

Water Provisioning

Another important variable affecting population dynamics at Berenty is water provisioning. Low-level water provisioning occurred in Gallery from before 1974 and was expanded in 1984 and again in 1991. Water provisioning in Scrub habitat began in 1991.

Ringtail Lemur Population Change

The Ringtail population in Malaza remained fairly stable between 1972 and 1985, fluctuating around a mean of 62 animals 2 years old or older (95% C.I. = 57-67 animals, $n=6$ years; Figure 3A). By 1991, when the entire population was next censused, it had increased to 107 animals (1-sample t -test comparing mean population size from 1972-1989 with population size in 1991, 2-tailed, $n=6$ years $p < 0.001$). Since 1991, numbers have remained similar (95% C.I. 121-139, $n=10$ years; Figure 3A).

The increase from the 1970's and 1980's to the 1990's reflects population growth in Gallery habitat. The number of adult Ringtails in Gallery averaged ca. 28 until 1985 (95% C.I. 25-31, $n=6$ years). By 1990 it had increased by 40% to 47. Between 1991 and 2000 the population fluctuated around 66 (95% C.I. 61-71, $n=10$ years; Figure 3B), a mean double that in the 70's and 80's (2-sample t -test, $n=16$ years, $p < 0.001$). Mean population density of Ringtails in Gallery habitat was 192 animals/km² between 1972 and 1985. This figure is comparable to Ringtail density in un-provisioned closed canopy forest habitats (e.g. Sussman 1972). Ringtail density in Gallery more than doubled to 413 animals/km² between 1990 and 2000. Population increase between 1985 and 1990, and between 1991 and 1997, follows expansions of water provisioning in Gallery in 1984 and 1991.

By contrast, despite the presence since 1991 of water provisioning in Scrub, the number of Ringtails in Scrub did not change significantly between the 1970's and the 1990's (2-sample t -test, $n=16$ years, $p > 0.05$). Ringtail population density in Scrub remains similar to un-provisioned populations. There was no significant change in population size between 1991 and 2000, but there is evidence of a trend of decrease between 1997 and 2000 (Figure 3C). In both Scrub and Gallery, numbers are low in the second or third year following drought, having

decreased in two consecutive years (see below; Figures 3B and 3C, droughts occurred in 1970, 1984, 1991-2, and 1997).

Brown Lemur Population Growth and Distribution

Between 1975 and 2000 the brown lemur population in Malaza increased steadily from 9 to 180 animals 2 years old or older (Figure 3A). By 2000, there were 107 additional animals in riverine forest adjacent to Malaza. For my analysis I considered only the animals ranging in Malaza. Initially, the Brown lemurs in Malaza used only Gallery habitat (O'Connor pers. comm.). Since 1995, the number of Brown lemurs in Gallery has averaged 76 animals (Figure 3B), or 516 animals/km², slightly greater than Ringtail population density. By 1990, 6 animals were using transitional Scrub forest adjacent to Gallery (J. Davidson, unpublished data). By 1996, there were 39 animals using the Scrub forest. The number of Brown lemurs in Scrub habitat increased to 100 in 2000, giving a density of 158 animals/km², more than double that of Ringtails. The increase shows no sign of leveling off (Figure 3C).

The increase in numbers of Brown lemurs in Scrub habitat between 1990-1993, and 1998-2000, cannot be explained by recruitment alone; immigration by animals born in Gallery must have contributed. There were 7 Gallery troops in 1990, and 10 from 1996 until 2000, much less growth than expected given Gallery Brown lemurs' high rate of juvenile recruitment. The number of Scrub troops increased much more rapidly during the same period, from 1 in 1990 to 7 in 1996 and 13 in 2000. There is no significant difference between sex ratios of the Scrub and Gallery animals for any census year (paired t-test, $n=6$ years, $p > 0.05$), indicating that both males and females are moving from Gallery to Scrub. Since female Brown lemurs tend to remain in their natal troop, it is likely that entire troops moved from Gallery habitat to Scrub.

Relationships Between Brown and Ringtail Lemur Populations

Contrary to my predictions based on apparent resource competition, the increasing Brown lemur population has not caused a decline in the Ringtail population in Malaza as a whole, or in Scrub or Gallery habitats. In Scrub habitat, the populations have changed independently (Pearson's Product Moment Correlation, $n=6$ years, $r = -0.57$, $p > 0.05$). In Gallery, there is a significant and strong positive correlation (Pearson's Product Moment Correlation, $n=8$ years, $r = +0.89$, $p < 0.01$).

Finite Rates of Increase of Ringtails

The finite rate of increase, λ , describes the proportional change in the size of the adult population from one year to the next. It integrates adult survival and recruitment of juveniles into the population. λ for Ringtails in Gallery between 1990 and 2000 averaged

slightly above replacement (C.V. = 0.15, 95% C.I. 0.94 – 1.16, $n=11$ years; Figure 4A). It was at or close to replacement in less than half the years. In other years, λ swung well above and well below replacement (range 0.85 - 1.28). The value of λ fluctuated with similar amplitude in Scrub (C.V. = 0.17, 95% C.I. 0.87 – 1.09, $n=9$ years; Figure 4A). Mean λ in Scrub was slightly, but not significantly, lower than in Gallery (2-sample t -test, $n=11$ years in Gallery and 9 years in Scrub, $p > 0.05$). Fluctuations in Scrub were not synchronous with fluctuations in Gallery. In the post-drought years 1992 and 1997, Scrub λ values peaked as Gallery hit its lowest values. Few data are available prior to 1990, because many census intervals exceeded 1 year, but λ during that period apparently fluctuated within the same range as between 1990-2000 (C.V. in Gallery = 0.12, $n=3$ years; Scrub = 0.02, $n=3$ years).

Juvenile Recruitment

The index I have used for juvenile recruitment (number of 1 year olds per adult female) incorporates both fecundity and survival of infants from birth to 1 year old. Juvenile recruitment per female (J/F) and λ were not correlated in either habitat.

Mean juvenile recruitment by Ringtails in Gallery between 1990 and 2000 was 0.36 (95% C.I. 0.3 – 0.42, $n=11$ years). Juvenile recruitment fluctuated from year to year, with a fairly narrow amplitude in Gallery (C.V. = 0.39, $n=11$ years; Figure 4B) and greater amplitude in Scrub (C.V. 0.60, $n=10$ years; Figure 4C). Mean juvenile recruitment in Scrub between 1990 and 2000 was 0.31 (95% C.I. 0.19 – 0.43, $n=10$ years), not significantly lower than in Gallery (2-sample t -test, unequal variances, $n=11$ years in Gallery and 10 years in Scrub, $p > 0.05$). Fluctuations in Scrub were synchronous with those in Gallery, but they were magnified. Mean juvenile recruitment from 1972-1985 was similar to that in 1990-2000 for both Scrub and Gallery (2-sample t -test, $n=17$ years in Gallery and 16 years in Scrub, $p > 0.05$). The coefficients of variation of juvenile recruitment were similar for both species.

Mean juvenile recruitment in Brown lemurs between 1990 and 2000 was 0.57 in Gallery (95% C.I. 0.46 – 0.56, $n=6$ years) and 0.45 in Scrub (95% C.I. 0.36 – 0.54, $n=6$ years). It was not significantly different in Scrub (Figure 4C) from in Gallery (Figure 4B; 2-sample t -test, $n=6$ years, $p > 0.05$) and varied asynchronously but with a similar, narrow amplitude (C.V. = 0.18 for Gallery, 0.23 for Scrub). Juvenile recruitment in Brown lemurs was significantly higher than in Ringtails (2-sample t -test, Gallery, Brown lemur $n=6$, Ringtail $n=11$: $p < 0.01$; Scrub, Brown lemur $n=6$, Ringtail $n=10$: $p < 0.05$) and varied less among years. Recruitment in the two species

did not vary synchronously, but the limited number of years with data for both species makes this comparison uncertain.

These results conspicuously fail to show a negative impact of the Brown lemur population on the Ringtail population's size, mean rate of increase, or mean level of juvenile recruitment. Since Brown lemurs were introduced, the Ringtail population has increased in size, although most of the increase took place when numbers of Brown lemurs were still small. Although the combined population density of Ringtails and Brown lemurs increased by almost 400% in Scrub and 450% in Gallery between the 1970's and the 1990's, mean λ and juvenile recruitment rates of Ringtails were not significantly affected. This suggested the Ringtail population was not experiencing density-dependent effects. To examine density-dependent effects more closely, I next examined the relationship between juvenile recruitment and intrinsic rates of increase in Ringtails, and density at both the population level and, for juvenile recruitment only, at the troop level. Because the relative importance of density-dependent and density-independent factors may change during periods of resource scarcity, I analysed post-drought years separately. In post-drought years, food availability at Berenty plummets (see discussion).

C. Does Density Affect Population Growth and Juvenile Recruitment?

Density Dependence at the Population Level

There was no relationship between Ringtail population density and Ringtail λ or juvenile recruitment in Gallery or Scrub habitat. In post-drought years, neither λ nor juvenile recruitment in Ringtails were affected by the population density of Brown lemurs, or by the combined population densities of both lemur species. In Post-drought years, Ringtail juvenile recruitment in both Gallery and Scrub declined at all population densities (see below; Figures 10A, 10B).

In regular and drought years, there was no effect of Brown lemur density on Ringtail λ or juvenile recruitment in Gallery. However, in Scrub there was a significant negative effect of Brown lemur density on Ringtail juvenile recruitment (Linear Regression, $R^2=0.77$, $F_{1,5} = 16.36$, $p=.009$; Figure 5A). This result is enigmatic since there is no evidence of a decline in Ringtail population density, nor of Ringtail λ , in Scrub habitat. Because Brown lemur density has only been at high levels in Scrub for 5 years, the effects of reduced recruitment on Ringtail population density in Scrub might not yet be evident.

