

ANGLIA RUSKIN UNIVERSITY

**INVESTIGATING POLYSPECIFIC COMMUNICATION  
AND ASSOCIATIONS BETWEEN PRIMATES AND BIRDS  
IN MADAGASCAR**

KIT STONER

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requirements of Anglia Ruskin University  
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ANGLIA RUSKIN UNIVERSITY

## ABSTRACT

FACULTY OF SCIENCE AND TECHNOLOGY

MASTER OF PHILOSOPHY

### INVESTIGATING POLYSPECIFIC COMMUNICATION AND ASSOCIATIONS BETWEEN PRIMATES AND BIRDS IN MADAGASCAR

KIT STONER

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Some species in co-evolved communities may rely on others to access resources or avoid predation, with knock-on effects for their survival if the dynamics of mixed species groups or interspecific communication are changed. Madagascar has some particularly vulnerable ecosystems and habitat fragmentation threatens the survival of lemurs and other animals. It is therefore essential that we understand the complex relationships between different species.

This study investigated whether ring-tailed lemurs, *Lemur catta*, and Verreaux's sifakas, *Propithecus verreauxi*, respond to specific bird calls, and if so, what is the function and habitat context of these responses. Whilst both are known to recognise each others' alarm calls and the calls of aerial predators, this is the first time that an experiment has tested their responses to non-predator bird alarm calls. The second half of the study explored whether these two species form associations with specific bird species, and the function of any associations formed.

A controlled playback experiment was used to test responses of the two lemur species to the following bird calls in different habitats: song of Madagascar magpie robin, *Copsychus albospectularis*, (control), green pigeon, *Treron australis*, song, white-headed vanga, *Artamella viridi*, call and crested drongo, *Dicrurus forficatus*, alarm call. The research was carried out at Berenty reserve in the south of Madagascar. Calls were presented in counterbalanced order to 21 different troops of lemurs. Group scans recorded lemur behaviour prior to and after playback. Focal sampling and group scans were used to record activity, habitat context and bird associations for each troop.

Both lemur species showed a significantly greater vigilant response to crested drongo alarm calls compared to their response to the control. Open and closed habitat did not have a significant effect on either species of lemurs' response to the crested drongo alarm calls. Neither lemur species were shown to seek out associations with specific bird species. The results suggest that the primary reason for these two lemur species listening to bird communication is predation avoidance rather than foraging efficiency. This research supports the suggestion that species in co-evolved communities may rely on others to avoid predation.

**Key words:** *Ring-tailed lemur, Verreaux's sifaka, polyspecific associations, interspecific communication*

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# **Investigating polyspecific communication and associations between primates and birds in Madagascar**

KIT STONER

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# Chapter 1: Introduction

## 1.1 Context

Associations among species are generally classified into three different categories: parasitism (where one species benefits at the expense of the other), mutualism (where both species benefit from the association), and commensalism (where one species benefits and the other is unaffected by the association) (Wilson 1975; Majolo & Ventura, 2004). Of the latter two categories, benefits commonly attributed to group living fall into two general categories: foraging efficiency and predation avoidance. However, group living may result in increased feeding competition and intraspecific aggression. Mixed species associations may provide these benefits without the associated costs (Terborgh, 1990; Chapman & Chapman, 1996; Windfelder, 2001; Oommen & Shanker, 2010; Oliveira & Dietz, 2011; Heymann & Hsia, 2015).

Perhaps the best known examples of mixed groups are mixed species flocks of birds (Morse, 1977; Greenberg, 2000). It is thought that birds may forage more efficiently due to beating (benefiting from insects flushed by flock members), social learning, minimising re-visitation of sites, and by allowing more time to feed (Krebs, 1973; Sullivan, 1984; Hino, 1998). Evidence suggests that mixed species flocks of birds are, at least in part, adaptations to reduce the risk of predation (Thiollay & Jullien, 1998; Thiollay, 1999). One important aspect of this is alarm calls; birds in mixed-species flocks have been shown to listen, read and respond to other species' aerial alarm calls (Munn, 1984; Sullivan, 1984; Goodale & Kotagama, 2008). Playback studies have been used for several species, for example, Sullivan (1984) demonstrated that downy woodpeckers, *Picoides pubescens*, foraging in mixed-species flocks of woodland birds increased their rate of scanning after the broadcast of alarm calls of chickadees, *Parus articapillus*, or tufted titmice, *P. bicolor*, (Fichtel, 2004).

Evidence suggests that interspecific communication *between* taxonomic mammal groups also takes place: bonnet macaques, *Macaca radiata*, responded with flight and/or scanning responses after the alarm calls of sambar deer, *Cervus unicolor*, as well as those of sympatric Nilgiri langurs, *Trachypithecus johnii*, and Hanuman langurs, *Semnopithecus entellus* (Fichtel, 2004). There is also evidence that mammals can recognise and respond to bird calls: Randler (2006) found that red squirrels, *Sciurus vulgaris*, responded to Eurasian jay, *Garrulus glandarius*, alarm calls with anti-predator behaviour, including increased vigilance, and Gunther's dik-diks, *Madoqua guentheri*, respond to bird alarm calls (Lea *et al.*,

2008; Kitchen *et al.*, 2010). There are examples of primates recognising and responding to bird calls, for example, vervet monkeys, *Chlorocebus pygerythrus*, to the alarm calls of superb starlings, *Spreo superbis*, (Seyfarth & Cheney, 1990), and conversely, birds responding to primates: hornbills, *Ceratogymna* spp., are known to discriminate between primate alarm calls (Rainey *et al.*, 2004; Kitchen *et al.*, 2010). In some cases the mammal/bird communication is mutualistic: for example, Von der Decken's hornbill, *Tockus deckeni*, and eastern yellow-billed hornbill, *Tockus flavirostris*, wait in trees near where dwarf mongooses, *Helogale parvula*, are sleeping for them to emerge, and the mongooses delay their departure if no birds are present. Hornbills warn for raptor species which do not predate them but which are mongoose predators; not, however, for raptors which are not mongoose predators (Rasa, 1983; Heymann & Hsia, 2015).

Evidence also suggests that some species may join mixed species groups to increase their ability to avoid predators. Different species may differ in their sensory ability to detect predators. These groups may be more efficient at detecting predators if two species scan in different ways, for example, one species may be more vigilant at lower levels of the forest and therefore better able to detect terrestrial predators, whilst others in a mixed species group may be vigilant at higher levels, scanning sideways and upwards to detect aerial and arboreal threats (Peres, 1993; Heymann & Buchanan-Smith, 2000; Stensland *et al.*, 2003; Harrison & Whitehouse, 2011). Red colobus monkeys, *Procolobus badius*, spend more time in mixed-species groups with black-and-white colobus, *Colobus guereza* (which scan in the upper canopy more than the other species in the group), red-tailed monkeys, *Cercopithecus ascanius*, blue monkeys, *C. mitis*, and grey-cheeked mangabeys, *Lophocebus albigena*, when the density of predators (chimpanzees, *Pan troglodytes*) is higher (Chapman & Chapman, 2000). It is also thought that red-tailed monkeys benefit from this association, by reducing their risk of aerial predation by crowned hawk-eagles, *Stephanoaetus coronatus* (Teelen, 2007).

Foraging benefits may be the main driver when associating species do not share predators. Insectivorous bird species are known to obtain flushed prey by following primate groups, for example, associations between double-toothed kites, *Harpagus bidentatus*, and primates such as squirrel monkeys, *Saimiri oerstedii*, and tamarins, *Saguinus mystax*, and *S. fuscicollis* (Heymann, 1992; Boinski & Scott, 1998; Haugaasen & Peres, 2008). Similarly, in Namibia, rock kestrels, *Falco rupicolus*, were seen to prey on Orthopterans that flew into the air following disturbance by chacma baboons, *Papio ursinus* (King & Cowlshaw, 2009).

Frugivorous mammals may form associations with sympatric frugivores in order to locate fruit, with their calls acting as a cue (Olupot *et al.*, 1998). Cords (1990) found that red-tailed monkeys use blue monkeys as a guide to food resources, and collared peccaries, *Tayassu tajacu*, have been observed actively following weeper capuchin, *Cebus olivaceus*, to locate fruiting-trees and take advantage of residual fruitfall (Robinson & Eisenberg, 1985; Haugaasen & Peres, 2008).

Rodrigues *et al.* (1994) noted that tanagers (Thraupidae) associated more with taxa that flush insects, including primates and other bird species, in times of low fruit and insect availability, suggesting there may be seasonal variation in associations (Hankerson *et al.*, 2006). Habitat context can also affect interspecific associations and communication. If birds associate with primates in order to gain flushed prey, these associations may be more frequent when primates move through denser vegetation and subsequently dislodge more insects (Hankerson *et al.*, 2006). Primate response to alarm calls can also be affected by habitat context (Enstam & Isbell, 2002). Evidence suggests that some species increase their use of exposed habitat when in mixed species groups, likely because of increased protection against predators (Cords, 1990).

## **1.2 Significance of study**

It is essential for conservation that we understand the complex relationships between species since these interactions, whether they be direct or indirect, are crucial to the functioning of ecosystems. Species in co-evolved communities may rely on others to access resources or avoid predation, with knock-on effects for their survival if the dynamics of the mixed groups are changed (Laland & Boorgert, 2010; Harrison & Whitehouse, 2011; Walsh, 2013; Heymann & Hsia, 2015). Madagascar has some particularly vulnerable ecosystems: over 80% of the island has already been stripped of vegetation cover and habitat fragmentation threatens the survival of lemurs and other animals in Malagasy forests (Bollen & Donati, 2006; Mittermeier *et al.*, 2005; Schwitzer *et al.*, 2013).

In a review of primate – non-primate associations (PNPAs), Heymann and Hsia (2015) reported that PNPAs are absent from Madagascar, including primate – bird associations. One of the reasons given for this is the relatively impoverished avian and mammalian fauna, providing few opportunities for such associations, particularly in comparison to main-land Africa, Asia and the Neotropics. The lack of such associations could also be partly explained by the fact that the majority of lemurs are nocturnal (Eppley *et al.*, 2014; Heymann & Hsia, 2015). However, two recent papers suggest that PNPAs may occur, and that certain

species of lemurs respond to bird alarm calls: an anecdotal example of an association between a group of southern bamboo lemurs, *Hapalemur meridionalis*, and giant coua, *Coua gigas*, has been published (Eppley *et al.*, 2014). In addition to this, the nocturnal Sahamalaza sportive lemur, *Lepilemur sahamalazensis*, has been shown to respond vigilantly to the alarm calls of the crested coua, *C. cristata*, and the Madagascar magpie robin, *Copsychus albospecularis* (Seiler *et al.*, 2013).

Harrison and Whitehouse (2011) suggest that by associating with other taxonomic groups, animals create a complex social environment that shapes their own ecology and behaviour. It can be difficult to see the full spectrum of interspecific relationships. Given this and the paucity of published literature on associations and communication between lemurs and (non-predatory) birds (the functions of which are, in the main, untested), there is merit in exploring this area further for different diurnal species of lemur.

### **1.3 Lemurs**

There are 99 species of lemur (as of 2013), 103 taxa including subspecies. All of these species belong to the primate order and are endemic to the island of Madagascar (Schwitzer *et al.*, 2013). Many lemur species are unique to one specific area of the country and some are rare, for example, the golden bamboo lemur, *Hapalemur aureus*, which is thought to have fewer than 1,000 individuals left in the wild (IUCN, 2014). According to Schwitzer *et al.* (2013), as many as 94% of lemurs are threatened with extinction with 24 species being classified as Critically Endangered and 49 classified as Endangered. In Madagascar, lemurs form a crucial part of the ecosystem, being the primary seed dispersers on an island with impoverished bird fauna and only three frugivorous species of bat (Wright *et al.*, 2011). For the purposes of this research, two relatively common species of lemur (ring-tailed lemur, *Lemur catta*, and Verreaux's sifaka, *Propithecus verreauxi*) were studied in order that sufficient data could be obtained and to pilot the methods used in captivity prior to fieldwork.

#### **1.3.1 Verreaux's sifaka**

Verreaux's sifaka is a large diurnal lemur belonging to the family Indridae which is only found in the southern and western parts of Madagascar (Tattersall, 1982; Fichtel & Kappeler, 2002; Fichtel, 2004; Lewis & Kappeler, 2005; Gould & Sauther, 2007; Mittermeier *et al.*, 2008). Like all lemurs, its conservation is of great concern and its status is currently listed as Endangered (IUCN, 2014). Troop sizes vary between sites; the average is between four and

eight individuals but there can be as many as 14 individuals (Norscia & Pelagi, 2008). Verreaux's sifaka is primarily folivorous (Howarth *et al.*, 1986; Wright, 1998) and leaves form the largest component of the sifaka diet throughout the majority of the year; over 88% in the dry season of May to July (Lewis & Kappeler, 2005). They are arboreal lemurs and spend the majority of their time in the lower and middle canopy, where they rest and feed (Howarth *et al.*, 1986; Fichtel & Kappeler, 2002; Lewis & Kappeler, 2005). This contrasts with the more frugivorous and terrestrial ring-tailed lemur. Birth dates vary between sites but are usually sometime between July and September (Jolly *et al.*, 2002; Lewis & Kappeler, 2005; Norscia & Pelagi, 2008).

### **1.3.2 Ring-tailed lemur**

The ring-tailed lemur is a diurnal lemur belonging to the family Lemnridae and is smaller than Verreaux's sifaka. They are found in the southern half of Madagascar and individuals are now largely restricted to isolated or relatively isolated fragments throughout their geographic range (Jolly, 1966; Sussman *et al.*, 2003; Garbutt, 2007). Like Verreaux's sifaka their status is currently listed as Endangered (IUCN, 2014). Ring-tailed lemur groups tend to be larger than those of Verreaux's sifaka and can be as large as 27 individuals (Jolly, 1966, Gould, 1996). They are more commonly between nine – 16 individuals (Simmen *et al.*, 2010), although smaller groups of four have been observed (pers. obs., 2012). Ring-tailed lemurs are opportunistic omnivores (Sauther *et al.*, 1999), and for gallery forest-dwelling populations, seasonal and sex differences in diet have been documented. In the wet season, the large majority of the ring-tailed lemur diet comprises ripe fruit, whereas in the dry season they have a greater reliance on unripe fruit and mature leaves (Sauther, 1994; Simmen *et al.*, 2003; 2006; Gould *et al.*, 2011). They are one of the more terrestrial species of lemur, with up to 70% of group travel being on the ground (Sauther, 1994). They usually give birth during September but it can be as early as August and occasionally as late as December (Jolly, 1966; Jolly *et al.*, 2002; Gemmill & Gould, 2008; Simmen *et al.*, 2010).

### **1.4 Birds co-occurring with lemurs in Madagascar**

There are just over 200 breeding species of bird in Madagascar, more than half of which are endemic to the country (Morris & Hawkins, 1998; Heymann & Hsia, 2015). Some of these birds are frugivorous, for example, the Madagascar green pigeon, *Treron australis*, and will feed in the same fruiting trees as frugivorous lemurs like the ring-tailed lemur. Other birds are insectivorous and are regularly observed in mixed species flocks, including the crested drongo, *Dicrurus forficatus*, common newtonia, *Newtonia brunneicauda*, Madagascar

paradise flycatcher, *Tersiphone mutata*, rufous vanga, *Shetba rufa*, blue vanga, *Cyanolanius madagascariensis*, ashy cuckoo shrike, *Coracina cinerea*, common jery, *Neomixis tenella*, and Madagascar white eye, *Zosterops maderaspatanus* (Eguchi *et al.*, 1993; Hino, 1998).