Juvenile recruitment in Brown lemurs in Scrub showed no relationship to population density when all years were analysed together (Figure 5B); in Gallery, there was a trend of declining juvenile recruitment at higher densities (Figure 5B). My data were insufficient to look for density dependent effects on λ in Brown lemurs, or for differences among regular, drought and post-drought years.

Density Dependence at the Troop Level

Since females of both species remain in their natal troop, I used the number of adult females per troop as an index of troop size (Jolly *et al.* 2002). The mean number of females per troop was larger for Ringtails in Gallery than in Scrub (Gallery: mean 5, median 5, range 1-10; Scrub: mean 4, median 3, range 1-8), and smaller overall in Brown lemurs (Gallery and Scrub: mean 3, median 3, range 1-6). There was no relationship between troop size and juvenile recruitment in Ringtails in either Gallery (Linear Regression, $R^2 = 0.02$, $F_{1,6} = 0.084$, $p = 0.78$) or Scrub (Linear Regression, $R^2 = 0.13$, $F_{1,5} = 0.75$, $p = 0.43$) in post-drought or regular/drought years.

In Brown lemurs in Gallery, juvenile recruitment decreased significantly with increasing troop size (Figure 6; Linear Regression, $R^2 = 0.73$, $F_{1,4} = 10.94$, $p = 0.03$). However, small sample sizes for the largest and smallest troop sizes here may mean that this result is not robust. In Scrub Brown lemurs, there was a trend for increasing juvenile recruitment at larger troop sizes (Figure 6; Linear Regression, $R^2 = 0.50$, $F_{1,4} = 3.98$, $p = 0.12$). Because λ is a population-level parameter, I could not compare it among troop sizes.

The Ringtail population has remained relatively stable for the last 10 years, and was stable at a smaller population size throughout the 70's and 80's. I found no evidence of density dependent effects on Ringtails in Gallery, although juvenile recruitment by Brown lemurs in Gallery habitat may have declined as combined population density has increased. Only in Scrub is there an apparent relationship between any Ringtail population parameter and Brown lemur population density. Yet this relationship is not correlated with a decline in population density. I therefore hypothesize that the Ringtail population at Berenty is limited in response to annual variability in water and/or food.

D. Does Rainfall Affect Population Growth and Juvenile Recruitment?

Data from the Beza Mahafaly Ringtail population, which does not receive water provisioning, suggests that Ringtails suffer mortality of adults and juveniles during and immediately after droughts, followed by very rapid population growth (Gould *et al.* 1999). Since water provisioning at Berenty may buffer adult mortality during droughts, I predicted that any effect of drought would show up in the years immediately following droughts. Thus, I analysed drought years and post-drought years separately. I explored the effect of the amount and variability of annual rainfall on λ and juvenile recruitment in Ringtails. Quantitative data on food availability were not available. However, rainfall and plant productivity are generally strongly positively correlated (van Schaik *et al.* 1993; Chapman and Balcomb 1998; Chapman *et al.* 1999; Janson and Chapman 1999), so I expected food to be more abundant during wetter wet seasons.

Rainfall Patterns

Mean rainfall per lemur-year at Berenty was 545mm (range 265 – 810mm). Both Dry and Wet season rainfall varied five-fold among years (Figure 7). Rainfall averaged 127mm (range 52 - 267mm, C.V. 0.50, $n=15$ years) for the Dry season and 415mm (range 147 – 729mm, C.V. 0.43, $n=15$ years) for the Wet season. Dry and Wet season rainfall were uncorrelated (Pearson's Product Moment Correlation, $n=15$ years, $r = +0.02$, $p > 0.05$). In 3 years (1983, 1991, 1996) there was drought in both seasons, and in two years each there was drought in only one season (Wet: 1990, 1991; Dry: 1992, 1995). Since most rain fell during the Wet season, all years with Wet season drought were drought years overall. Mean Wet season rainfall was 221mm (95% C.I. 177 – 265mm, $n=5$ years) in drought years and 501mm (95% C.I. 397 – 605mm, $n=10$ years) in regular years; Wet season rainfall was heavy in about half these years.

Effects of Rainfall on Demography of Ringtails

Regression analyses showed no effect of amount of dry season rainfall or "change in rainfall" on λ or juvenile recruitment in Ringtails. There was also no significant effect of amount of wet season rainfall on λ or juvenile recruitment in Gallery Ringtails. Incorporating a one-, two-, or three-year time lag produced similar results. In Scrub there was no significant effect of wet season rainfall on λ , but juvenile recruitment decreased significantly with increasing rainfall (Linear Regression, $R^2 = 0.43$, $F_{1,8} = 7.49$, $p < 0.05$; Figure 8). This paradoxical result is likely an artifact of decreased recruitment in post-drought years as

compared to drought years (see below). There was no apparent effect after a one-, two-, or three-year time lag.

Drought and Post-drought Effects on Demography of Ringtails and Brown Lemurs

I analysed drought and non-drought years in chronological sequence. Lambda values in Scrub, and juvenile recruitment in Scrub and Gallery, were affected not by amount of rainfall, but by the amount of time since the last drought (Figures 9, 10A, 10B). Again, there was no visible effect on λ in Gallery Ringtails; there was no significant difference among years with drought, regular, or 1- or 2-year post-drought wet season rainfall for Gallery (One-way ANOVA, $F_{3,9} = 1.05, p = 0.42$). In Scrub there was only a very weak trend for λ to decrease in post-drought years (One-way ANOVA, $F_{3,7} = 0.588, p = 0.64$; Figure 9).

Although survival of adult Ringtails was not affected by drought, juvenile recruitment was reduced after droughts. In Gallery, juvenile recruitment in regular and drought years was nearly twice as high as in the second year post-drought, though the difference was not significant (Figure 10A; One-way ANOVA, $F_{3,10} = 2.440, p = 0.13$). This effect was magnified in Scrub: in the first two years post-drought, less than 10% of females (95% C.I. = 0.04 – 0.13, $n=5$ years) in Scrub habitat reared an infant that survived its first year. Juvenile recruitment was almost three times greater in drought and regular years than in the first year post-drought, and five times greater than in the second year post-drought (Figure 10B; One-way ANOVA, $F_{3,8} = 8.665, p < 0.01$). Dry season droughts showed a similar pattern. However, demographic data were available for only one year in which there was a dry season drought without a wet season drought, so it was not possible to distinguish the effects of the different seasons fully.

While the post-drought effect on juvenile recruitment was profound in Ringtails, there was no such effect on Brown lemurs in Gallery (Figure 10C). In fact, there was a trend for recruitment of Brown lemurs to increase after droughts in Scrub (Figure 10C), though this may be an artifact of small sample size.

Although I detected no effect of the amount of rainfall on Ringtails when I analysed all years together, an effect emerged when I analysed drought years separately. Drier droughts had a greater impact on Ringtail demography: juvenile recruitment by Ringtails in Scrub and Gallery, and λ of Ringtails in Scrub, decreased in the first year post-drought with decreasing rainfall in the drought year. This relationship was significant only for λ in Scrub (Linear Regression, for juvenile recruitment in Scrub, $F_{1,1} = 65.62, R^2 = 0.98, p = 0.08$; for λ in Scrub, $F_{1,1} = 382.1, R^2 = 0.99, p = 0.03$; for juvenile recruitment in Gallery, $F_{1,1} = 11.88, R^2 = 0.92, p = 0.18$). There was no relationship in Scrub or Gallery between amount of drought year rainfall and Ringtail juvenile

recruitment or λ in the drought year itself, or in the second year post-drought. There was also no relationship in Gallery between drought year rainfall and λ one year post-drought. Juvenile recruitment by Brown lemurs was not affected by rainfall amount in drought years.

These results demonstrate that Ringtails and Brown lemurs at Berenty respond differently to drought. While Brown lemurs experience no apparent effect of drought, juvenile survival in Ringtails decrease dramatically following droughts, particularly in Scrub habitat. In contrast to the high mortality seen during drought years in a Ringtail population without water provisioning (Gould *et al.* 1999), the effect of drought on Ringtails at Berenty is apparent only in post-drought years.

Summary

In summary, these data suggest that Brown lemurs and Ringtails at Berenty share key resources to a significant degree, but that competition with Brown lemurs has not resulted in a decline in the Ringtail population. The populations share overlapping territories, diets and foraging habits. Intriguingly, juvenile recruitment in Ringtail lemurs is significantly more sensitive to drought than is juvenile recruitment in Brown lemurs.

Discussion

My study had two goals: to examine the factors affecting Ringtail and Brown lemur population density at Berenty Reserve, and to determine whether the introduced Brown lemur population is having a negative impact on the size of the native population of Ringtail lemurs there. These two populations occupy an area that previously contained a single stable population of Ringtails a quarter the size of the current combined population. Though their current combined density is similar to that of Ringtails and Brown lemurs in natural sympatry, their ecology is not. In contrast with the diet and habitat partitioning seen in natural sympatry, I have shown here that Ringtails and Brown lemurs at Berenty overlap extensively in diet and habitat use, even during periods of food scarcity (Figures 1C, 2A, 2B, 2C). Based on this, I predicted a negative demographic impact of the increasing Brown lemur population on the Ringtail population at Berenty.

I found evidence of recent density-dependent effects on both species (Figures 5A, 5B, 6), but no obvious negative effect of Brown lemurs on the size of the Ringtail population (Figures 3B, 3C). Despite the dramatic increase in the number of animals utilizing the same limiting resources, the number of Ringtails at Berenty has not declined, and the number of Brown lemurs continues to increase (Figure 3A). Given the degree of interspecific diet and habitat use overlap seen at Berenty, this outcome is completely unexpected.

To manage Berenty's important Ringtail lemur population, we need to understand what influenced the last 15 years of population change at Berenty, and to predict what will happen if Berenty's Brown lemur population continues to increase. Three of my findings in particular are central to addressing these questions: A) the high degree of interspecific diet overlap (Figure 1C), B) the density-independent crashes in Ringtail recruitment that follow droughts (Figures 10A, 10B), and C) the lack of effect of Brown lemurs on Ringtail numbers (Figures 3B, 3C). Sections A, B, and C of the following discussion examine my three key results that affect the continued coexistence of these two populations. In section C, I also explore the role of water provisioning on lemur interactions at Berenty.

A. Interspecific Diet Overlap and Population Density

Interspecific Diet Overlap

Twenty-three years after their introduction to Berenty, Brown lemurs and Ringtails overlapped in diet and habitat use dramatically more than in other sympatric populations (Sussman 1972; Ganzhorn 1985, 1986). Overlap was greater at Berenty because the Ringtails behaved as they do in natural sympatry, but the Brown lemurs did not. Ringtails at Berenty, as in all known populations, had generalist ranging behaviour and a diet dominated by a few plant species, particularly *Tamarindus indica*, and rounded out with many lightly used food species (e.g. Sussman 1972; Ganzhorn 1985, 1986; Sauther 1991; Rasamimanana and Rafidinarivo 1993; Yamashita 2002; Simmen *et al.* 2003). In contrast, the Berenty Brown lemurs were not the specialised arboreal folivores described in other studies of populations sympatric with Ringtails (Sussman 1972; Ganzhorn 1985).

The flexible behaviour of Berenty's Brown lemurs is not surprising. Brown lemurs exhibit much variation among habitat types and populations (e.g. Sussman 1972; Ganzhorn 1985, 1986; Overdorff, 1991, 1993, 1996; Simmen *et al.* 2003; Scholz and Kappeler 2004). Their diets are flexible, allowing them to respond to small-scale changes in food availability over time and space. Unlike Ringtails, they can exist at high density while feeding primarily on mature leaves (Sussman 1972). Yet, they are highly frugivorous where fruit is plentiful (Overdorff 1991). At Berenty, they opportunistically feed on insects, lizards, bird eggs and even baby Ringtail lemurs (Jolly *et al.* 2000; Walker pers. comm.; Jolly and Pinkus unpublished data).

Thus, Brown lemurs sometimes act as serial specialists (this study; Jolly pers. com; see also Ganzhorn 1986) at the population and troop level. On average, the seven Brown lemur troops in this study acted much like Ringtails. They foraged at similar heights, ranged in overlapping habitat, and shared the majority of their diets. The only diet component that differed consistently between species was new leaves, which were eaten less by Brown lemurs, as found in other studies (Berenty: Jolly *et al.* unpublished, Simmen *et al.* 2003; captivity: Ganzhorn 1986). However, there was far more variation in diet and foraging heights among individual Brown lemur troops than among Ringtail troops.

High overlap during periods of food scarcity occurs occasionally in sympatric primate populations (e.g. Gautier-Hion 1980; Waser 1980; Richard and Dewar 1991; Vasey 2000), but usually diets diverge most when food is most scarce (Gautier-Hion 1980; Terborgh 1983; Overdorff 1991; Richard and Dewar 1991; Tutin *et al.* 1997). When primates of similar body size eat the same diet, divergence in microhabitat or feeding height tends to increase (e.g. Gautier-Hion 1980; Gautier-Hion 1988; Vasey 2000; see also Waser 1980; Terborgh 1983; Ganzhorn 1988; Ganzhorn and Kappeler 1996). In my study, this did not occur. Two

dimensions along which sympatric primates' diets diverge, feeding substrate and leaf chemistry, were not measured in my study and deserve exploration (e.g. Emmons *et al.* 1983; Glander and Rabin 1983; Harcourt and Nash 1986; Ganzhorn 1986, 1988, 1989; Tomlin and Cranford 1994; Vasey 2000).

Interspecific Differences in Diet and Competitive Ability

Serial specialisation gives Brown lemurs greater resilience than Ringtails to temporal variation in resource availability (see Figures 10B and 10C). However, Brown lemurs' use of closed canopy forests (Sussman 1972; Hawkins 1999) suggests that they are poorly adapted to edge habitat. They have less flexible thermoregulatory behaviour than Ringtails (Ganzhorn 1985), and travel shorter distances than Ringtails in dry forest (Sussman 1972; Ganzhorn 1985; this study). Brown lemurs follow a strategy of conserving energy and water by ranging in shady habitat, moving relatively little, and subsisting on food types that are abundant nearby. Conserving water may be especially important for dry forest populations of Brown lemurs because, compared to Ringtails, their diets contain fewer young leaves, leaves from succulent plants, or fleshy fruit (this study; Sussman 1972). In contrast, the rigid foraging behaviour of Ringtails works well in edge habitats with limited resources (see Gould *et al.* 1999; Wright 1999; Godfrey *et al.* 2003). Surveys of naturally sympatric Brown and Ringtail lemur populations suggest that Ringtails in sympatry regularly make use of both closed-canopy forest and scrubby edge habitat, while Brown lemurs remain in the forest (Sussman 1972; Hawkins 1999; Sussman *et al.* 2003).

Interspecific Differences in Diet and Population Density

The demography of Brown lemurs in dry forests has been little studied. However, long-term demographic studies have compared Ringtails' and white sifakas. Sifakas are obligate folivores that share the same range as Ringtail lemurs. White sifakas have a similar intrinsic rate of natural increase to Ringtails (0.24 versus 0.27, Ross 1992), do not eat fruit, and experience less mortality following droughts than Ringtails (Richard *et al.* 2000, 2002; Godfrey *et al.* 2004).

Brown lemurs have a demography that resembles white sifakas, though they can increase more rapidly in population density (Ross 1992; Godfrey *et al.* 2004; this study). Their broad diet includes all items eaten by Ringtails and white sifakas. The diets of Brown lemurs and Ringtails at Berenty overlapped extensively during the period of scarcity sampled in this study. Yet, Brown lemur numbers at Berenty continued to grow in the years of this study when Ringtail numbers fell, particularly in post-drought years. Though they sometimes eat mainly fruit, Brown lemurs, like white sifakas, may be limited by leaf rather than fruit availability. The availability

of high quality leaves is more predictable than the availability of fruit, and is not directly correlated with total rainfall (Janson and Chapman 1999). As a result, lows in leaf availability are not as severe as lows in fruit availability. It seems that, during extreme fruit scarcity, Brown lemurs switch to a folivorous diet. Generalising until resources become scarce, and then specialising, can allow populations of facultative specialists to out-compete obligate generalists (Robinson and Wilson 1998).

Behavioural Dominance of Brown Lemurs Over Ringtails

Brown lemurs at Berenty clearly dominate Ringtails in contest competition. Though Brown lemurs and Ringtails seldom interact in natural sympatry (Sussman 1972), Brown lemurs dominate other lemur species both in rainforest and in captivity at Duke Primate Center (Overdorff 1991; K. Glander pers. comm.). At Berenty, Brown lemurs dominate Ringtail lemurs at food and water sources (personal observation, N. Koyama, A. Jolly, J. Walker, pers. comm.). In areas of high population density, each Ringtail troop's range is overlapped by several Brown lemur troops, and some Ringtail troops spend 25% of their feeding time in patches occupied by Brown lemurs (current study; Jolly *et al.* unpublished). During my study, Brown lemur and Ringtail troops entered food patches occupied by the other species regularly. These intrusions were twice as likely to lead to aggressive conflict when Brown lemurs invaded patches occupied by Ringtails (Pinkus, unpublished data). It seems likely that, if the density of Brown lemurs continues to increase, contest competition with Ringtails will intensify, perhaps with negative results for Ringtails.

B. Ringtail Recruitment and the Role of *Tamarindus indica*

At Berenty, *T. indica* trees, and possibly other species, bear mast fruit crops during droughts that occur about every 7 years (Jolly *et al.* 2002; Figure 7), then dramatically decrease fruit production over the next one to two years (personal observation; Jolly *et al.* 2002; Simmen *et al.* 2003). Throughout Ringtails' range, areas with higher densities of *T. indica* trees support higher densities of Ringtails (Gould *et al.* 1999; Hawkins 1999; Sussman *et al.* 2003).

T. indica Fruit as a Keystone Resource for Ringtails

Food availability in southern Malagasy dry forests is low during the late dry season, even in years of average food abundance (Ganzhorn *et al.* 2003). At Berenty, female Ringtails end gestation and begin lactation during the late dry season (Koyama *et al.* 2001; Jolly *et al.* 2002). Energy appears to be particularly limiting for female Ringtail lemurs during gestation and lactation (Young *et al.* 1991; Pereira 1993; Pereira *et al.* 1999; Godfrey *et al.* 2004). A female's

ability to rear surviving offspring in consecutive years may depend on weight gain during this time (Pereira 1993). Thus, Ringtail populations are particularly vulnerable to food shortages during the late dry season. The density-dependent effect of Brown lemurs on Ringtail recruitment in Scrub during average rainfall years (Figure 5A) may indicate increasing interspecific competition for *T. indica* fruit.

Plant species that produce abundant and reliable fruits are keystone resources for frugivorous primates (e.g. Overdorff 1991; Tutin *et al.* 1997; Sauther 1998; Peres 2000; Jolly *et al.* 2002). *T. indica* fruit is a keystone dry season resource for Ringtails, and is often the dominant component of their diet (Sussman 1972; Sauther 1991; Rasamimanana and Rafidinarivo 1993; Yamashita 2002; Merti-Millhollen *et al.* 2003; this study). For this reason, droughts affect Ringtails more severely than sympatric species with more folivorous diets (Gould *et al.* 1999; Richard *et al.* 2000; Jolly *et al.* 2002; this study).