Madagascar is home to several species of raptor, some of which are known to predate on lemurs. In Ranomafana National Park large and small lemurs are killed by raptors, including the Madagascar harrier hawk, *Polyboroides radiatus*, and the Henst's goshawk, *Accipiter henstii* (Karpanty, 2006). At Kirindy Forest and Berenty and Bealoka reserves Verreaux's sifaka are preyed on by harrier hawks (Karpanty & Goodman, 1999; Fichtel & Kappeler, 2011), and may account for 48.4% of the biomass of the hawks' diet (Karpanty & Goodman, 1999).

## 1.5 Objectives of study

Several playback experiments were developed in order to test for recognition by lemurs of different bird calls. The experimental part of this research therefore explores the following questions:

- Do ring-tailed lemurs and Verreaux's sifakas respond to specific bird calls?
- What is the function and habitat context of these responses?

Both ring-tailed lemurs and Verreaux's sifakas are known to use acoustic cues to recognise predators, responding to each others' alarm calls and to the calls of aerial predators (Oda, 1998; Fichtel, 2004). Further, ring-tailed lemurs have been shown to respond to the alarm calls of the ground coua and helmeted guinea fowl, *Numida meleagris* (Sauter, 1989). Recent research shows that another species of lemur, the Sahamalaza sportive lemur, can distinguish between the alarm calls and contact calls/songs of the crested coua and the Madagascar magpie robin (Seiler *et al.*, 2013).

**Prediction 1:** Both species will respond to specific bird calls in different ways.

**Prediction 2:** Both species will respond to alarm calls with vigilant behaviour.

Whilst research shows that foraging-focused interspecific communication does take place (Olupot *et al.*, 1998; Haugaasen & Peres, 2008), there is little published literature on lemur/bird communication in relation to foraging and it is thought that this is not likely to occur (Heymann & Hsia, 2015). However, fruit is sparse in Madagascar between June and

September and primates in other parts of the world have been known to use the calls of different species as a way of finding food (Cords, 1990; Olupot *et al.*, 1998; Haugaasen & Peres, 2008). If such communication does take place, it is most likely to be between frugivorous birds and more frugivorous lemurs, such as the ring-tailed lemur.

**Prediction 3:** Ring-tailed lemurs will respond more than Verreaux's sifakas to the calls of frugivorous bird species.

Although lemurs are in danger from aerial predation when in the upper canopy and terminal branches, it is thought that lemurs are in greater danger in open canopy areas, particularly during terrestrial travel, as the ground is a preferred striking location for the Madagascar harrier hawk (Sauther, 1989; 2002).

**Prediction 4:** Both lemur species will respond vigilantly to alarm calls more in open habitats.

The second half of the study aims to explore the following questions:

- Do ring-tailed lemurs and Verreaux's sifakas form associations with specific bird species?
- What is the function and habitat context of any associations formed?

**Prediction 5:** Ring-tailed lemurs will form associations with frugivorous birds more than Verreaux's sifakas.

**Prediction 6:** Lemur species will not influence the number of associations motivated by predator avoidance, i.e. with alarm-calling birds.

**Prediction 7:** Lemur species will form more associations with alarm-calling birds in open habitats.



## Chapter 2: Methods

### 2.1 Study site

Berenty Reserve sits next to the Mandrare River (S 25.00°; E 46.30°) and comprises 200 ha of protected, privately owned land (Jolly & Pride, 1999; Jolly *et al.*, 2002; Mertl-Milhollen *et al.*, 2003; Norscia & Pelagi, 2008). It is broadly divided into five zones: Ankoba (largely regrown from cleared ground), Tourist Front (a part of the western boundary), Gallery (natural forest, with canopy blocking >50% of the sky), Scrub (drier natural forest, >50% open to the sky) and the Spiny Forest (deciduous woody plants/deciduous/evergreen succulents), and is essentially a 'habitat island' (Jolly *et al.*, 2002) (figure 1). The wet season at Berenty falls between November and April, with the dry season lasting from May to October. The mean rainfall is approximately 500mm per year but it does fluctuate, with severe droughts occurring in some years (Jolly *et al.*, 2002; Simmen *et al.*, 2003; Jolly *et al.*, 2006). This research took place in the cooler months of the dry season: July to mid August 2012. Temperature at Berenty ranges between  $\leq 4^{\circ}\text{C}$  at night during the dry season up to  $40^{\circ}\text{C}$  during the day in the wet season (Simmen *et al.*, 2003; Jolly *et al.*, 2006).



**Figure 1: Aerial view of Berenty Reserve (with zones labelled). Courtesy of Barry Ferguson and Centre Ecologique de Libanona, [www.libanona.com](http://www.libanona.com) (Jolly *et al.*, 2006)**

There are a number of environmental challenges at Berenty Reserve. Alongside native plant species such as *Tamarindus indica* and *Ficus* spp., there are numerous introduced plants such as *Azadirachta indica*, *Cordia sinensis* and *Pithecellobium dulce* (Simmen *et al.*, 2003; Norscia & Pelagi, 2008; pers. obs., 2012). The introduction of exotic plant species, alongside provisioning by tourists and an artificial supply of water, has led to an artificially high population of lemurs which, in turn, leads to greater competition for resources (Jolly *et al.*, 2002; Norscia & Pelagi, 2008). This is somewhat increased by the introduction of the red-fronted brown lemur hybrid, *Eulemur fulvus rufus* x *Eulemur collaris*, in 1975 (Blumenfeld-Jones *et al.*, 2006; Jolly *et al.*, 2006; Pinkus *et al.*, 2006).

Three diurnal lemur species are present at Berenty: the red-fronted brown lemur hybrid, ring-tailed lemur and Verreaux's sifaka. In addition to this there are three nocturnal lemurs: the grey-brown mouse lemur, *Microcebus griseorufus*, grey mouse lemur, *M. murinus*, and white-footed sportive lemur, *Lepilemur leucopus* (Jolly *et al.*, 2006; Simmen *et al.*, 2006; Garbutt, 2007; Norscia & Pelagi, 2008; Donati *et al.*, 2009). Whilst fossa, *Cryptoprocta ferox*, are not present at Berenty, domestic dogs and cats are known to predate lemurs, alongside larger raptors such as the Madagascar harrier hawk and the Madagascar buzzard, *Buteo madagascariensis*, which are also present. Fifty-two species of resident birds have been recorded out of a total of 99 species seen (Jolly *et al.*, 2006).

## 2.2 Study subjects

The population density of ring-tailed lemurs at Berenty is 2.5 individuals/ha in the gallery forest, 5.0 individuals/ha at the tourist front, and 1.3 individuals/ha in the scrub and spiny forest (Jolly *et al.*, 2002; Pride, 2005; Gould *et al.*, 2011). In 2002 a total of 103 troops were counted. In general the troops close to the Tourist Front are larger in number (Jolly *et al.*, 2002). At this site ring-tailed lemurs usually give birth in September or October (Jolly *et al.*, 2002); this research was carried out in July and the first half of August and so no ring-tailed lemur infants were present. Tamarind, *Tamarindus indica*, fruit and leaves form an important part of the ring-tailed lemur diet at Berenty (Yamashita, 2002; Mertl-Millhollen *et al.*, 2003; Simmen *et al.*, 2003; 2006; Gemmill & Gould, 2008, pers. obs., 2012).

Like the ring-tailed lemur, the population of Verreaux's sifaka at Berenty is dense and group size can be quite large ( $\leq 9$  or 10 individuals) (Jolly *et al.*, 2006; Norscia & Pelagi, 2008). In Ankoba the population density is estimated at 2.75 individuals/ha, with the density in the Malaza gallery-transitional zone being 1.86 individuals/ha, 0.41 individuals/ha in the Malaza scrub area and 1.91 individuals/ha in the spiny forest parcel (Norscia & Pelagi, 2008). During

this study, infants started to appear with some troops during July. The diet of Verreaux's sifakas at Berenty is different to that of the ring-tailed lemurs; whilst they also eat tamarind fruit and leaves, their diet is far more eclectic, with a greater reliance on foliage (Simmen *et al.*, 2003).

A total of 11 ring-tailed lemur troops and 14 Verreaux's sifaka groups were followed during this study. The species and number of individuals in each group is shown in table 1. It also highlights whether an infant was present in the troop. Only 21 of these troops were included in the playback analysis.

**Table 1: List of lemur groups studied in period July-August 2012**

<b>Group ID</b>	<b>Species</b>	<b>Maximum no of lemurs seen in troop</b>	<b>Infant present in troop</b>
R1	Ring tailed lemur	11	No
R2	Ring tailed lemur	11	No
R3	Ring tailed lemur	12	No
R4	Ring tailed lemur	12	No
R5	Ring tailed lemur	7	No
R6	Ring tailed lemur	4	No
R7	Ring tailed lemur	11	No
R8	Ring tailed lemur	4	No
R9	Ring tailed lemur	12	No
R10	Ring tailed lemur	10	No
R11	Ring tailed lemur	8	No
S1	Verreaux's sifaka	10	No
S2	Verreaux's sifaka	6	No
S3	Verreaux's sifaka	7	Yes
S4	Verreaux's sifaka	8	Yes
S5	Verreaux's sifaka	6	Yes
S6	Verreaux's sifaka	10	No
S7	Verreaux's sifaka	9	No
S8	Verreaux's sifaka	4	No
S9	Verreaux's sifaka	10	No
S10	Verreaux's sifaka	8	Yes
S11	Verreaux's sifaka	8	Yes
S12	Verreaux's sifaka	6	Yes
S13	Verreaux's sifaka	5	No
S15	Verreaux's sifaka	8	No

## 2.3 Playback stimuli

The calls of four abundant bird species were played to ring-tailed lemurs and Verreaux's sifakas. Bird calls were sourced from the free online archive Xeno-canto, from Pro-Sounds Effects and the Bird Sounds of Madagascar CD (Ranft & Hawkins, 2007). Where possible calls recorded at Berenty were chosen to reduce the impact of potential geographical variation in calls. The same recording of each bird was used in all of the trials and only birds commonly found at Berenty were used. In order to test possible reasons for responses to call, if any, four different native bird calls were selected for playback:

- 1) Frugivorous bird song – Madagascar green pigeon, *Treron australis*. Only true frugivorous bird found at Berenty and shares some food preferences with ring-tailed lemurs. Call not recorded at Berenty.
- 2) Insectivorous mixed species flock bird contact call – White-headed vanga, *Artamella viridis*. Mixed species flock bird found in Berenty as comparison to frugivorous bird. Call not recorded at Berenty.
- 3) Insectivorous bird **alarm** call – Crested drongo, *Dicrurus forficatus*. Drongo alarm calls are well studied, and often used by other bird species in Madagascar and other countries (Goodale & Kotagama, 2005; Satischandra *et al.*, 2010; Flower, 2011). Call recorded at Berenty.
- 4) Control – the song of the Madagascar magpie robin, *Copsychus albospectularis*, was used as the control. The robin is a very common bird at Berenty. Call recorded at Berenty. ([www.xeno-canto.org/species/Copsychus-albospectularis](http://www.xeno-canto.org/species/Copsychus-albospectularis))

## 2.4 Playback procedure

Calls were played back using a Sony Minidisk MZ-R900/L and a portable, battery-powered SME-AFS field speaker (Saul Mineroff Electronics; Elmont, NY). The loudspeaker was placed at least 30m away from the lemur troop and approximately 10m from the observers. Where possible the speaker was hidden behind vegetation. Playback was undertaken after troops had been observed for at least 30 minutes to minimise confounding variables such as distraction by the observers. Calls were only presented when the lemurs were engaged in a quiet activity and when no natural alarm calls (lemur or bird) had occurred in the preceding five minutes.

Lemur behaviour immediately prior to, and following, each treatment was recorded using a group scan of up to 30 seconds depending on the size of the group (table 2 for operational definitions of behaviour) (Martin & Bateson, 2007). The control, vanga and pigeon calls were presented in a counter-balanced randomised order with one minute of silence between each call. The drongo alarm call was presented at the end of the sequence to limit the potential impact on lemur response to the other calls. Playback took place between 7.45 – 16.30 local time, with a balance between morning (7.00 – 12.00) and afternoon (12.01 – 17.00) treatments to allow comparisons (table 3 for response behaviour categories). Calls were presented to groups in different habitat contexts to allow comparison (table 4 for habitat categories). Habitat context and the position of each individual in the canopy or on the ground was recorded prior to each call (table 5 for position categories).

Ten different ring-tailed lemur groups and 11 sifaka groups were played the four bird calls. No lemur group was played the calls more than four times in a two month period. This limited both pseudoreplication and disturbance to the lemurs.

**Table 2: Operational definitions of behaviour. Used for group scans, focal sampling and prior to playback**

Behaviour	Code	Description
Feeding	FE	Individual placing food item into mouth or chewing.
Travelling	T	Individual moving through or between trees or on the ground.
Resting	R	Individual sitting or lying quietly, eyes closed or open but without attentive scanning. Not engaged in other activities.
Vigilant	V	Individual looking up towards a specific direction or scanning the environment.
Grooming	G	Individual grooming itself or another troop member.
Other	O	Activities not covered by the above descriptions, including playing.

**Table 3: Operational definitions of behaviour in response to playback**

Behaviour	Code	Description
No reaction	N	Individual continued with previous quiet activity
Look up	L	Individual looked up towards speaker
Scan	S	Visual scan of the sky, ground or towards the speaker
Vocalisation	V	Distinct alarm call vocalisation
Flee	F	Flight away from the speaker
Advance towards speaker	A	Movement towards the speaker

**Table 4: Definitions of habitat categories**

Defined as open canopy		Defined as closed canopy	
Upper canopy	Lower canopy	Upper canopy	Lower canopy
0-25% coverage	0-25% coverage	50-75% coverage	0-25% coverage
0-25% coverage	25-50% coverage	50-75% coverage	25-50% coverage
0-25% coverage	50-75% coverage	50-75% coverage	50-75% coverage
0-25% coverage	75+% coverage	50-75% coverage	75+% coverage
25-50% coverage	0-25% coverage	75+% coverage	0-25% coverage
25-50% coverage	25-50% coverage	75+% coverage	25-50% coverage
25-50% coverage	50-75% coverage	75+% coverage	50-75% coverage
25-50% coverage	75+% coverage	75+% coverage	75+% coverage

**Table 5: Definition of position in canopy or on the ground**

Position in canopy		Position on ground	
G	Ground	N/A	In tree
B	Bottom third of tree	<5m	Less than 5m from nearest tree
M	Medium third of tree	5-10m	5-10m from nearest tree
T	Top third of tree	> 10m	More than 5m from nearest tree

## **2.5 Activity and association data collection**

Prior to fieldwork being carried out, observations of captive ring-tailed lemurs were carried out at Shepreth Wildlife Park, Cambridgeshire. A small troop of lemurs (five individuals) live on a small island in the middle of a lake, and observations were carried out from the side of the lake using binoculars. Observations took place 29 January – 23 February (total of 12 hours) and 8 May – 14 June 2012 (total of 14 hours). Observations only took place in dry weather; in wet weather the lemurs stayed in their shelter and were not visible. The captive studies enabled sampling techniques to be practised and operational definitions of behaviour to be developed.