Lemur Recruitment During T. indica Fruit Crop Failures

Juvenile recruitment in Ringtails at Berenty fell in the first two years following droughts. This effect was strongest in Scrub habitat (Figure 10B; cf. Figure 10A), and was independent of population density, as is typical of the effects of environmental variability on populations (e.g. Davis *et al.* 2003). Ringtail population declines at Berenty (e.g. years 1985, 1994 and 1998; Figure 3B and 3C) also occurred following droughts. Since recruitment and population growth rate are average to high in drought years (Figures 9, 10A, 10B), this effect is unlikely to be caused by low water availability. Decreased recruitment and growth rate after droughts in my study probably represent the effects of rainfall on food availability, particularly *T. indica* fruit (Jolly *et al.* 2002). In years when *T. indica* fruit are scarce, high adult/juvenile mortality and reproductive failure also occur in Ringtails at Beza Mahafaly (Gould *et al.* 1999; Jolly *et al.* 2002; Godfrey *et al.* 2004; Figures 10A and 10B).

C. Can Water Provisioning Explain the Lack of Impact of Brown Lemurs on Ringtails at Berenty?

Because Brown lemurs are behaviourally dominant and resilient to fruit shortages, interspecific competition for *T. indica* fruit should have greater consequences for Ringtails. Yet Ringtail numbers at Berenty have not declined as Brown lemurs have increased in density, resource partitioning has not occurred, and Ringtails in Gallery habitat are currently stable at the highest population density of any known wild Ringtail population. This surprising outcome may

be the result of the different effects of water provisioning on Ringtails and Brown lemurs. In this section, I explore the hypothesis that the Brown lemur introduction in 1975, and expanded water provisioning in 1984 and 1991, interact at Berenty to create densities and distributions of lemurs that do not occur in natural sympatry.

Distribution of Brown lemurs at Berenty May Reflect Water Provisioning

The distribution of Brown lemurs at Berenty is strongly influenced by the distribution of water troughs. In the decade following expanded water provisioning, Brown lemur numbers in Gallery habitat increased and then stabilised (Figure 3B). Their numbers in Gallery were still increasing in 1991 when water provisioning expanded for the second time; their distribution in Gallery subsequently expanded to include newly provisioned areas (this study). Since water provisioning began in Scrub habitat at Berenty in 1991, Brown lemurs have colonized Scrub habitat, reaching three times the density of Ringtails, and are continuing to increase (Figure 3C). In natural sympatry with Ringtails at Anserananomby, Brown lemurs were confined to closed-canopy forest (Sussman 1972).

The absolute water requirements for Brown lemurs are unknown, but they will travel considerable distances to reach water. In a dry forest in Western Madagascar during the dry season, Brown lemurs traveled up to 3km to drink water, while sympatric white sifakas met their water requirements by eating leaves with high water content (Scholz and Kappeler 2004). Brown lemurs living in dry forest generally have access to a river or stream (Sussman 1972; Hawkins 1999; Scholtz and Kappeler 2004). Although lemurs at Berenty are never more than 1km from the Mandrare River, it is not an inviting place for an arboreal species to drink: there is no vegetation cover on the long expanse between the bank and the dry season trickle of water, and there is considerable human and livestock traffic along the riverbed. Although Ringtails do drink from the river (Jolly pers. comm.), Brown lemurs have not been observed to do so during the day. The correlation between Brown lemur distribution and water provisioning at Berenty suggests that Brown lemurs might not range in Scrub in the absence of water provisioning.

High Ringtail Density in Gallery May Reflect Water Provisioning

Standing water does not seem to be a limiting resource for Ringtail lemurs in Scrub at Berenty; even before water provisioning, their numbers rarely declined in drought years. Numbers of Ringtails in Scrub have not changed markedly since water provisioning began in Scrub habitat, likely because Ringtails in Scrub habit can obtain sufficient water by eating succulents and other plants with high moisture content (Jolly pers. com.; Budnitz and Dainis 1975; Randriamboavonjy 2003). In Gallery habitat, there are far fewer water-rich plants than in

Scrub, and troops rely more heavily on standing water. Ringtails in Gallery habitat more than doubled their density in the decade after water provisioning expanded for the second time. During that decade, dry season food shortages occurred 40% of the time. While it is not certain that water provisioning caused the population increase in Gallery, increased food availability is an unlikely explanation. Large increases in population density in response to food or water provisioning are common in primates and other vertebrates (Krebs *et al.* 1995; Newton 1998; Fleagle *et al.* 1999). Populations of long-lived species typically increase within 10 years after food or water is supplemented (Fleagle *et al.* 1999). Ringtail populations have a high intrinsic rate of increase (Ross 1992) and should respond rapidly to provisioning.

There are other plausible explanations for the increase in Ringtail density in Gallery following the late 1980's. These include: changes in hunting pressure; rebounding from a disease outbreak prior to the 1970's; increased food provisioning by tourists; or changes in forest structure. Neither disease nor hunting should have impacted Gallery habitat more than Scrub, and researchers resident at Berenty in the 1970's and 1980's did not observe hunting or signs of disease (A. Mertl-Millhollen, K. Dainis pers. com.). In addition, given Ringtails' high intrinsic rate of increase following declines, the population should have rebounded prior to the 1990's. On Barro Colorado, howler monkeys, whose intrinsic rate of natural increase is well below that of Ringtails (0.18 vs. 0.27, Ross 1992), rebounded within 8 years from an outbreak of yellow fever that halved their population (Chapman *et al.* 1999). Food provisioning has certainly affected the density of the troops ranging in the developed tourist area of the reserve (Jolly *et al.* 2002), but the growth rate and recruitment of Gallery troops are not correlated with these changes. Finally, changes in forest structure may have affected Ringtail density, but the increase in Ringtail density was too rapid to be explained by successional changes in the forest. In conclusion, none of these alternative explanations seems likely at Berenty.

Relative Densities in Gallery May Reflect Water Provisioning

The combined density of Brown and Ringtail lemurs in Gallery habitat was stable from 1995 through 2000 at a density similar to their combined density in natural sympatry (*e.g.* Sussman 1972). However, the proportions of the two species differed between these two situations. Ringtail density in Gallery at Berenty was twice that of Ringtails in natural sympatry (Sussman 1972), while Brown lemur density in Gallery has stabilised at half that in natural sympatry. These results suggest flexibility in the relative densities at which sympatric Ringtails and Brown lemurs can maintain stable populations in closed-canopy forest.

Water provisioning in Gallery habitat at Berenty may have allowed Gallery Ringtails to reach unusually high density by increasing the number of territories with access to water. These territories are likely a limiting resource for Ringtails living in closed canopy forest. With no water limitation, and more territories available, Gallery Ringtail troops increased in both size and number, stabilising around a new, higher population density. That is, at Berenty, water provisioning lets Ringtails in Gallery forest compete successfully with Brown lemurs. Though my analysis did not show an effect of Brown lemur density on Ringtails in Gallery and interspecific food competition with Brown lemurs occurs (see above), it does not seem that this food competition is having a negative impact on Gallery Ringtails.

A further factor here is that juvenile recruitment in Scrub Ringtails is declining with increasing Brown lemur density (Figure 5A). The population growth rate for Scrub Ringtails in post-drought years also appears to have decreased since Brown lemurs appeared in Scrub (Figure 4A), but it is too soon to tell if this trend is robust. High Brown lemur density in Scrub is recent and has not yet led to a decline in numbers of Ringtails. However, food competition with Brown lemurs in Scrub may reduce the high recruitment needed for Ringtails to recover from post-drought food shortages. Ringtails are adapted to rebound rapidly from population declines, but their diet and use of edge habitat in natural sympatry (Sussman 1972; Hawkins 1999) suggest they may be less able to do so while competing for food with Brown lemurs. In summary, with less access to standing water and greater intraspecific food competition, Brown lemurs might exhibit the more conservative range use seen in other dry forest populations (Sussman 1972; Ganzhorn 1985, 1986). Under these conditions, interspecific diet and habitat use overlap would be relatively low.

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Tables and Figures

Table 1: Daytime activity of Ringtails and Brown lemurs at Berenty

Percent of 5-minute scan samples between 6am and 6pm spent feeding, and resting or sleeping, in Gallery and Scrub habitats (for each species $n=4$ troops in Gallery; $n=3$ troops in Scrub). Data are presented as 95% confidence intervals. In both habitats, Brown lemurs fed significantly less (2-sample t-tests, 1-tailed, $p < 0.01$) and slept or rested significantly more (2-sample t-tests, 1-tailed, $p < 0.05$) than Ringtails.

Lemur Species	% Time Feeding (95% C.I.)		% Time Resting (95% C.I.)	
	GALLERY	SCRUB	GALLERY	SCRUB
RINGTAIL	0.27 – 0.45	0.28 – 0.40	0.44 – 0.64	0.37 – 0.69
BROWN	0.16 – 0.26	0.10 – 0.22	0.62 – 0.72	0.67 – 0.85

Table 2: Resource types fed on by Brown and Ringtail lemurs. Abbreviations appear in Figures 1A and 1B.

Abbreviation	Species/Description
ACA	<i>Acacia royumae</i>
ACW	Caterpillar (unknown sp.)
AZI	<i>Azima tetracantha</i>
CEB	<i>Celtis bifida</i>
CEG	<i>Celtis gomphophylla</i>
CEP	<i>Celtis philippensis</i>
COM	<i>Combretum albiflorum</i>
COR	<i>Cordia rothii</i>
COV	<i>Cordia varo</i>
CRE	<i>Crataeva excelsa</i>
CRG	<i>Crataeva greveana</i>
DRT	Soil/Clay
EGG	Bird egg (unknown species)
ERI	<i>Erigeron</i> sp.
FIC	<i>Ficus</i> spp.
INS	Insect (unknown species)
IPO	<i>Ipomoea cairica</i>
KIL	<i>Tamarindus indica</i>
LIT	Leaf litter (unknown plant species)
MAE	<i>Maerua filiformis</i>
NEO	<i>Neotina isoneura</i>
OPU	<i>Opuntia vulgaris</i>
PHR	Secretions from the homopteran <i>Phromnia rosea</i>
PHY	<i>Phyllanthus casticum</i>
QUI	<i>Quivisianthe papinae</i>
RIN	<i>Rinoria greveana</i>
SAL	<i>Salvadorea angustifolia</i>
SIS	<i>Agave sisalana</i>
TER	<i>Terminalia mantaly</i>
U1E1	Unknown plant sp.
U1E2	Unknown plant sp.
U1EB	Unknown plant sp.
U1ST	Unknown plant sp.
U1YB	Unknown plant sp.
U2YB	Unknown plant sp.
WOO	Rotting wood (unknown species)

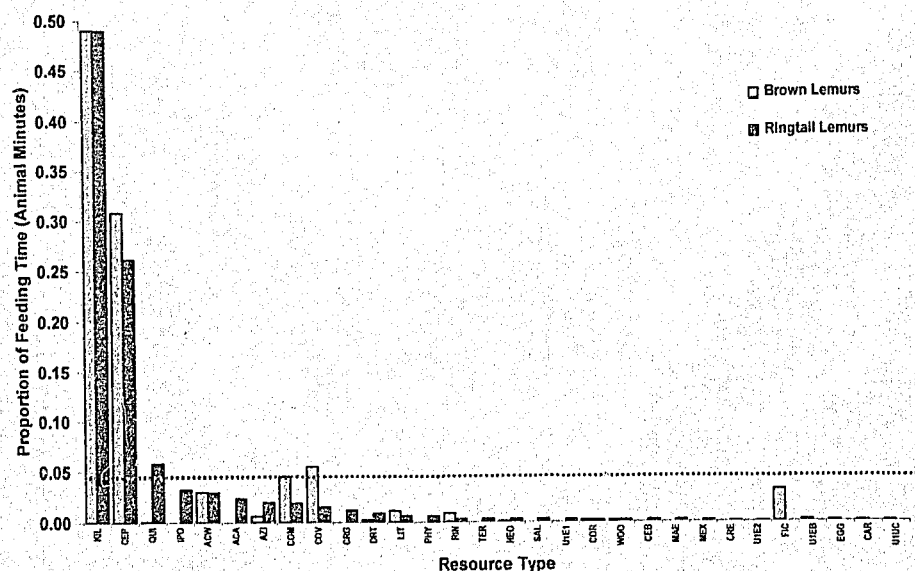


Figure 1A: Diet overlap between Ringtails and Brown Lemurs in Gallery habitat. Bars above the dashed line are resource types that make up more than 4% of the species' diet; these resources were used to calculate diet breadth. Resource types are species of plant or insect fed on by either lemur species.

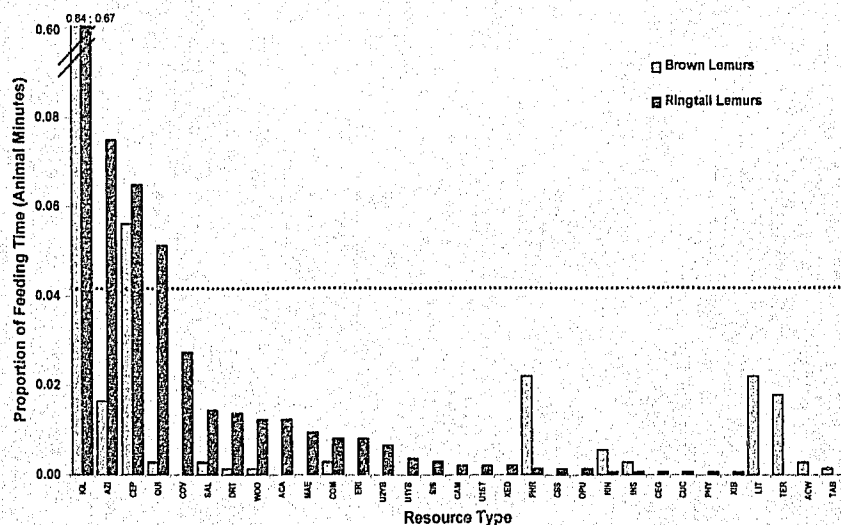


Figure 1B: Diet overlap between Ringtails and Brown lemurs in Scrub habitat. Scale expanded to show less used species. Bars above the dashed line are resources making up more than 4% of the species' diet; these resource were used to calculate diet breadth. Resource types are species of plant or insect fed on by either lemur species.

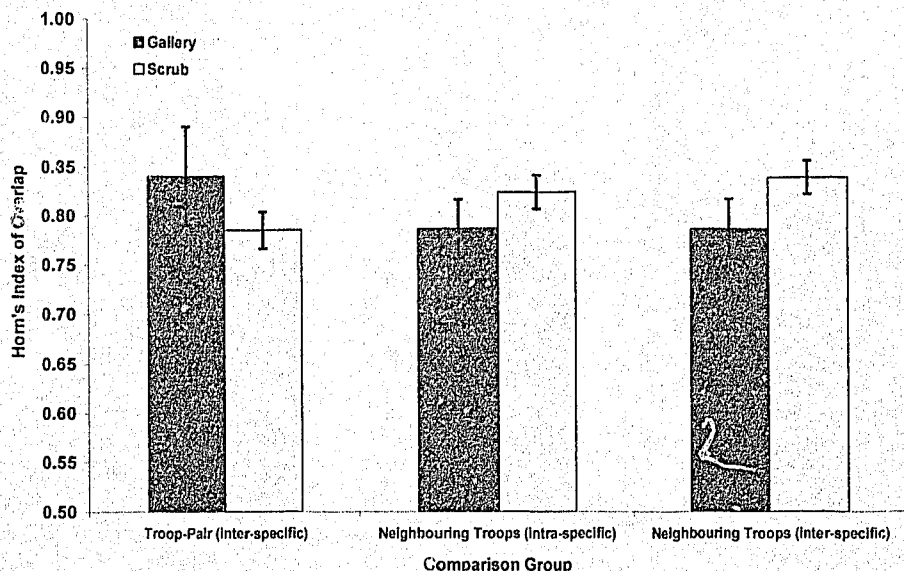


Figure 1C: Inter- and intra-specific overlap of food types eaten by troop pairs and neighbouring troops in Gallery and Scrub habitat. Each bar represents the mean value of Horn's Index of Overlap between pairs of troops. Comparison groups are paired troops of a) one Ringtail and one Brown lemur troop in overlapping ranges, b) two troops of the same species in adjacent ranges, and c) one Ringtail and one Brown lemur troop in adjacent ranges. Error bars are ± 1 SE for the mean of Horn's index of Overlap for paired troops.

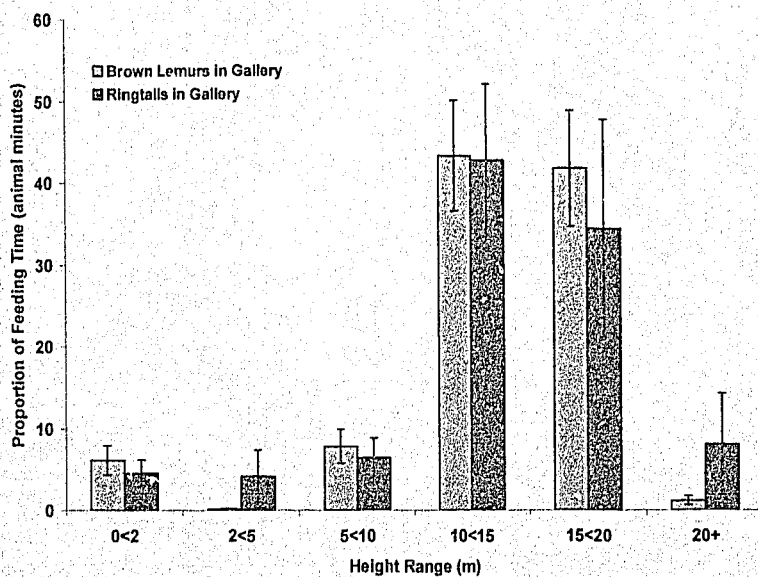


Figure 2A: Mean feeding heights of Brown and Ringtail lemurs in Gallery habitat. Error bars are ± 1 SE.

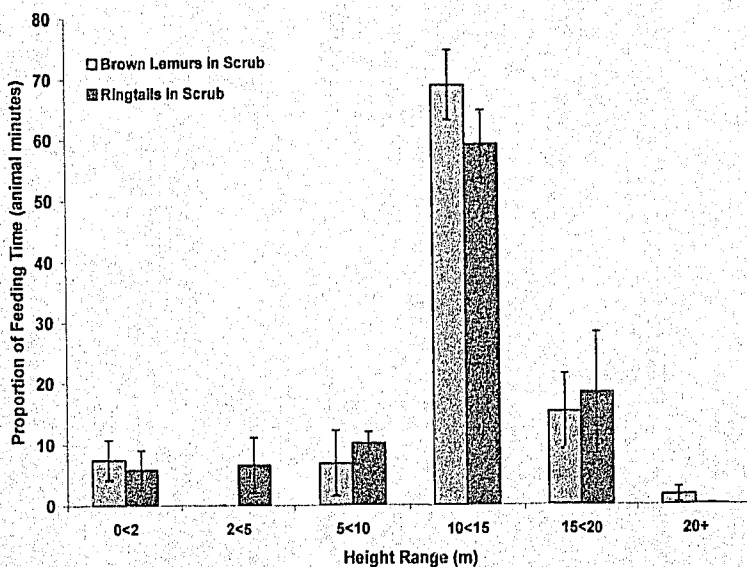


Figure 2B: Mean feeding heights of Ringtails and Brown lemurs in Scrub habitat. Error bars are +/- 1SE.