The first week of the field work at Berenty was used to test the behavioural categories against wild animals, and for the researcher and field assistant to familiarise themselves with the field techniques and to test inter-observer reliability. This time also enabled the team to familiarise themselves with key bird calls.

Behavioural and bird association data were collected from those troops used for playback, through a combination of focal sampling and group scans. The habitat context was recorded for all forms of data collection (table 4).

### **2.5.1 Focal sampling**

Two minute individual follows were carried out every half hour with continuous recording of time spent feeding and vigilant (Martin & Bateson, 2007). Focal animals were observed in rotation so that males, females and juveniles were sampled equally and the data shown in tables 5 and 6 were recorded. Vibrating timers were used by the research team to ensure that focal sampling took place at the correct time and for the correct duration.

**Table 6: Data recorded on focal individuals**

Date	Total feeding time (in seconds)
Time	Total time vigilant (in seconds)
Species	Food resource (Fruit / plant / other)
ID	Food species if known
Status (M, F, J)	Number of birds in association*
Canopy height (see table 6)	Bird species in association
Distance from nearest tree if on ground (see table 6)	Type of bird**
*A bird was defined as in association with the troop if it was within 10m of a troop member. ** Birds were defined as Frugivore, Insectivore, Omnivorous, Unknown. Table 7 lists birds sighted and their definitions.	

Before undertaking fieldwork the researcher and field assistant measured distances from a tree and practised estimating distance. Estimations were then used in the field (table 5).

Bird groupings were defined prior to fieldwork based on information from Birds of Madagascar (Morris and Hawkins, 1998) and relevant scientific papers (table 7).

**Table 7: Definitions of bird groups**

Bird group	Bird species
<b>Frugivorous birds</b>	Lesser vasa parrot ( <i>Coracopsis nigra</i> )
	Greater vasa parrot <i>Coracopsis vasa</i> )
	Green pigeon ( <i>Treron australis</i> )
<b>Insectivorous birds*</b>	Common jery ( <i>Neomixis tenella</i> )
	Common newtonia ( <i>Newtonia brunneicauda</i> )
	*Crested coua ( <i>Coua cristata</i> )
	*Crested drongo ( <i>Dicrurus forficatus</i> )
	Giant coua ( <i>Coua gigas</i> )
	Hook-billed vanga ( <i>Vanga curvirostris</i> )
	Madagascar bee-eater ( <i>Merops superciliosus</i> )
	*Madagascar paradise flycatcher ( <i>Terpsiphone mutata</i> )
	*Madagascar magpie robin ( <i>Copsychus albospectularis</i> )
<b>Omnivorous/other</b>	Common myna ( <i>Acridotheres tristis</i> )
	Grey-headed lovebird ( <i>Agapornis canus</i> )



	Madagascar bulbul ( <i>Hypsipetes madagascariensis</i> )
	Madagascar coucal ( <i>Centropus toulou</i> )
	Madagascar turtle dove ( <i>Nesoenas picturata</i> )
	Madagascar white eye ( <i>Zosterops maderaspatanus</i> )
	Namaqua dove ( <i>Oena capensis</i> )
	Pied crow ( <i>Corvus albus</i> )
	Sakalava weaver ( <i>Ploceus sakalava</i> )
	Souimanga sunbird ( <i>Nectarinia souimanga</i> )

\* additionally defined as alarm-calling birds (Goodale & Kotagama, 2005; Ito & Mori, 2010; Satischandra *et al.*, 2010; Flower, 2011, Seiler *et al.*, 2013).

### 2.5.2 Group scans

Group scans were carried out at 15 minute intervals from when a troop was found in the morning to 4.30pm the same day. Scans took up to 30 seconds, depending on the size of the group (Martin & Bateson, 2007). The behavioural categories shown in table 2 were recorded for each individual lemur. Additional contextual data was recorded as for focal animals (tables 5 and 6): date, time, species, food resource if feeding, canopy height/position on ground and birds in association with the troop.

Twenty-five different lemur troops were followed to minimise disturbance and pseudoreplication during the playback experiments. This meant that it was not usually possible to identify individual lemurs in group scans. However, gender was recorded for individuals where possible.

## 2.6 Data analyses

### 2.6.1 Data preparation

Prior to data being collected, the researcher and field assistant trialed a number of group scans and focal samples to ensure that both team members were interpreting behavioural categories and calculating time periods in the same way. Data collected by the researcher and field assistant were also compared at the end of each day to ensure accuracy. Data were removed where they were not clear.

**Focal data:** Where a group had been followed more than once the first set of data was not included in the analysis to avoid any duplication of groups. Field skills improved throughout

the season and so later data were deemed more robust. Focal data were not included in the analysis where the full two minutes were not achieved (for example, if the individual moved out of sight). Pivot tables in Microsoft Excel 2003 were used to calculate means where more than one set of focal data was collected for a particular individual. They were also used to group data into troop format for the purposes of analysing the bird association data.

**Group scans:** Duplicate group data were removed as for the focal data. Scans where only one individual could be observed were also removed. Pivot tables in Microsoft Excel 2003 were used to ensure that only one set of bird association data was applied to each group scan.

**Playback data:** Duplicate group data were removed as above. Data were not included in the analysis when lemurs changed to a 'non-restful' activity as a result of external stimuli, for example, another troop of lemurs approaching or an alarm call from another lemur troop, before all four calls were played. A non-restful activity was defined as any activity other than resting, feeding or grooming.

### **2.6.2 Statistical analyses**

All statistical analyses were conducted using SPSS 20. The majority of data were not normally distributed and so non-parametric tests were used. The  $\alpha$ -level was set at 0.05 for all tests. Results are reported following the conventions of the journal, *Animal Behaviour* (Elsevier, 2014).

The Wilcoxon signed-rank test was used in order to determine whether there were any statistically significant differences between the response of lemurs to the green pigeon, white-headed vanga and crested drongo calls, and to the control. To explore the effect of explanatory variables (for example, time of day or canopy height before playback) on lemur responses to bird calls Generalised Linear Models (GLMs) were used. A two-way classification chi-square was used to test whether the order of the calls had a significant impact on lemur response.

A Mann-Whitney U test was used to test the difference between lemur species in their time spent vigilant or feeding. The Wilcoxon signed-rank test (or Friedman test where more than two categories) was used to test the difference between lemur vigilance and feeding patterns in different contexts or times. Where a Friedman test found significance, post hoc analysis using the Wilcoxon signed-rank test was carried out to pinpoint which categories were significant.

A Mann-Whitney U test was used to test the difference between the two lemur species in their time spent in association with different groups of birds. The Wilcoxon signed-rank test and Friedman test were used as above to test bird associations in different habitat contexts or times in season/day.

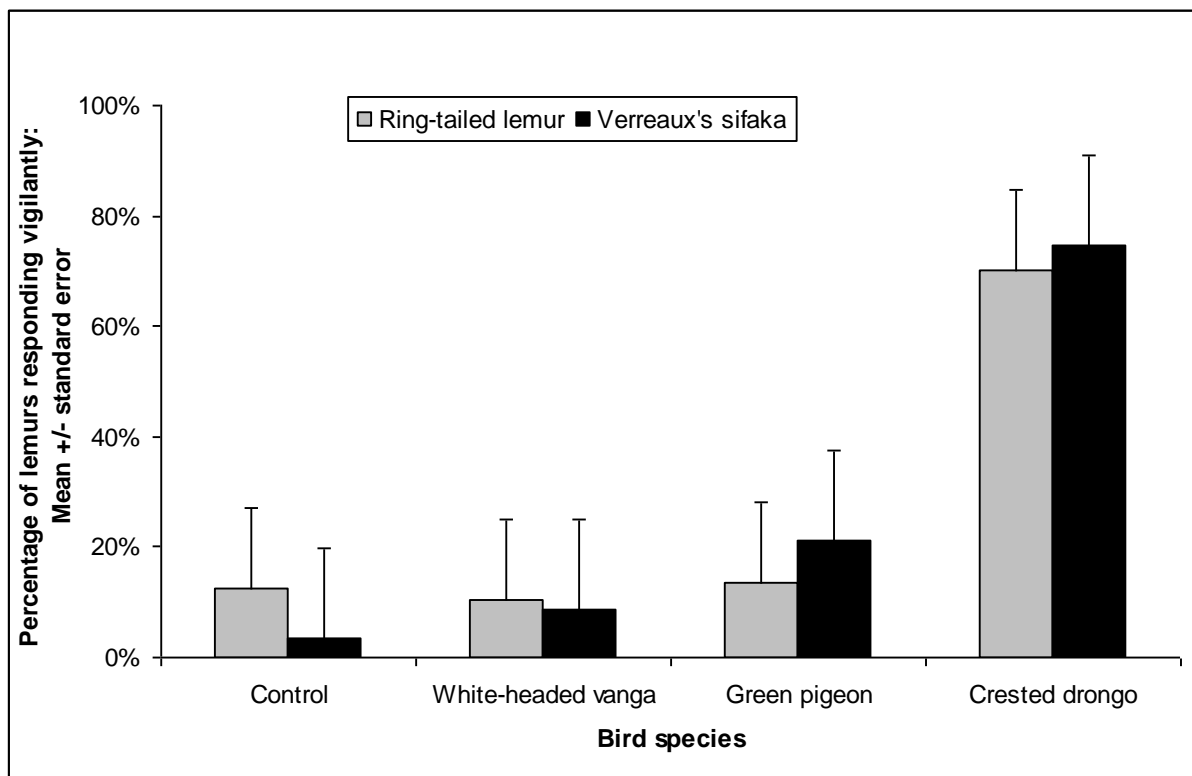
## **2.7 Ethical approval and permissions**

This research was conducted with the permission of the owners of Berenty Reserve (the de Heaulme family) and Alison Jolly, research co-ordinator at Berenty. It was ethically approved by Anglia Ruskin University.

## Chapter 3: Results

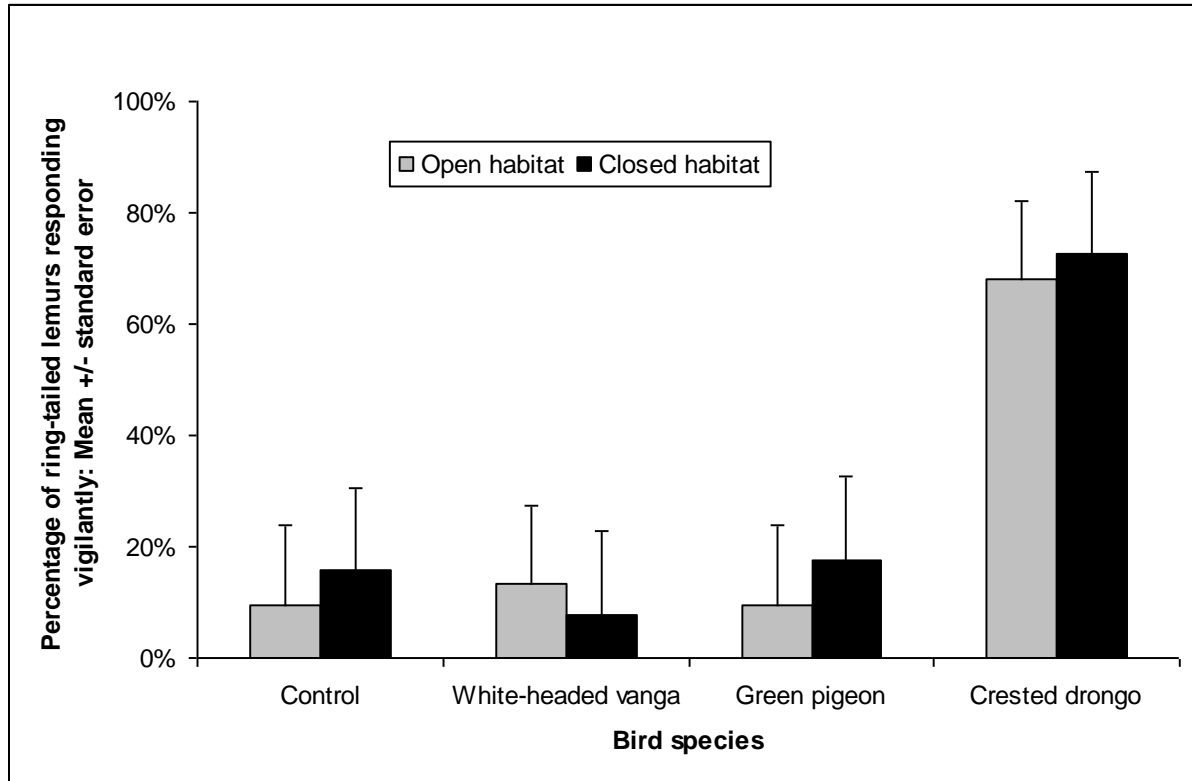
### 3.1 Playback results

Ring-tailed lemurs (70%) and Verreaux's sifakas (75%) responded vigilantly to crested drongo alarm calls across a mixture of habitats (Wilcoxon signed-rank test *Ring-tailed*:  $T = 65$ ,  $N = 104$ ,  $P = 0.000$ ; *Sifaka*:  $T = 86$ ,  $N = 114$ ,  $P = 0.000$ ). A far smaller number of Verreaux's sifakas responded vigilantly to the green pigeon (21%) but this was still significant when compared to the control (Wilcoxon signed-rank test:  $T = 40.5$ ,  $N = 114$ ,  $P = 0.000$ ). Only 13% of ring-tailed lemurs responded to the pigeon with vigilant behaviour and this was not significant (Wilcoxon signed-rank test:  $T = 90$ ,  $N = 104$ ,  $P = 0.819$ ). The white-headed vanga call did not elicit a significant vigilant response from either lemur species (Wilcoxon signed-rank test: *Ringtail*:  $T = 76.5$ ,  $N = 104$ ,  $P = 0.617$ ; *Sifaka*:  $T = 19.5$ ,  $N = 114$ ,  $P = 0.083$ ) (figure 2).



**Figure 2: Comparison of vigilant response by two lemur species to four native bird calls. SE shown.**

Ring-tailed lemurs responded vigilantly to crested drongo alarm calls in both closed (Wilcoxon signed-rank test:  $T = 16$ ,  $N = 51$ ,  $P = 0.000$ ) and open (Wilcoxon signed-rank test:  $T = 17$ ,  $N = 53$ ,  $P = 0.000$ ) habitats but the response was slightly higher in closed habitat (73% vs. 68%). The other calls did not produce a significant response (figure 3 and table 8).