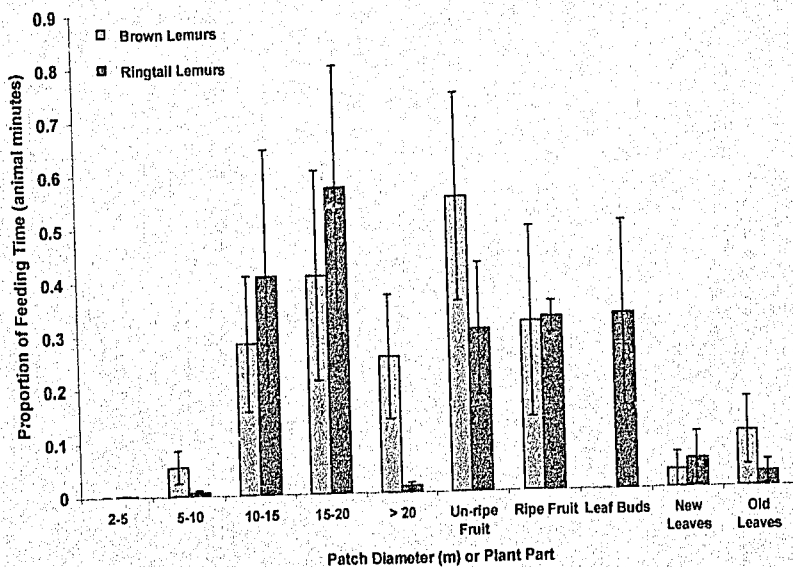


Figure 2C: Patch size and plant part utilised by Brown and Ringtail lemurs in Scrub habitat. Error bars are ± 1 SE.

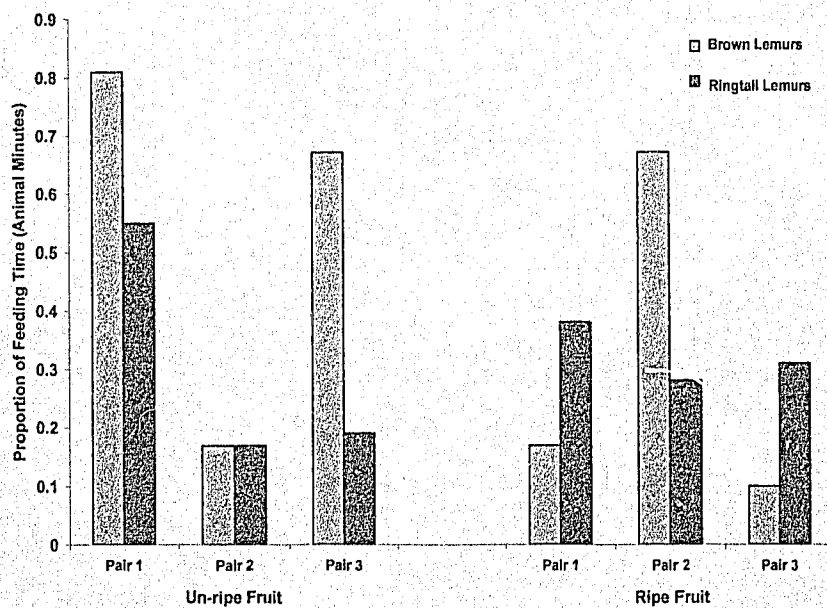


Figure 2D: *Tamarindus indica* fruit consumption by three troop-pairs in Scrub habitat.

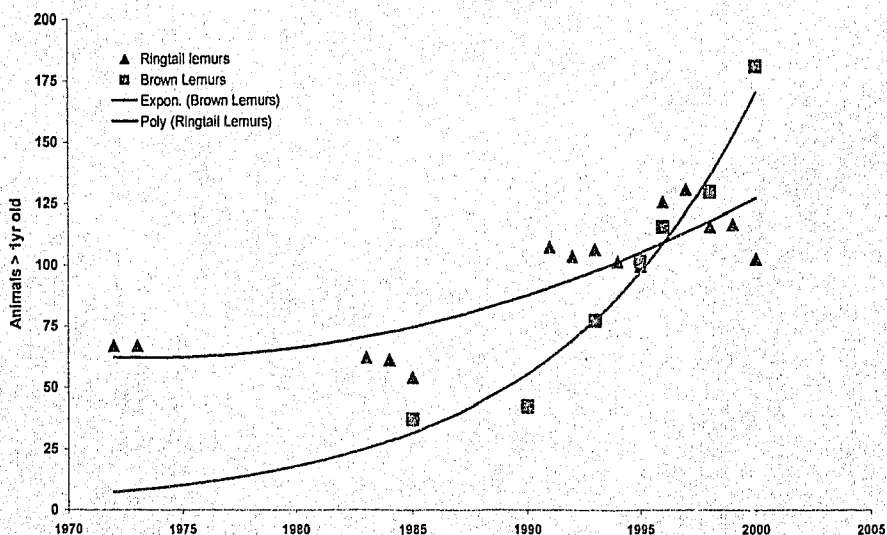


Figure 3A: Ringtail and Brown lemur population size in Malaza 1972-2000. Data are complete counts of adult animals, done in the birth season. Exponential equation fitted for Brown lemurs, $R^2 = 0.95$; Polynomial equation fitted for Ringtails, $R^2 = 0.74$

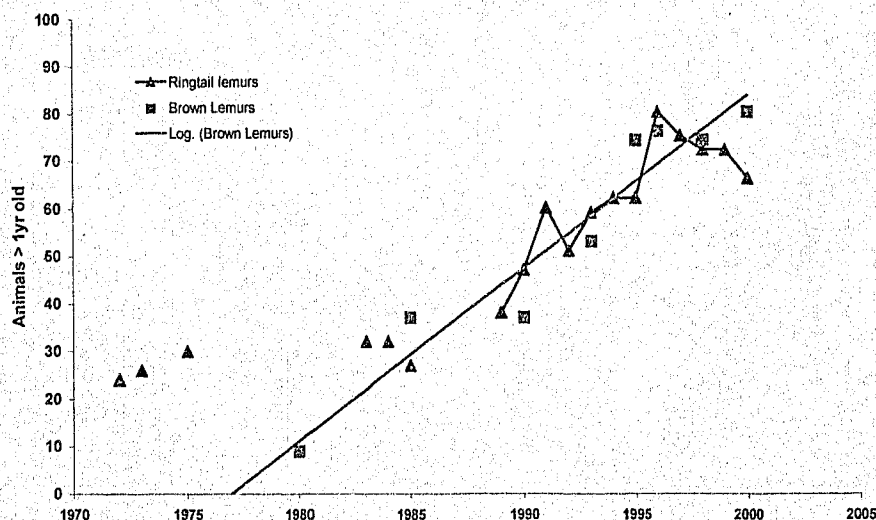


Figure 3B: Ringtail and Brown lemur numbers in Gallery habitat, 1972-2000. Logarithmic equation fitted for Brown lemurs, $R^2 = 0.93$.

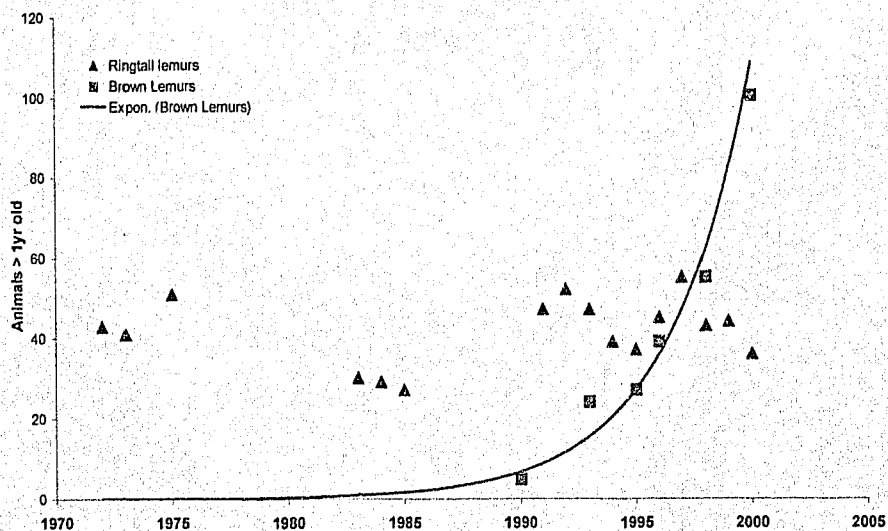


Figure 3C: Ringtail and Brown lemur numbers in Scrub habitat, 1972-2000. Exponential equation fitted for Brown lemurs; $R^2 = 0.94$.

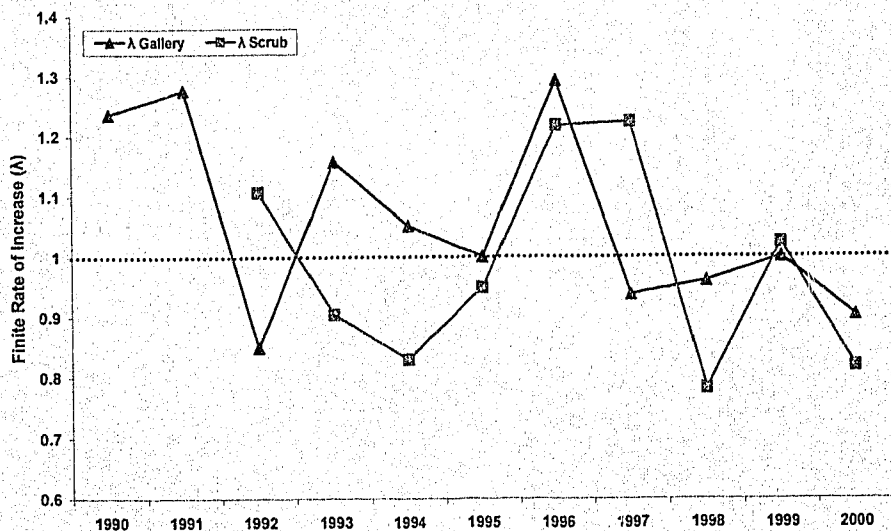


Figure 4A: Finite rate of increase (λ) of Ringtail lemurs in Gallery and Scrub habitats, 1990-2000. $\lambda = N_{t+1}/N_t$ for adults. The dotted line indicates λ at replacement.

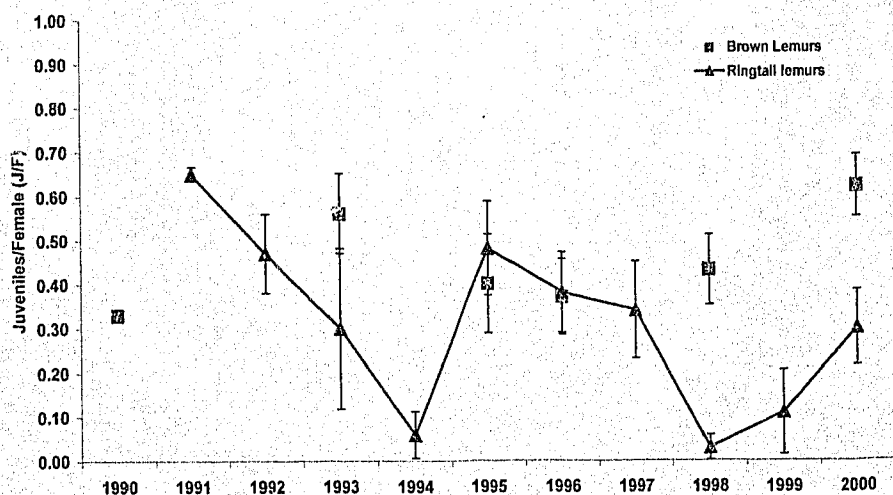


Figure 4B: Juvenile recruitment in Ringtail and Brown lemurs in Scrub habitat, 1990-2000. Data are ratios of 1-year olds to adult females (J/F) from complete population counts taken in birth season. Error bars are ± 1 SE.

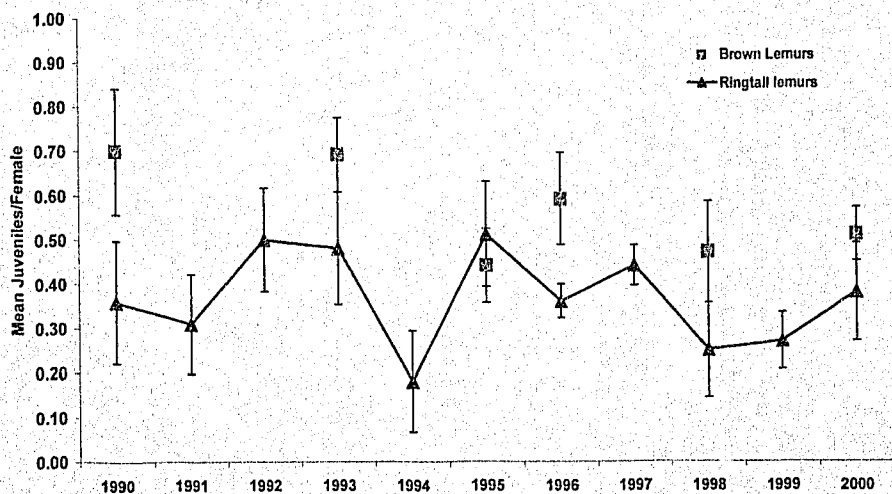


Figure 4C: Juvenile recruitment in Ringtail and Brown lemurs in Gallery habitat, 1990-2000. Error bars are $\pm 1SE$.

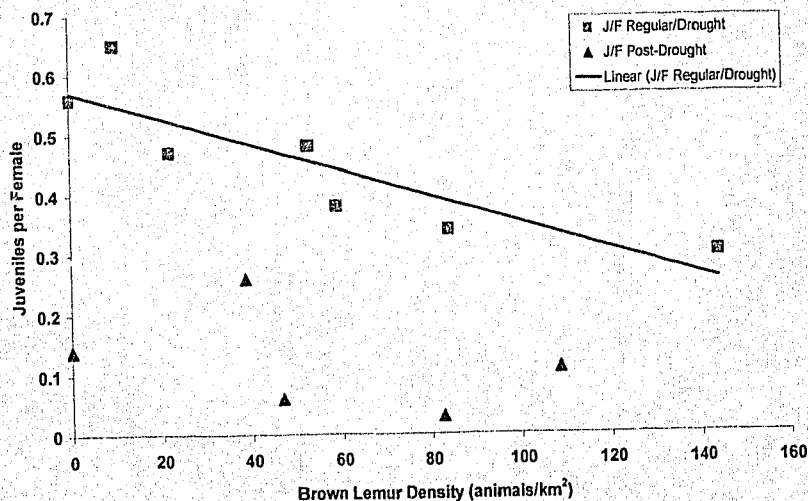


Figure 5A: Juvenile recruitment to Ringtails in Scrub habitat as a function of Brown lemur density in regular/drought years vs. post-drought years. In regular/drought years $y = -0.002x + 0.57$; $R^2 = 0.77$.

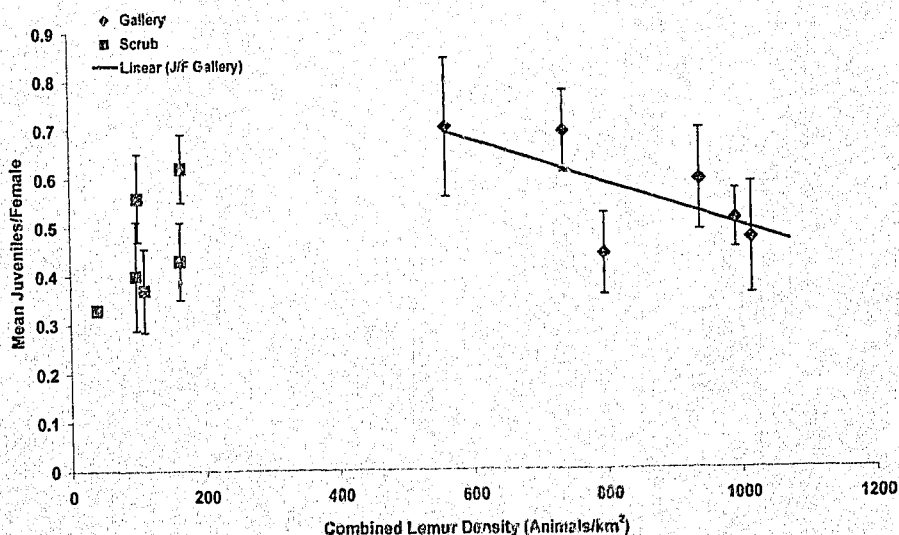


Figure 5B: Population level density dependence of Brown lemur juvenile recruitment. J/F is shown as a function of combined density of Ringtail and Brown lemurs in the previous year. In Gallery, $y = -0.0004x + 0.94$; $R^2 = 0.48$. Error bars are ± 1 SE.

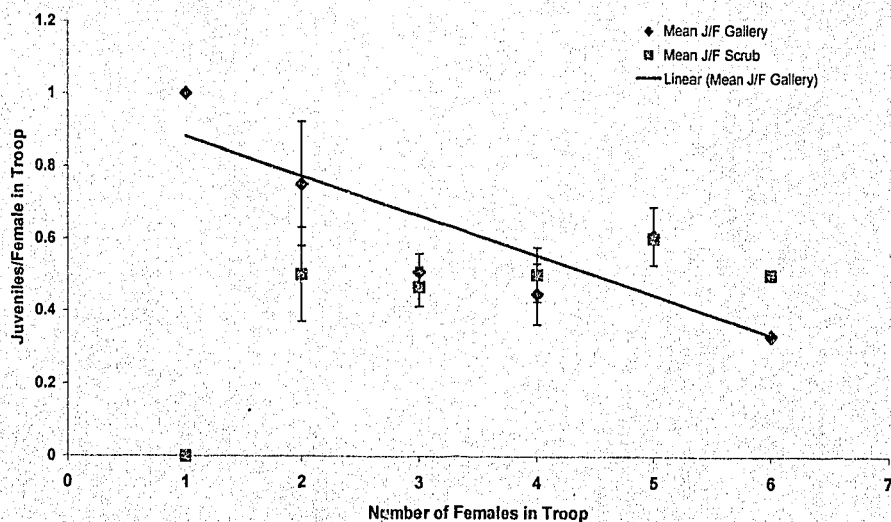


Figure 6: Troop level density dependence of Brown lemur juvenile recruitment. Mean J/F within individual troops is shown as a function of size of troop in the same year. For Gallery, $J/F = -0.11x + 0.99$; $R^2 = 0.73$. Error bars are ± 1 SE.