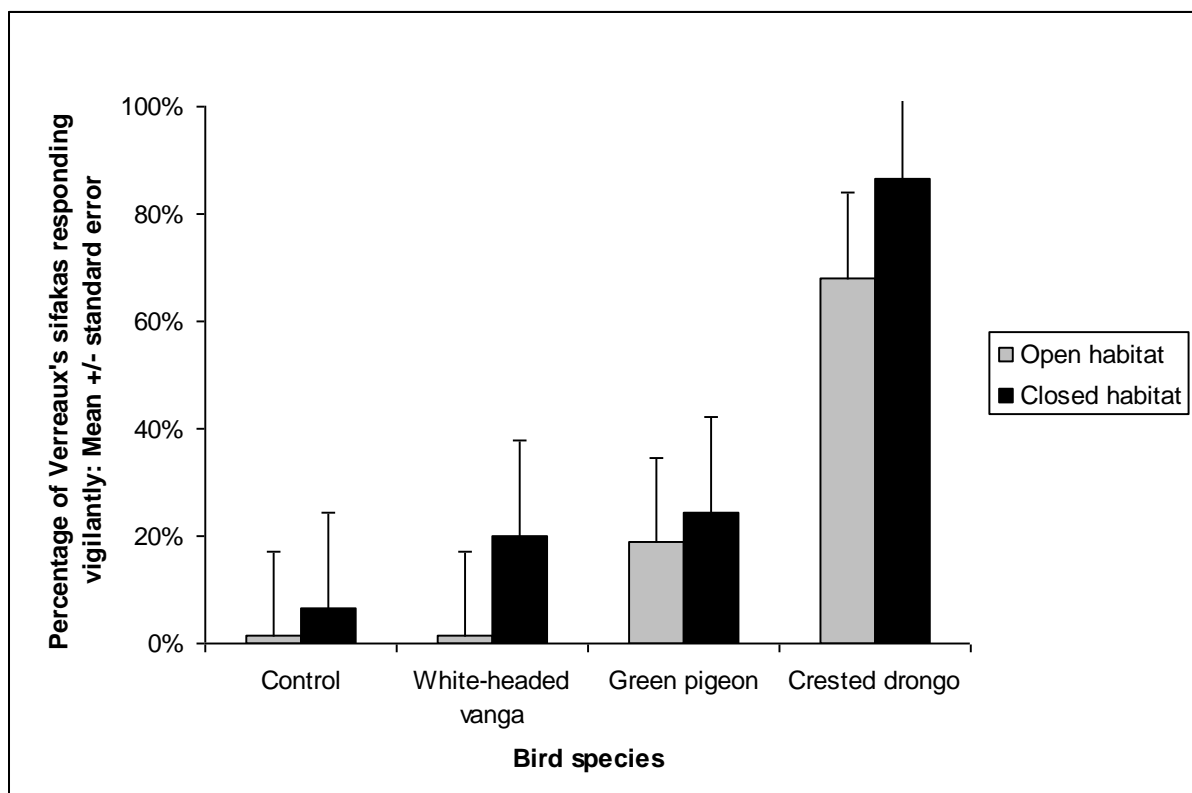


**Figure 3: Comparison of vigilant response by ring-tailed lemurs to four native bird calls in different habitats. SE shown.**

**Table 8: Response of ring-tailed lemurs to bird calls and the significance of the result using Wilcoxon signed-rank test**

Lemur species	Bird call	Habitat	T	N/n	P	Result
Ring-tailed lemur	White-headed vanga	Open	4.5	53	0.480	Not significant
		Closed	4.5	51	0.157	Not significant
	Green pigeon	Open	5.5	53	1.000	Not significant
		Closed	5	51	0.739	Not significant

Like ring-tailed lemurs, Verreaux's sifakas responded vigilantly to crested drongo alarm calls in both closed (Wilcoxon signed-rank test:  $T = 19$ ,  $N = 45$ ,  $P = 0.000$ ) and open (Wilcoxon signed-rank test:  $T = 24.5$ ,  $N = 69$ ,  $P = 0.000$ ) habitats but the response was higher in closed habitat (87% vs 68%). Sifakas also had a significant vigilant response to the green pigeon in both open (Wilcoxon signed-rank test:  $T = 7.5$ ,  $N = 69$ ,  $P = 0.001$ ) and closed (Wilcoxon signed-rank test:  $T = 13$ ,  $N = 45$ ,  $P = 0.021$ ) habitats. The white-headed vanga call did not elicit a significant vigilant response from Verreaux's sifakas (Wilcoxon signed-rank test: *Open*:  $T = 1.5$ ,  $N = 69$ ,  $P = 1.000$ ; *Closed*:  $T = 11$ ,  $N = 45$ ,  $P = 0.058$ ) (figure 4). Generalised Linear Models showed that habitat type (open or closed) was not a significant explanatory variable for the response to any of the bird calls .



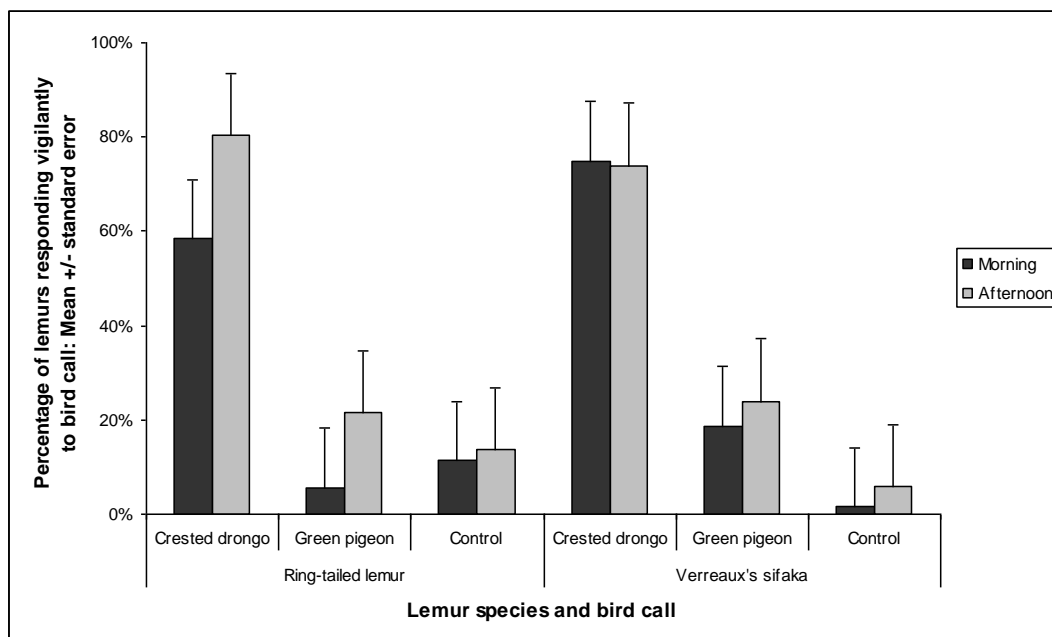
**Figure 4: Comparison of vigilant response by Verreaux's sifakas to four native bird calls in different habitats. SE shown.**

Generalised Linear Models were used to test the effect of other environmental variables on the vigilant lemur responses to bird calls. Neither habitat type, time of day, month, canopy position, upper or lower canopy density or activity prior to playback were significant predictors of the response by either lemur species to the control (magpie robin song).

Time of day was a significant explanatory variable for the ring-tailed lemur response to crested drongo alarm calls, with more responses recorded in the afternoon (80%) than the morning (58%). The same was true of their response to the green pigeon calls with 22% more responding vigilantly in the afternoon than in the morning (6%). Time of day was not significant for the response by Verreaux's sifakas to crested drongo alarm calls or green pigeon calls (table 9 and figure 5).

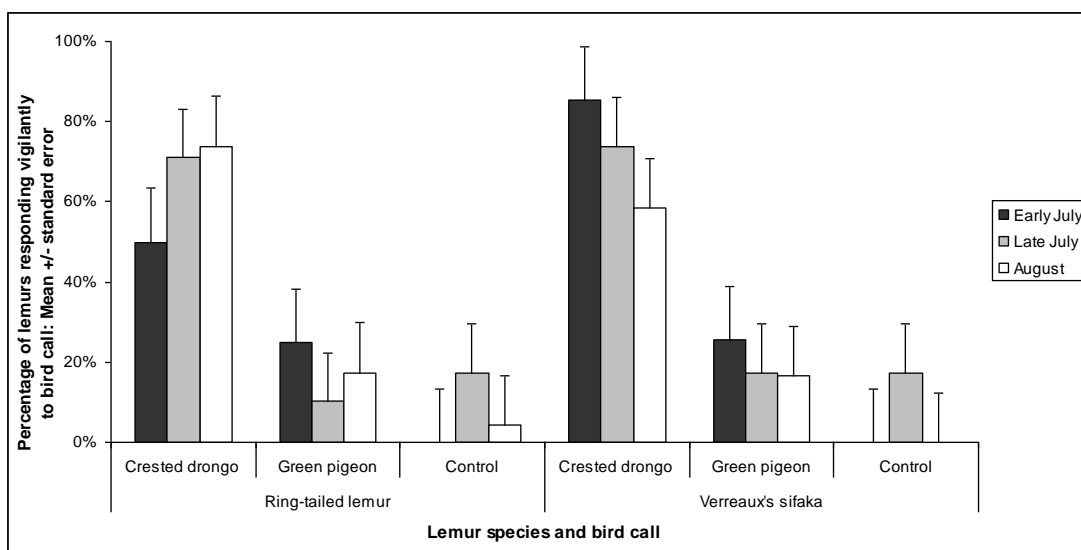
**Table 9: Results of single Generalised Linear Models showing significance of explanatory variables for ring tailed lemur and Verreaux's sifaka responses to the green pigeon and crested drongo playback.**

Explanatory variable	Ring-tailed lemurs	Verreaux's sifakas
Habitat type (open v closed)	GP: $X^2_4 = 1.463$ , $P = 0.227$ CD: $X^2_1 = 0.516$ , $P = 0.473$	GP: $X^2_1 = 0.715$ , $P = 0.398$ CD: $X^2_1 = 1.136$ , $P = 0.286$
Time of day	<b>GP: <math>X^2_1 = 4.939</math>, <math>P = 0.026</math></b> <b>CD: <math>X^2_1 = 5.644</math>, <math>P = 0.018</math></b>	GP: $X^2_1 = 0.464$ , $P = 0.496$ CD: $X^2_1 = 0.015$ , $P = 0.903$
Month in season	GP: $X^2_2 = 2.214$ , $P = 0.331$ CD: $X^2_2 = 2.310$ , $P = 0.315$	GP: $X^2_2 = 1.229$ , $P = 0.541$ <b>CD: <math>X^2_2 = 7.914</math>, <math>P = 0.019</math></b>
Canopy position prior to playback	GP: $X^2_4 = 4.723$ , $P = 0.317$ CD: $X^2_4 = 4.877$ , $P = 0.300$	GP: $X^2_2 = 1.878$ , $P = 0.391$ CD: $X^2_2 = 5.133$ , $P = 0.077$
Upper canopy density	GP: $X^2_3 = 1.489$ , $P = 0.685$ CD: $X^2_3 = 3.460$ , $P = 0.326$	GP: $X^2_3 = 4.144$ , $P = 0.246$ CD: $X^2_3 = 2.753$ , $P = 0.431$
Lower canopy density	GP: $X^2_3 = 3.230$ , $P = 0.357$ <b>CD: <math>X^2_3 = 12.451</math>, <math>P = 0.006</math></b>	GP: $X^2_3 = 1.685$ , $P = 0.640$ CD: $X^2_3 = 4.906$ , $P = 0.179$
Activity prior to playback	GP: $X^2_4 = 0.259$ , $P = 0.992$ CD: $X^2_4 = 0.798$ , $P = 0.939$	GP: $X^2_3 = 0.093$ , $P = 0.993$ CD: $X^2_3 = 0.463$ , $P = 0.927$
GP = green pigeon CD = crested drongo Significant results are in <b>bold</b>		



**Figure 5: Comparison of vigilant response by ring-tailed lemurs and Verreaux's sifakas to bird calls in the morning and the afternoon. SE shown.**

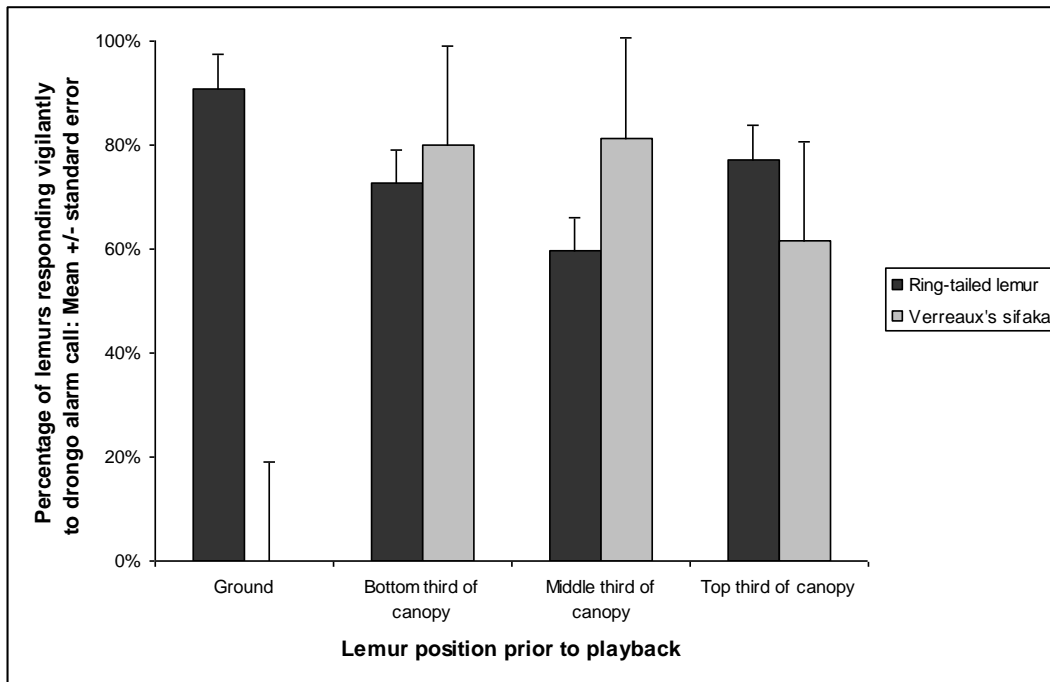
For Verreaux's sifakas, the month had a significant effect on their response to crested drongo alarm calls, with more responding in early July (85%) than in late July (74%) or August (58%) (table 9). More ring-tailed lemurs responded vigilantly to crested drongo calls in late July and August than in early July but this was not significant (table 9 and figure 6). The month was not a significant explanatory variable for response to green pigeon song in either lemur species (table 9 and figure 6).



**Figure 6: Comparison of vigilant response by ring-tailed lemurs and Verreaux's sifakas to bird calls in different months. SE shown.**

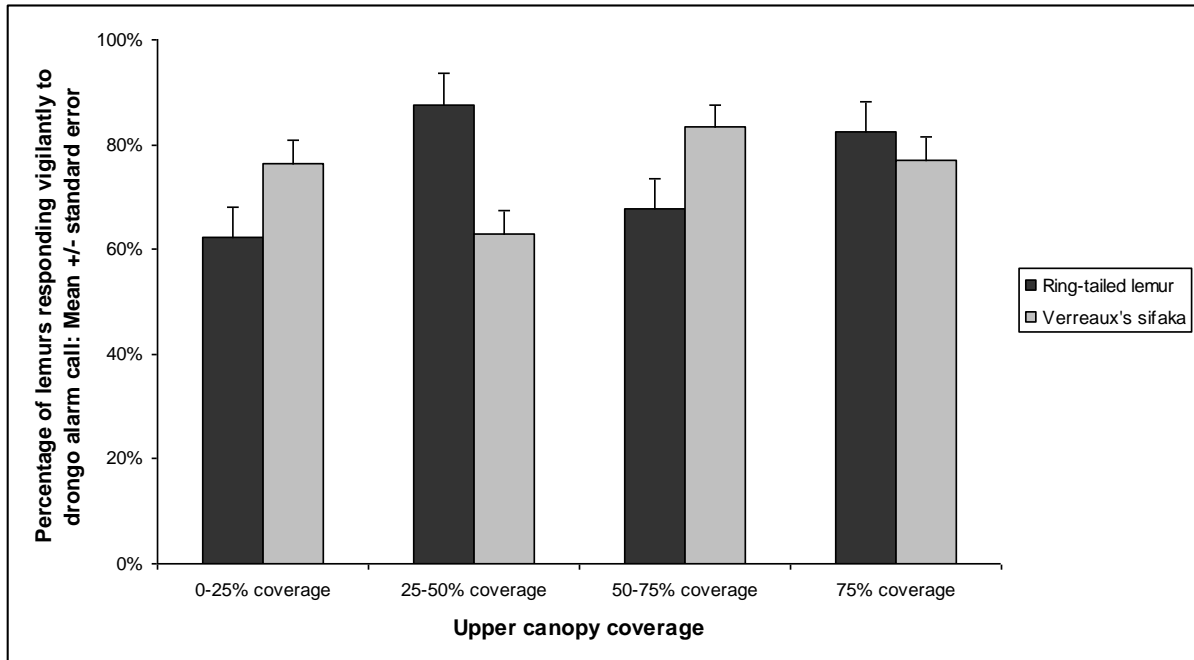


Position in the canopy prior to playback was not a significant explanatory variable for response to the crested drongo alarm call in either lemur species (table 9). The greatest vigilant response to crested drongo calls was by ring-tailed lemurs who were on the ground prior to playback. Sifakas were rarely found resting on the ground and so playback only took place when they were in the canopy (figure 7).



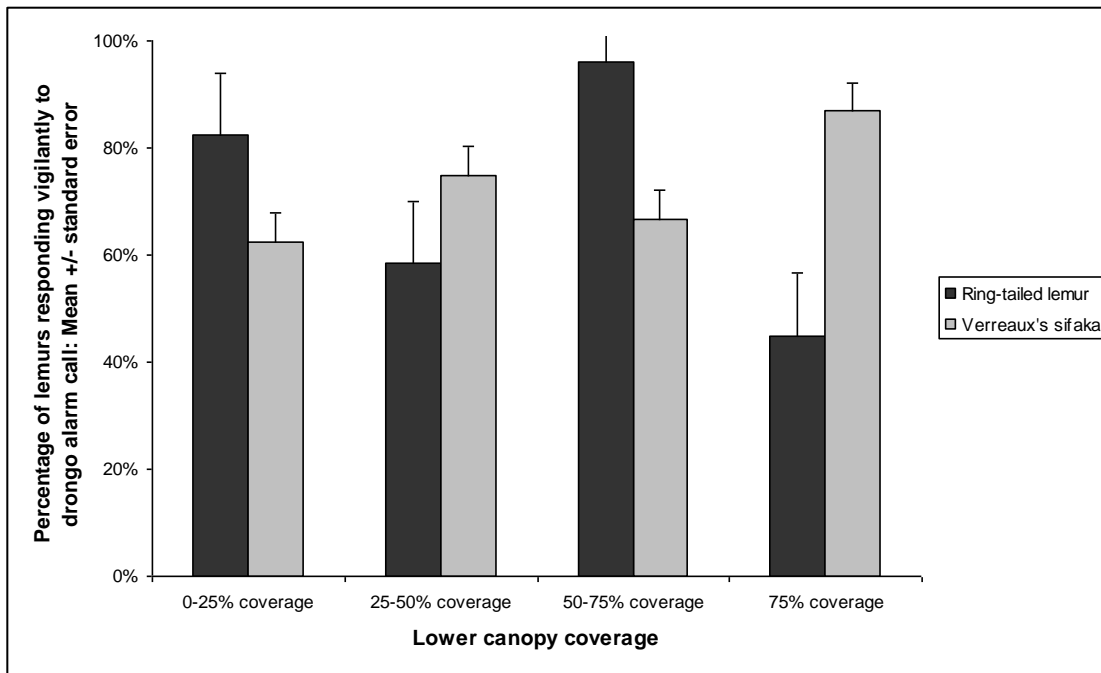
**Figure 7: Comparison of vigilant response by ring-tailed lemurs and Verreaux's sifakas to crested drongo alarm call at different canopy heights. SE shown.**

Upper canopy coverage was not found to be a significant explanatory variable for response to the drongo alarm call by either lemur species (table 9). Following a crested drongo alarm call in habitats of varying degree of upper canopy cover, 62-88% of ring-tailed lemurs and 63-83% Verreaux's sifakas were vigilant (figure 8).



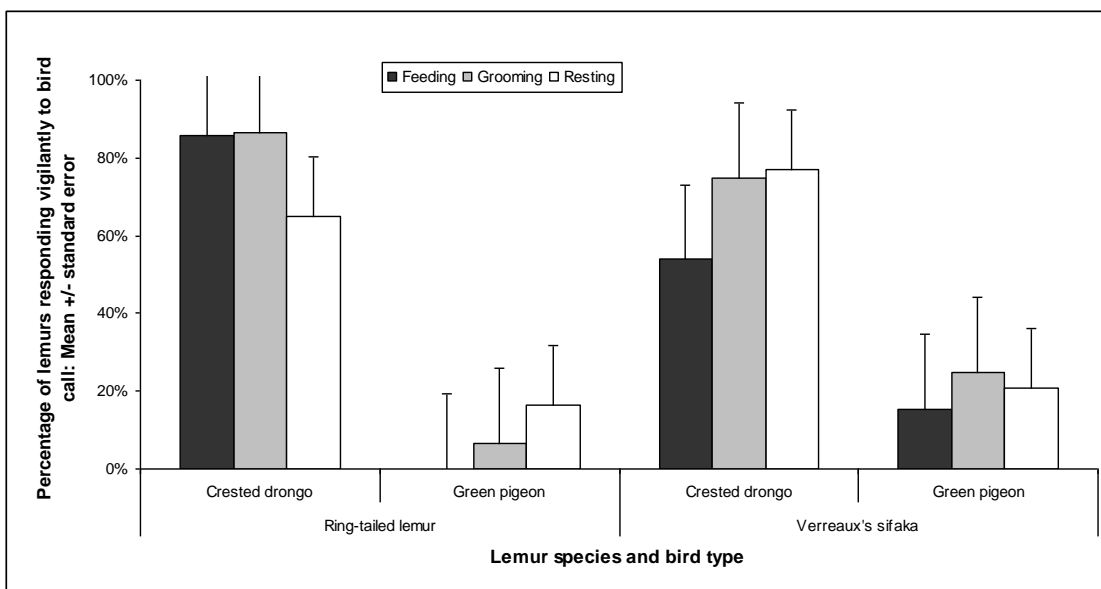
**Figure 8: Comparison of vigilant response by ring-tailed lemurs and Verreaux's sifakas to crested drongo alarm call in different upper canopy coverage. SE shown.**

Ring-tailed lemurs showed greatest vigilance in response to a crested drongo alarm call when in 50-75% lower canopy coverage (96%) and this was a significant explanatory variable (table 9 and figure 9). Lower canopy coverage was not a significant explanatory variable for response to the drongo alarm call by Verreaux's sifakas (table 9 and figure 9).



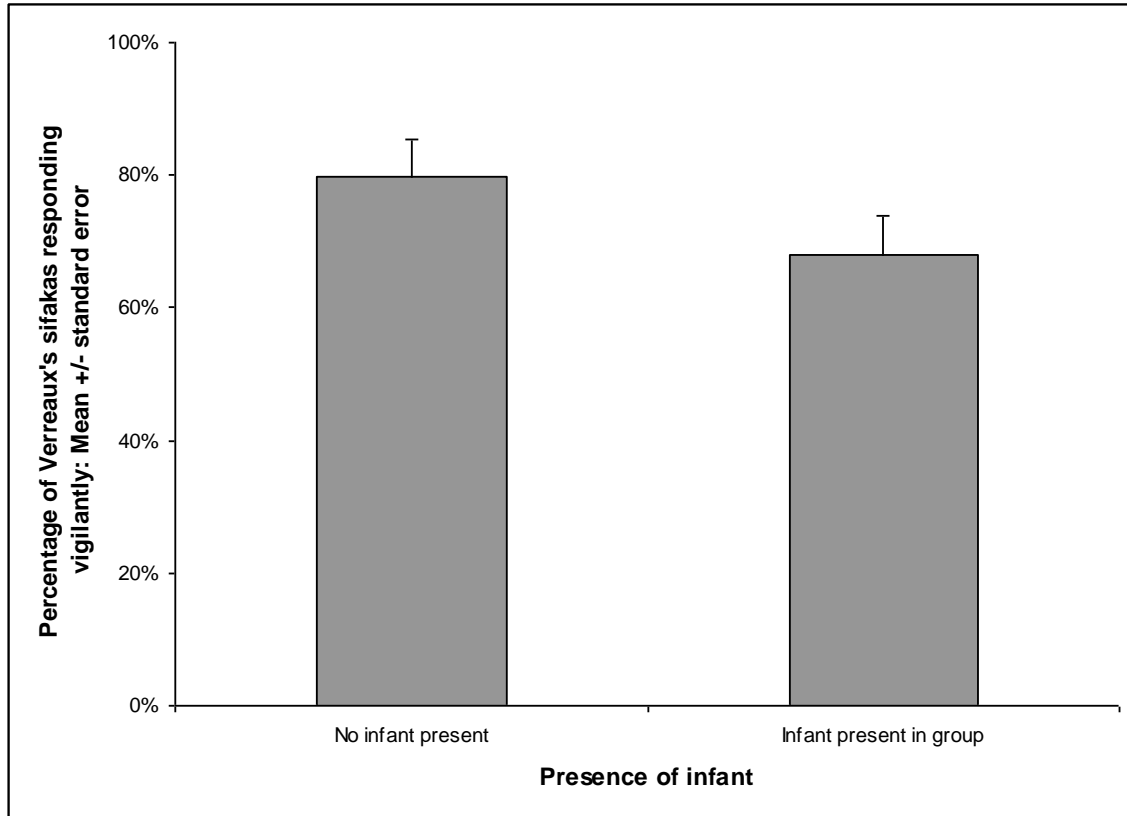
**Figure 9: Comparison of response by ring-tailed lemurs and Verreaux's sifakas to crested drongo alarm call in different lower canopy coverage. SE shown.**

Activity prior to playback was not a significant explanatory variable for vigilant response to the crested drongo alarm call or the green pigeon call by either lemur species (table 9 and figure 10).



**Figure 10: Activity of ring-tailed lemurs and Verreaux's sifakas prior to playback and subsequent vigilant response of both lemur species to the crested drongo alarm call and green pigeon song. SE shown.**

Whilst groups of sifakas *with* an infant had a lower rate of vigilance in response to a crested drongo alarm call than groups *without* an infant (figure 11), presence of an infant was not a significant explanatory variable for response to the alarm call (Generalised linear model:  $X^2_2 = 4.822$ ,  $P = 0.090$ ).



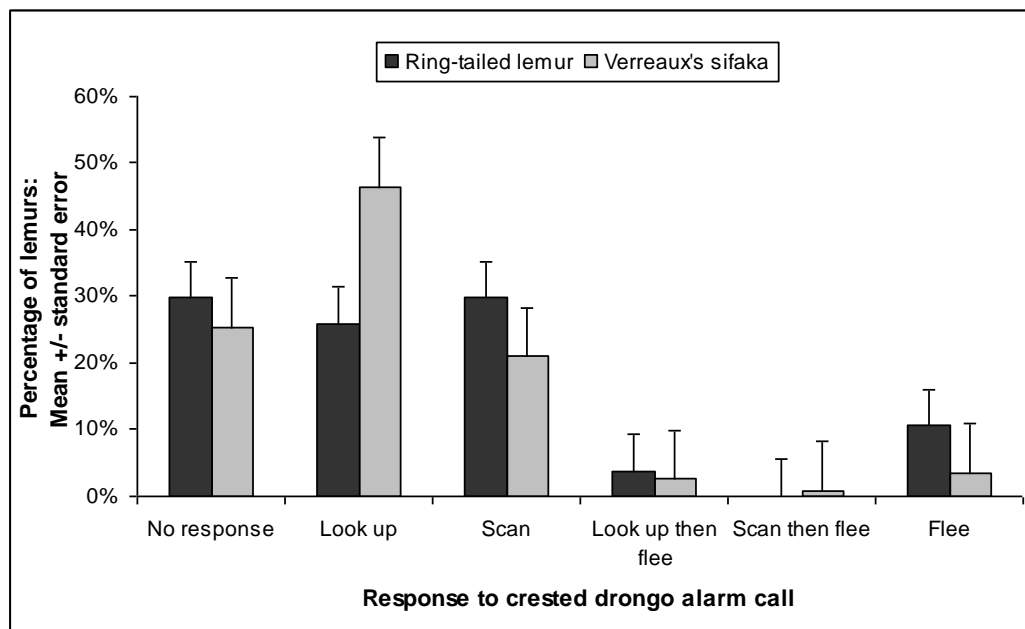
**Figure 11: Response of Verreaux's sifakas to crested drongo alarm call depending on whether an infant is present in the troop. SE shown.**

A chi square test showed a significant relationship between the order of calls and the response of ring-tailed lemurs to crested drongo alarm calls (two-way classification chi-square:  $X^2_5 = 15.463$ ,  $P < 0.05$ ) but not for the response of Verreaux's sifakas to drongo alarm calls (two-way classification chi-square:  $X^2_5 = 5.578$ ,  $P > 0.05$ ). There was a significant relationship between the order of calls and the response of Verreaux's sifakas to green pigeon songs (two-way classification chi-square:  $X^2_5 = 11.954$ ,  $P < 0.05$ ) but not for the response of ring-tailed lemurs (two-way classification chi-square:  $X^2_5 = 6.493$ ,  $P > 0.05$ ) (table 10).