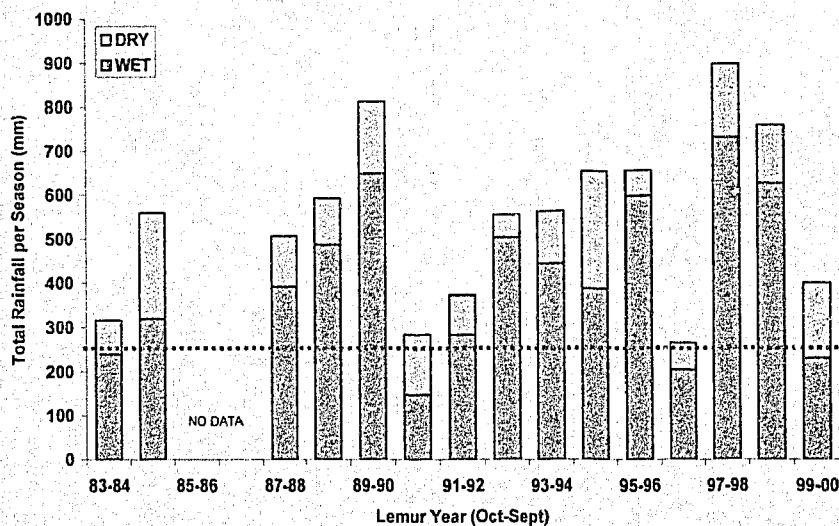


Figure 7: Rainfall per Lemur Year Oct 1, 1983 to Sept 30, 2000. Dry Season is April-September; Wet Season is October-March. Drought years have wet season rainfall at or below the dotted line (less than 60% of mean wet season rainfall).

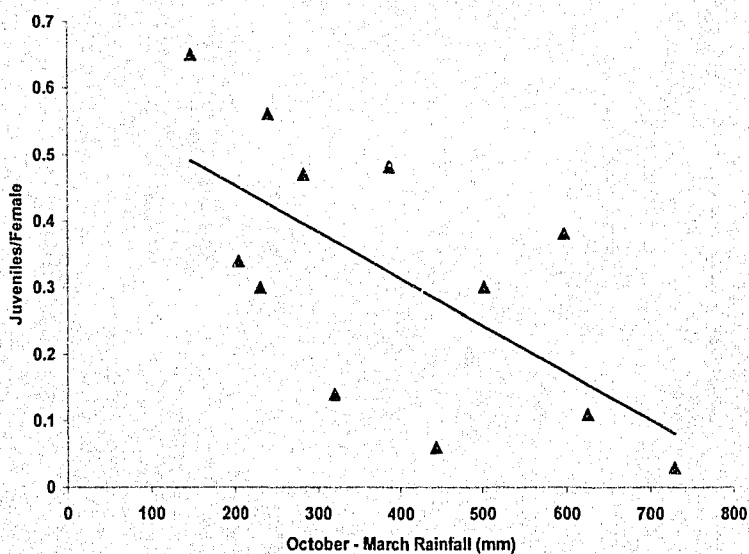


Figure 8: Effect of amount of wet season rainfall on J/F in Ringtail lemurs in Scrub habitat. J/F in October of lemur-year N is shown as a function of Wet season rainfall in lemur-year N-1. $J/F = -0.0007(\text{rainfall}) + 0.59$; $R^2 = 0.43$.

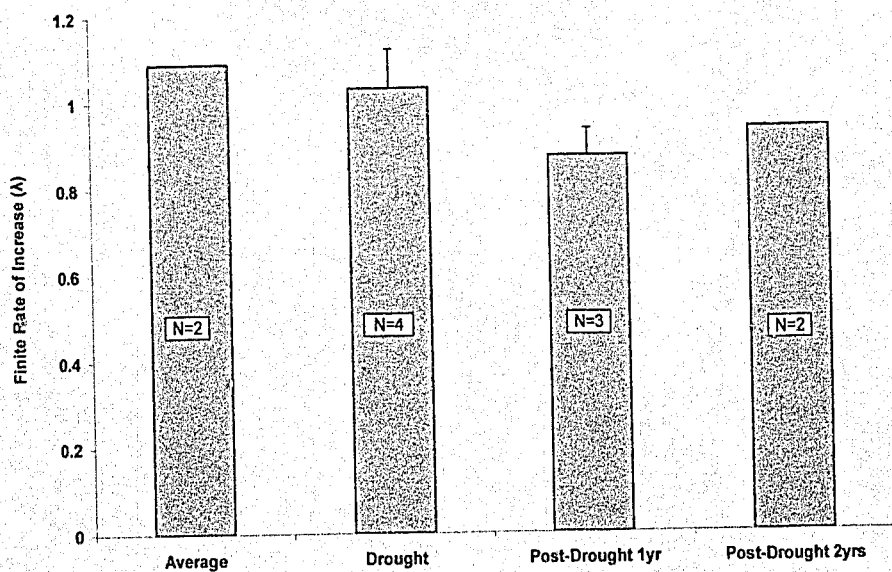


Figure 9: Finite rate of increase (λ) of Ringtail lemurs in Scrub habitat in Wet season Drought and Post-drought years. Years with wet season rainfall more than 3SE below the mean are considered drought years. Error bars are ± 1 SE.

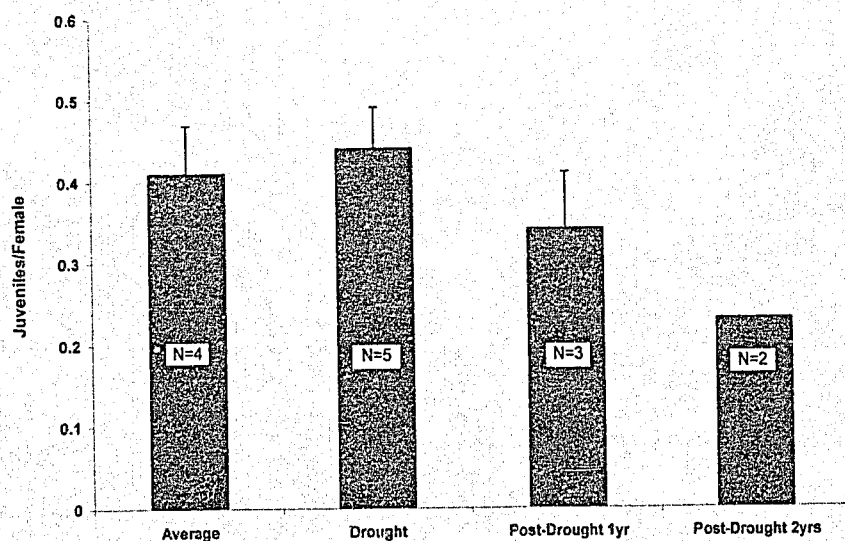


Figure 10A: Juvenile recruitment (J/F) by Ringtail lemurs in Gallery habitat in Wet season Drought and Post-drought years. Error bars are +/- 1SE.

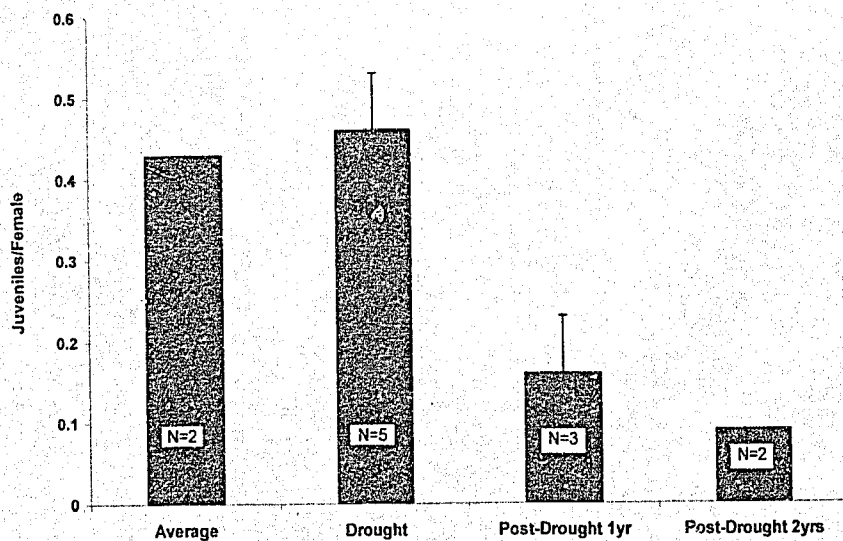


Figure 10B: Juvenile recruitment (J/F) by Ringtail lemurs in Scrub in Wet season Drought and Post-drought years. Error bars are $\pm 1SE$.

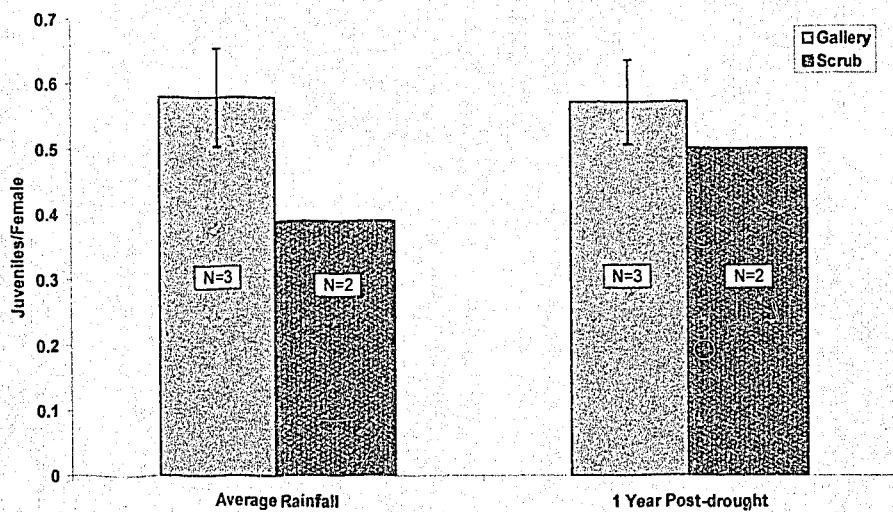


Figure 10C: Juvenile recruitment by Brown lemurs in Wet season Average rainfall and Post-drought years. Error bars are ± 1 SE.