**Table 10: Response of the two lemur species to drongo and pigeon calls for different call orders**

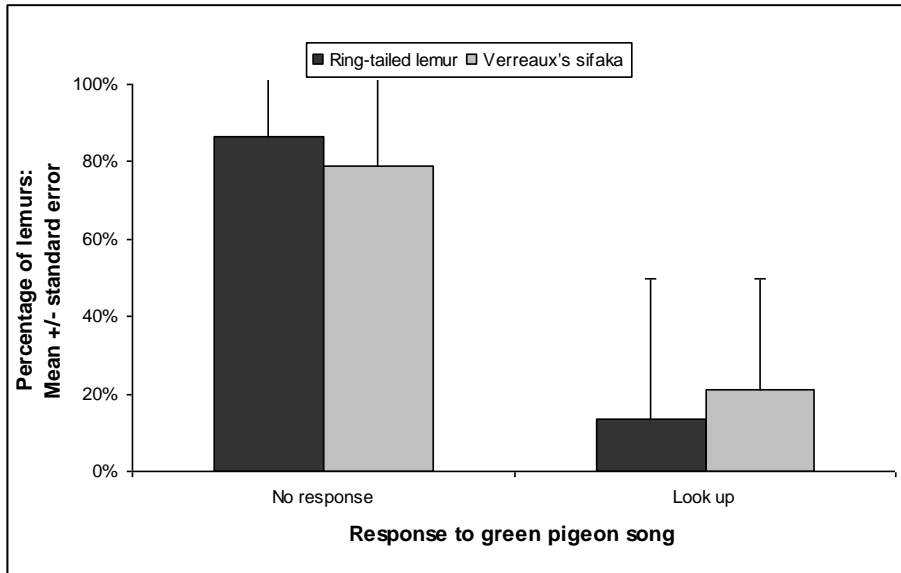
Order of calls*	Ring-tailed lemur		Verreaux's sifaka	
	Vigilant response to drongo	Vigilant response to pigeon	Vigilant response to drongo	Vigilant response to pigeon
PCVD	30.77%	7.69%	85.00%	25.00%
PVCD	100.00%	0.00%	63.64%	0.00%
CPVD	70.83%	8.33%	75.00%	33.33%
CVPD	68.57%	11.43%	89.47%	42.11%
VPCD	100.00%	37.50%	71.43%	0.00%
VCPD	88.24%	23.53%	66.67%	15.56%
*C=control, V= white-headed vanga, P=green pigeon, D=crested drongo				

To explore the hypotheses more fully, graphs of the *type* of response to bird calls were created. For ring-tailed lemurs the greatest response to the crested drongo alarm call was scanning (30%) with 25% looking up in response to the call (table 3 in methods lists definitions of responses). Four percent of ring-tailed lemurs looked up and then fled, with 11% fleeing immediately after hearing the call. In contrast, 46% of Verreaux's sifakas looked up in response to the crested drongo alarm call, and 21% scanned. Only 1% scanned then fled, and 4% fled immediately after hearing the call. Both species fled away from the speaker rather than towards it (figure 12).



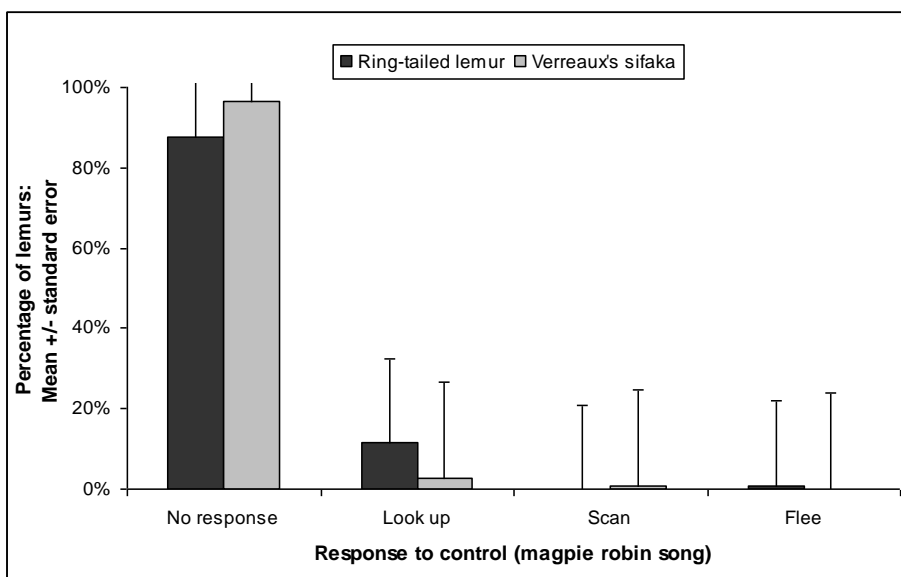
**Figure 12: Different types of response of both lemur species to the crested drongo alarm call. SE shown.**

The response to the green pigeon song by both lemur species was different. Neither species responded to these calls by scanning or fleeing. The only response was to look up, with ring-tailed lemurs looking up 13% of the time and Verreaux's sifakas looking up 21% of the time (figure 13).



**Figure 13: Different types of response of both lemur species to the green pigeon song. SE shown.**

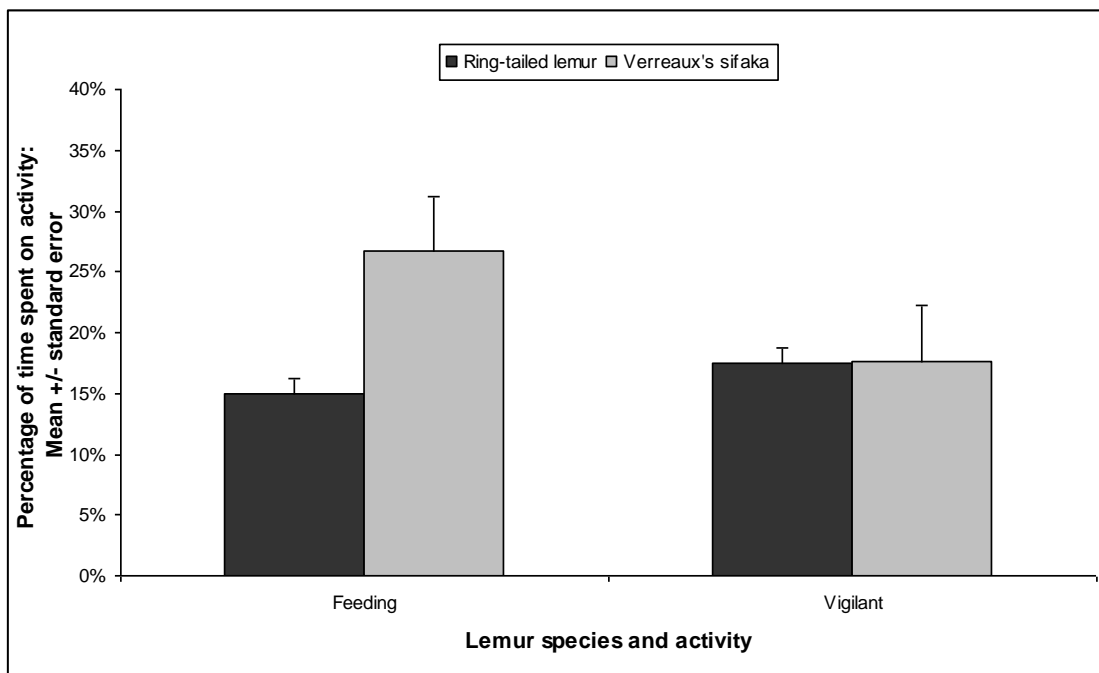
Where there was a response to the control (magpie robin song) by ring-tailed lemurs it was to look up, with one exception when a juvenile fled. There was minimal response by Verreaux's sifakas with 3% looking up and one individual scanning (figure 14).



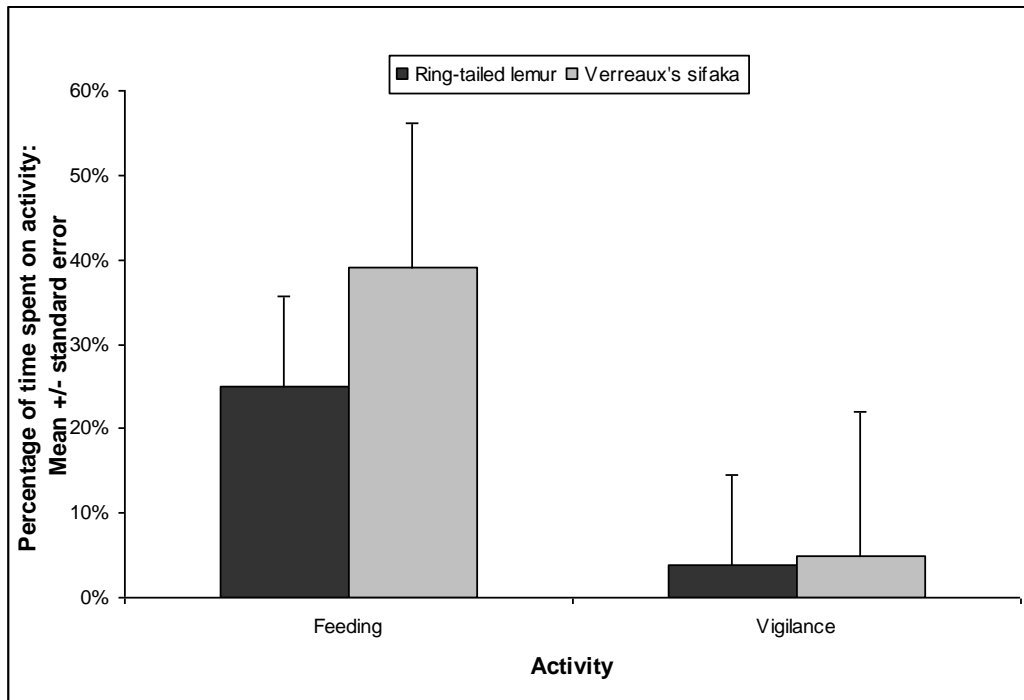
**Figure 14: Different types of response of both lemur species to the control (magpie robin song). SE shown.**

### 3.2 Activity results

According to the focal sampling data, Verreaux's sifakas spent significantly more time feeding (27%) than ring-tailed lemurs (15%) (Mann-Whitney U test:  $U = 3329$ ,  $n_1 = 97$ ,  $n_2 = 104$ ,  $P = 0.000$ ). There was no significant difference in the time spent vigilant between the two lemur species (Mann-Whitney U test:  $U = 4965$ ,  $n_1 = 97$ ,  $n_2 = 104$ ,  $P = 0.849$ ) (figure 15a). Group scan data showed a lower level of vigilance overall (figure 15b). This suggests that this method is less likely to pick up instances of vigilance and so focal data is used to explore feeding and vigilance in different contexts.

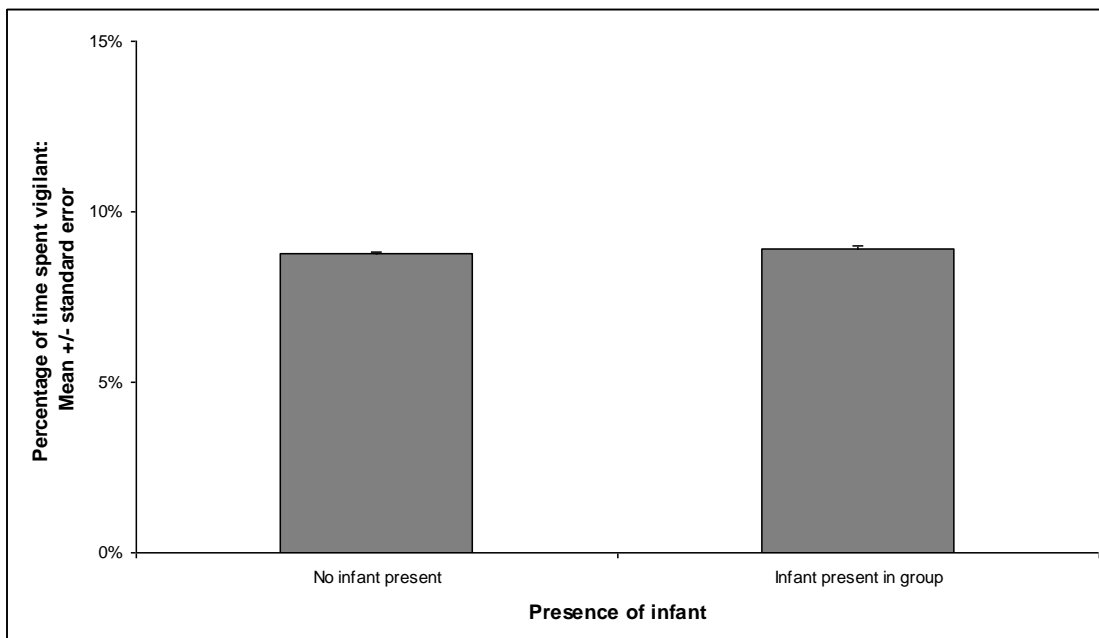


**Figure 15a: Comparison of mean percentage of time spent feeding and vigilant by ring-tailed lemurs and Verreaux's sifakas. Based on focal sampling. SE shown.**



**Figure 15b: Comparison of mean percentage of time spent feeding and vigilant by ring-tailed lemurs and Verreaux's sifakas. Based on group scans. SE shown.**

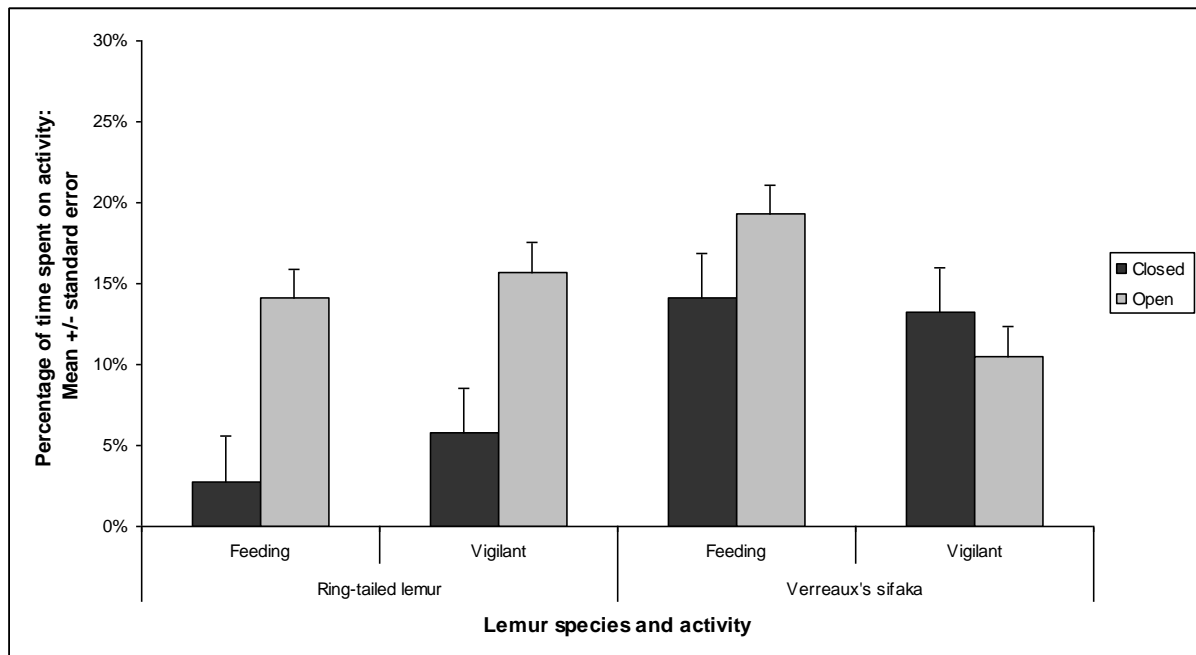
It should be noted that the presence of an infant in the group did not significantly affect the vigilance levels of Verreaux's sifakas (Wilcoxon signed-rank test:  $T = 2359$ ,  $N = 104$ ,  $P = 0.950$ ) (figure 16).



**Figure 16: Comparison of mean percentage of time spent vigilant by Verreaux's sifakas when an infant was or wasn't present in the group. Based on focal sampling. SE shown.**

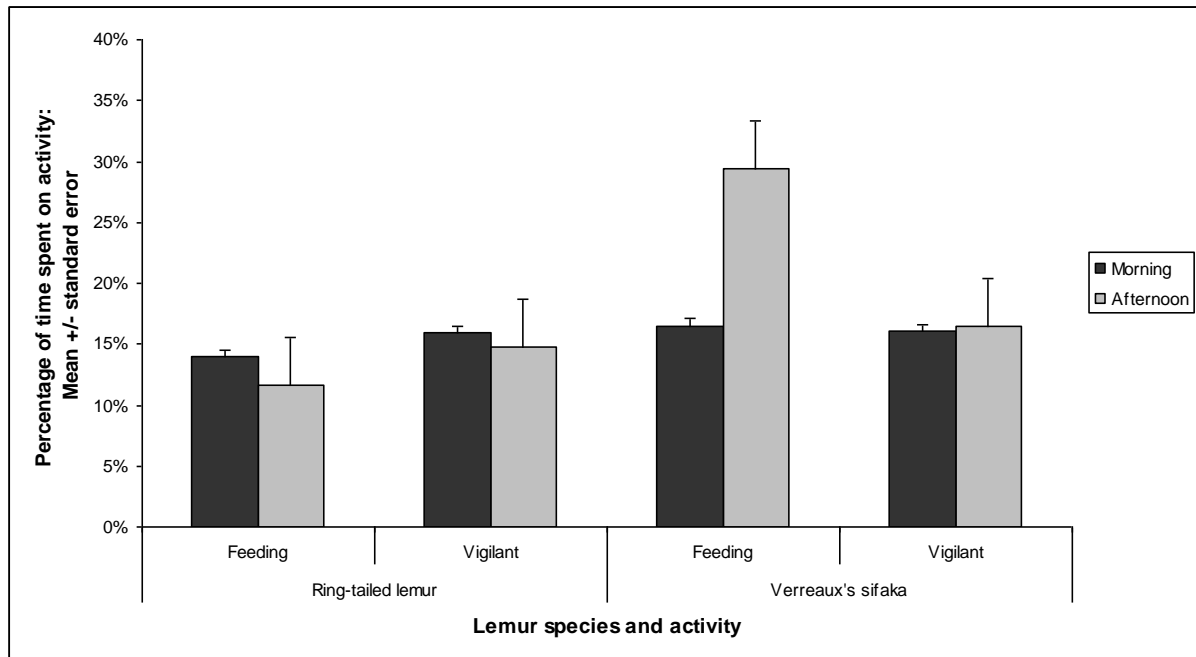


Ring-tailed lemurs were significantly more vigilant in an open habitat (16%) than in closed (6%) (Wilcoxon signed-rank test:  $T = 858$ ,  $N = 97$ ,  $P = 0.000$ ). There was no significant difference in the level of vigilance by Verreaux's sifakas in open and closed habitats (Wilcoxon signed-rank test:  $T = 2699$ ,  $N = 104$ ,  $P = 0.247$ ). Ring-tailed lemurs spent significantly more time feeding in an open habitat (14%) as compared to closed habitat (3%) (Wilcoxon signed-rank test:  $T = 191$ ,  $N = 97$ ,  $P = 0.000$ ). Verreaux's sifakas also spent more time feeding in an open habitat but this was not significant (Wilcoxon signed-rank test:  $T = 1395$ ,  $N = 104$ ,  $P = 0.082$ ) (figure 17).



**Figure 17: Comparison of mean percentage of time spent feeding and vigilant by ring-tailed lemurs and Verreaux's sifakas in open and closed habitats. Based on focal sampling. SE shown.**

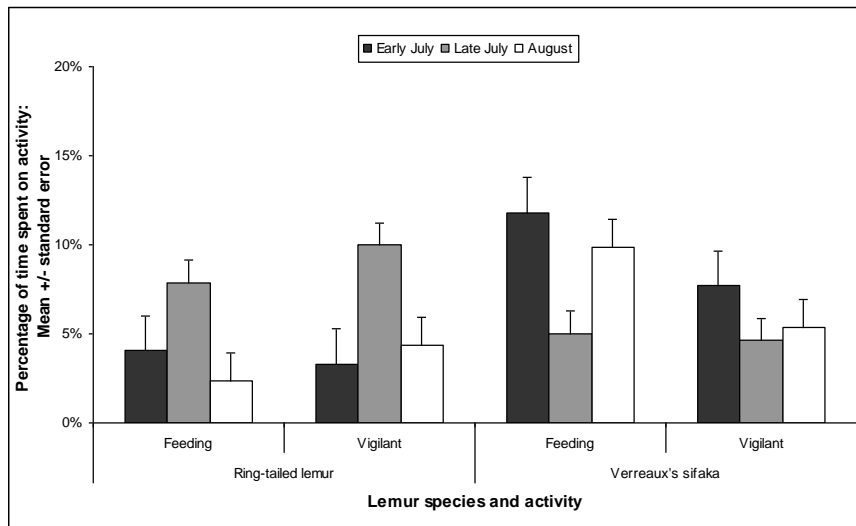
Verreaux's sifakas spent significantly more time feeding in the afternoon (29%) than the morning (17%) (Wilcoxon signed-rank test:  $T = 1127$ ,  $N = 104$ ,  $P = 0.003$ ). There was no significant difference between the time that ring-tailed lemurs spent feeding (Wilcoxon signed-rank test:  $T = 754$ ,  $N = 97$ ,  $P = 0.557$ ) or vigilant (Wilcoxon signed-rank test:  $T = 1966.5$ ,  $N = 97$ ,  $P = 0.542$ ) in the morning and the afternoon. Verreaux's sifakas showed no significant difference between their level of vigilant behaviour in the morning and afternoon (Wilcoxon signed-rank test:  $T = 2222$ ,  $N = 104$ ,  $P = 0.828$ ) (figure 18).



**Figure 18: Comparison of mean percentage of time spent feeding and vigilant by ring-tailed lemurs and Verreaux's sifakas in the morning and afternoon. Based on focal sampling. SE shown.**

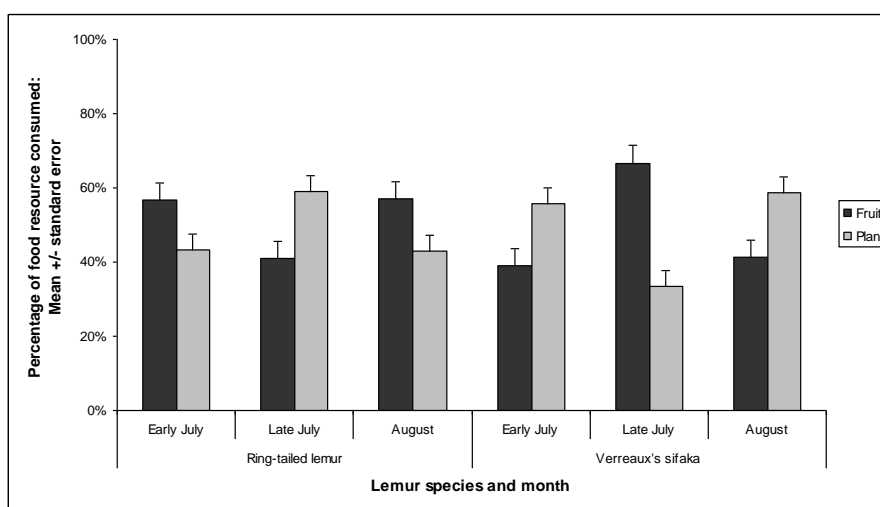
Levels of vigilance by ring-tailed lemurs across the study – early July (3%), late July (10%) and August (4%) – were significantly different (Friedman test:  $X^2_2 = 10.907$ ,  $N = 97$ ,  $P = 0.004$ ). Vigilance in early and late July were shown to be significantly different (Wilcoxon signed-rank test:  $T = 520$ ,  $N = 97$ ,  $P = 0.001$ ) as was vigilance in late July and August (Wilcoxon signed-rank test:  $T = 1500$ ,  $N = 97$ ,  $P = 0.012$ ). Verreaux's sifakas were more vigilant in early July (7.68%) than late July (4.62%) and August (5.36%) (Friedman test:  $X^2_2 = 12.639$ ,  $N = 104$ ,  $P = 0.002$ ). There was only a significant difference in the levels of vigilance between early and late July (Wilcoxon signed-rank test:  $T = 1497$ ,  $N = 104$ ,  $P = 0.048$ ).

Ring-tailed lemurs spent 4% of their time feeding in early July, 8% in late July and a little less time (2%) in August (Friedman test:  $X^2_2 = 13.885$ ,  $N = 97$ ,  $P = 0.001$ ). There was a significant difference in the time spent feeding between late July and August (Wilcoxon signed-rank test:  $T = 640.5$ ,  $N = 97$ ,  $P = 0.006$ ). Verreaux's sifakas spent more time feeding in early July (12%) than the other two periods (Friedman test:  $X^2_2 = 13.071$ ,  $N = 104$ ,  $P = 0.001$ ). There was only a significant difference in the time spent feeding between early and late July (Wilcoxon signed-rank test:  $T = 465.5$ ,  $N = 104$ ,  $P = 0.004$ ) (figure 19).



**Figure 19: Comparison of mean percentage of time spent feeding and vigilant by ring-tailed lemurs and Verreaux's sifakas in different months. Based on focal sampling. SE shown.**

Both lemur species ate a variety of different food types throughout the study period but for the purposes of figure 20 they have been classified into two groups: fruit and plant. The definition of plant is any part of the plant that is not fruit, for example, leaves and flowers.

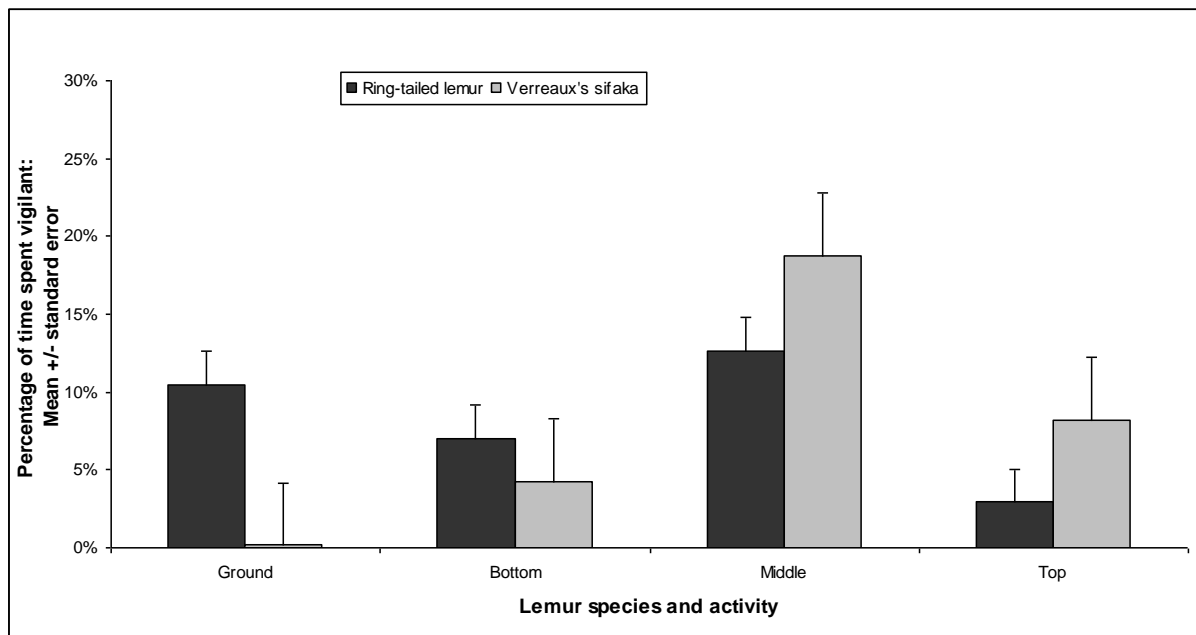


**Figure 20: Comparison of percentage of resource consumed by ring-tailed lemurs and Verreaux's sifakas in different months. Based on group scans. SE shown.**

Ring-tailed lemurs were most vigilant when on the ground or in the middle third of the tree (Friedman test:  $X^2_4 = 61.054$ ,  $N = 97$ ,  $P = 0.000$ ). Verreaux's sifakas were most vigilant in the middle third of the tree (Friedman test:  $X^2_4 = 151.607$ ,  $N = 104$ ,  $P = 0.000$ ) (see figure 21). The significant results of the post hoc analysis are listed in table 11.

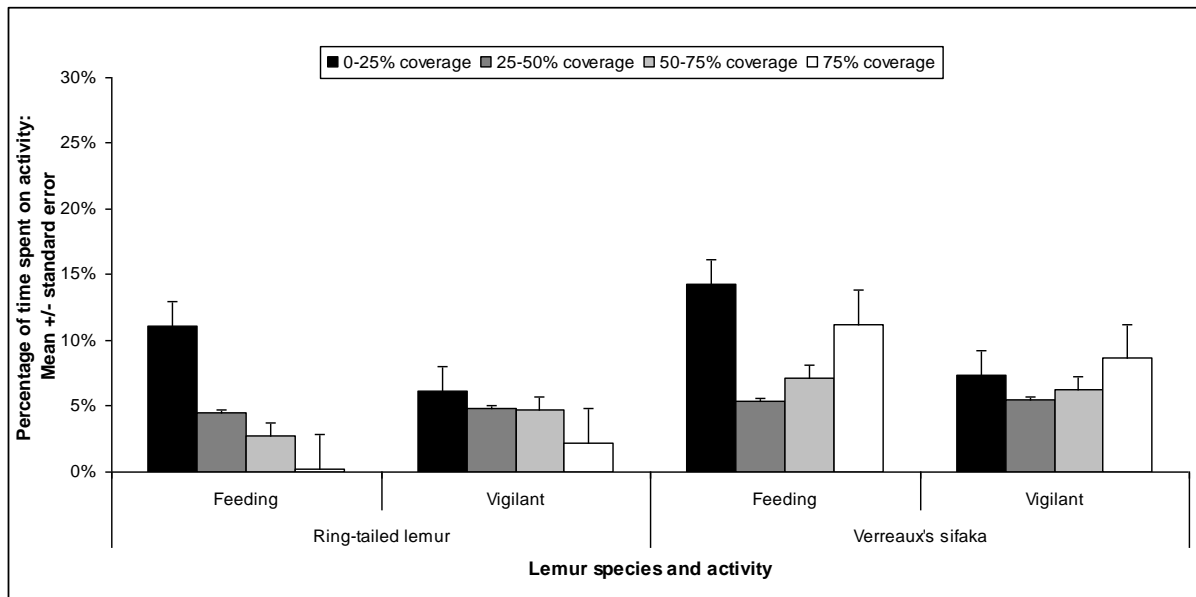
**Table 11: Post hoc analysis of lemur vigilance when at different canopy heights or on the ground using Wilcoxon signed-rank test. Significant results shown.**

Lemur species	Location 1	Location 2	T	N/n	P
Ring-tailed lemur	Bottom	Middle	670	97	0.001
	Ground	Top	692	97	0.001
	Middle	Top	1902	97	0.000
Verreaux's sifaka	Bottom	Ground	145	104	0.001
	Bottom	Middle	509	104	0.000
	Bottom	Top	567	104	0.003
	Ground	Middle	2415	104	0.000
	Ground	Top	38	104	0.000
	Middle	Top	2836	104	0.000



**Figure 21: Comparison of mean percentage of time spent vigilant by ring-tailed lemurs and Verreaux's sifakas when at different canopy heights or on the ground. Based on focal sampling. SE shown.**

Upper canopy coverage significantly affected the time that Verreaux's sifakas spent vigilant (figure 22 and table 12) (Friedman test:  $X^2_3 = 50.783$ ,  $N = 104$ ,  $P = 0.000$ ). Time spent vigilant was significantly different between 0-25% upper canopy coverage and 75%+ upper canopy coverage (Wilcoxon signed-rank test:  $T = 210$ ,  $N = 104$ ,  $P = 0.000$ ) as it was between 25-50% and 50-75% upper canopy (Wilcoxon signed-rank test:  $T = 72$ ,  $N = 104$ ,  $P = 0.001$ ) and in 25-50% and 75%+ upper canopy (Wilcoxon signed-rank test:  $T = 156.5$ ,  $N = 104$ ,  $P = 0.000$ ). Upper canopy coverage did not significantly affect the time that ring-tailed lemurs spent vigilant (figure 22) (Friedman test:  $X^2_3 = 5.168$ ,  $N = 104$ ,  $P = 0.160$ ).



**Figure 22: Comparison of mean percentage of time spent feeding and vigilant by ring-tailed lemurs and Verreaux's sifakas at different upper canopy coverage. Based on focal sampling. SE shown.**

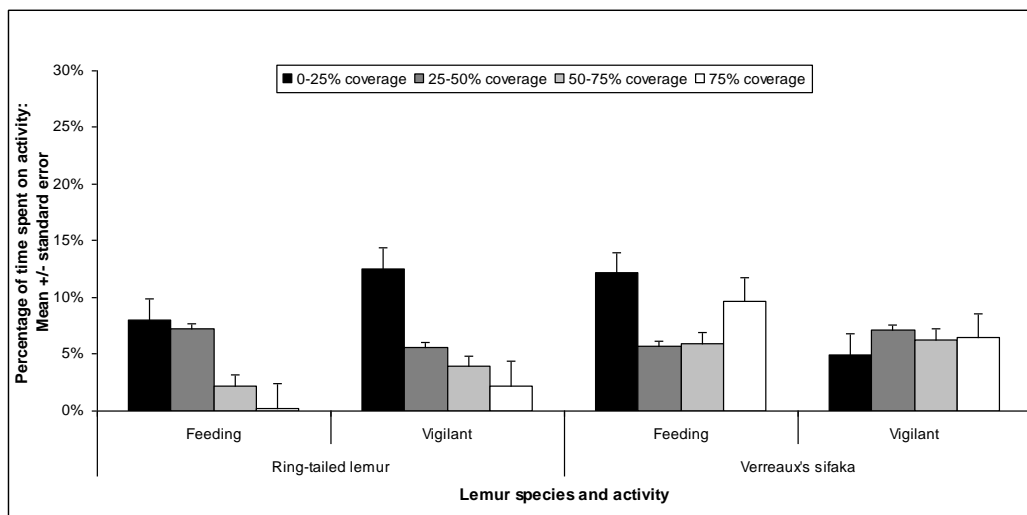
Upper canopy coverage significantly affected the time that ring-tailed lemurs (Friedman test:  $X^2_3 = 43.126$ ,  $N = 97$ ,  $P = 0.000$ ) and Verreaux's sifakas (Friedman test:  $X^2_3 = 11.402$ ,  $N = 104$ ,  $P = 0.010$ ) spent feeding (figure 22). The significant results of the post hoc analysis are listed in table 12.

**Table 12: Post hoc analysis of lemur feeding in different upper canopy coverage using Wilcoxon signed-rank test, testing the differences between feeding in canopy density 1 and canopy density 2. Significant results shown.**

Lemur species	Canopy density 1	Canopy density 2	T	N/n	P
Ring-tailed lemur	0-25% coverage	25-50% coverage	740.5	97	0.004
	0-25% coverage	50-75% coverage	821.5	97	0.001
	0-25% coverage	75%+ coverage	628	97	0.000
	25-50% coverage	75%+ coverage	98	97	0.004
	50-75% coverage	75%+ coverage	72	97	0.010
Verreaux's sifaka	0-25% coverage	25-50% coverage	971.5	104	0.004
	0-25% coverage	50-75% coverage	853.5	104	0.017
	0-25% coverage	75%+ coverage	136	104	0.000
	50-75% coverage	75%+ coverage	78	104	0.000

Lower canopy coverage significantly affected the time that ring-tailed lemurs spent vigilant (figure 23) (Friedman test:  $X^2_3 = 42.354$ ,  $N = 97$ ,  $P = 0.000$ ). The significant results of the post hoc analysis are listed in table 13. Lower canopy coverage did not significantly affect the time that Verreaux's sifakas spent vigilant (Friedman test:  $X^2_3 = 2.053$ ,  $N = 104$ ,  $P = 0.561$ ).

Lower canopy coverage significantly affected the time that ring-tailed lemurs spent feeding (figure 23) (Friedman test:  $X^2_3 = 28.817$ ,  $N = 97$ ,  $P = 0.000$ ). The significant results of the post hoc analysis are listed in table 13. Lower canopy coverage did not significantly affect the time that Verreaux's sifakas spent feeding (Friedman test:  $X^2_3 = 2.446$ ,  $N = 104$ ,  $P = 0.485$ ).

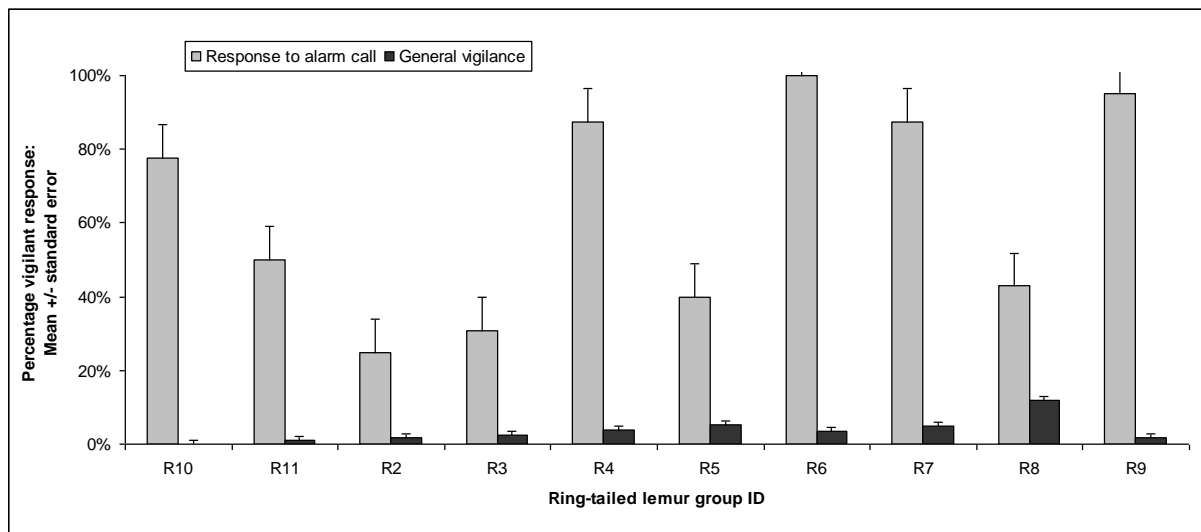


**Figure 23: Comparison of mean percentage of time spent feeding and vigilant by ring-tailed lemurs and Verreaux's sifakas at different lower canopy coverage. Based on focal sampling. SE shown.**

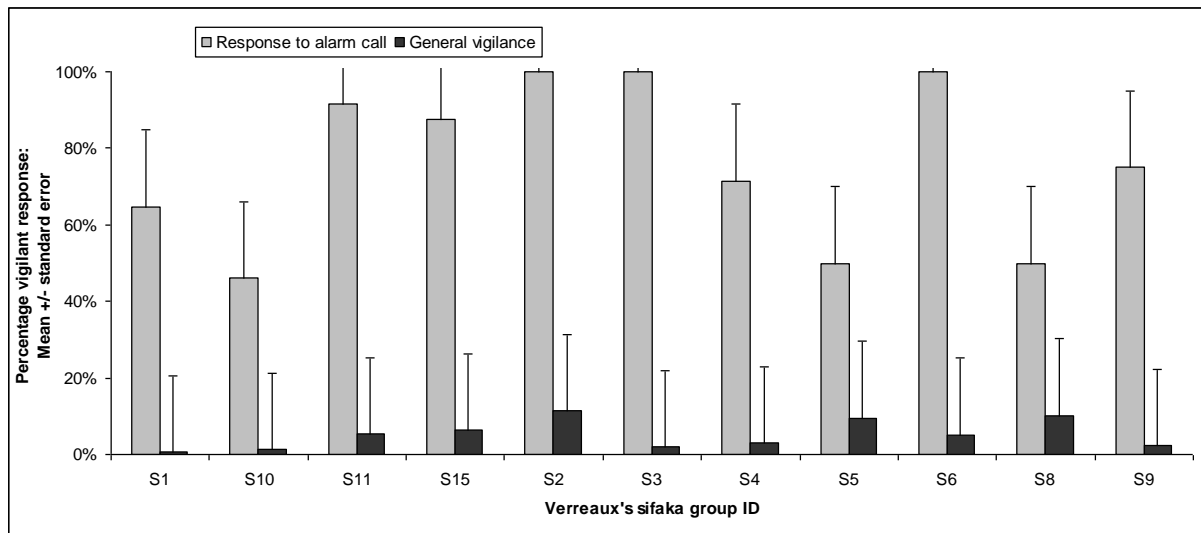
**Table 13: Post hoc analysis of ring-tailed lemurs feeding and being vigilant in different lower canopy coverage using Wilcoxon signed-rank test. Significant results shown.**

Activity	Location 1	Location 2	T	N/n	P
Vigilance	0-25% coverage	25-50% coverage	1881.5	97	0.001
	0-25% coverage	50-75% coverage	1566	97	0.000
	0-25% coverage	75%+ coverage	252	97	0.000
	25-50% coverage	50-75% coverage	275	97	0.010
Feeding	0-25% coverage	75%+ coverage	404	97	0.000
	25-50% coverage	50-75% coverage	289	97	0.016
	25-50% coverage	75%+ coverage	222	97	0.000
	50-75% coverage	75%+ coverage	49	97	0.028

Figures 24 and 25 show the mean percentage of time spent vigilant by different troops of lemurs as compared to the vigilant response to drongo alarm calls. The four troops who spent most time vigilant were R8, S2, S5 and S8. Troops that had a 100% vigilant response to drongo alarm calls were R6, S2, S3 and S6.

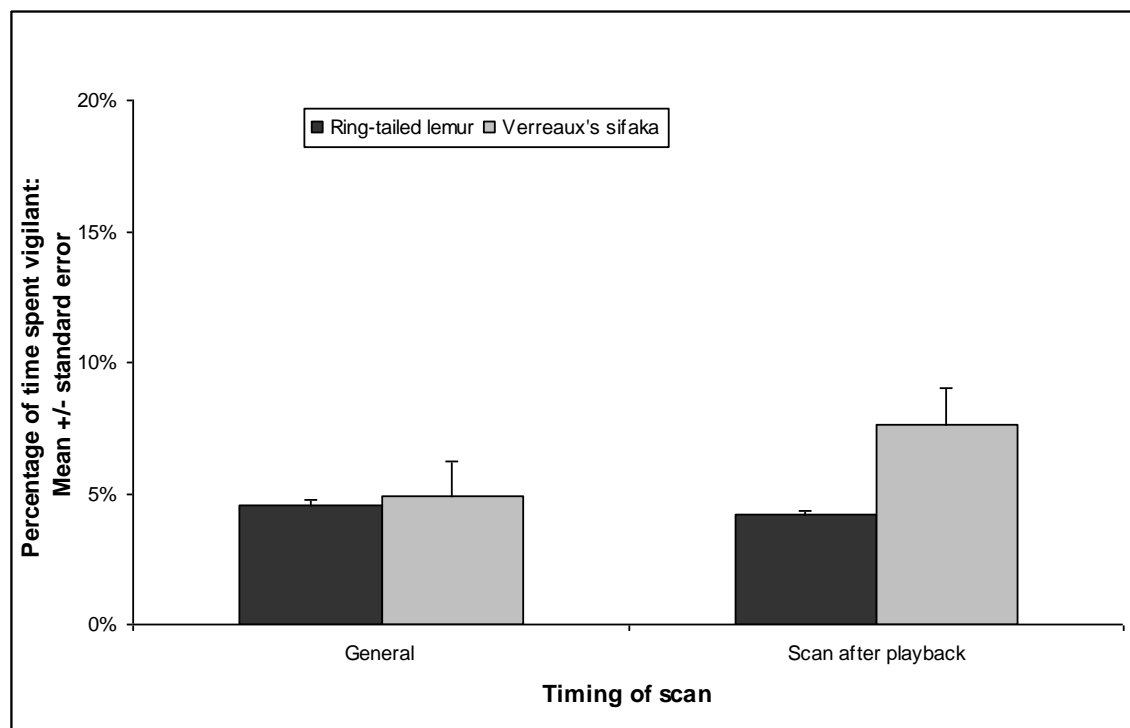


**Figure 24: Comparison of mean percentage of time spent vigilant by different troops of ring-tailed lemurs against the vigilant response to the crested drongo alarm call. Based on group scans. SE shown.**



**Figure 25: Comparison of mean percentage of time spent vigilant by different troops of Verreaux's sifakas against the vigilant response to the crested drongo alarm call. Based on group scans. SE shown.**

Figure 26 shows time spent vigilant by playback troops as compared to vigilance at the group scan which took place 10-15 minutes after playback. There was no significant difference between the two for either lemur species (Mann-Whitney U test: *Ring-tailed lemur*:  $U = 1217$ ,  $n_1 = 12$ ,  $n_2 = 214$ ,  $P = 0.613$ . *Verreaux's sifaka*:  $U = 1391$ ,  $n_1 = 12$ ,  $n_2 = 271$ ,  $P = 0.222$ ).



**Figure 26: Comparison of mean percentage of time spent vigilant by ring-tailed lemurs and Verreaux's sifakas in playback troops, as compared to vigilance on the scan which took place 10-15 minutes after playback. Based on group scans. SE shown.**



### 3.3 Association results

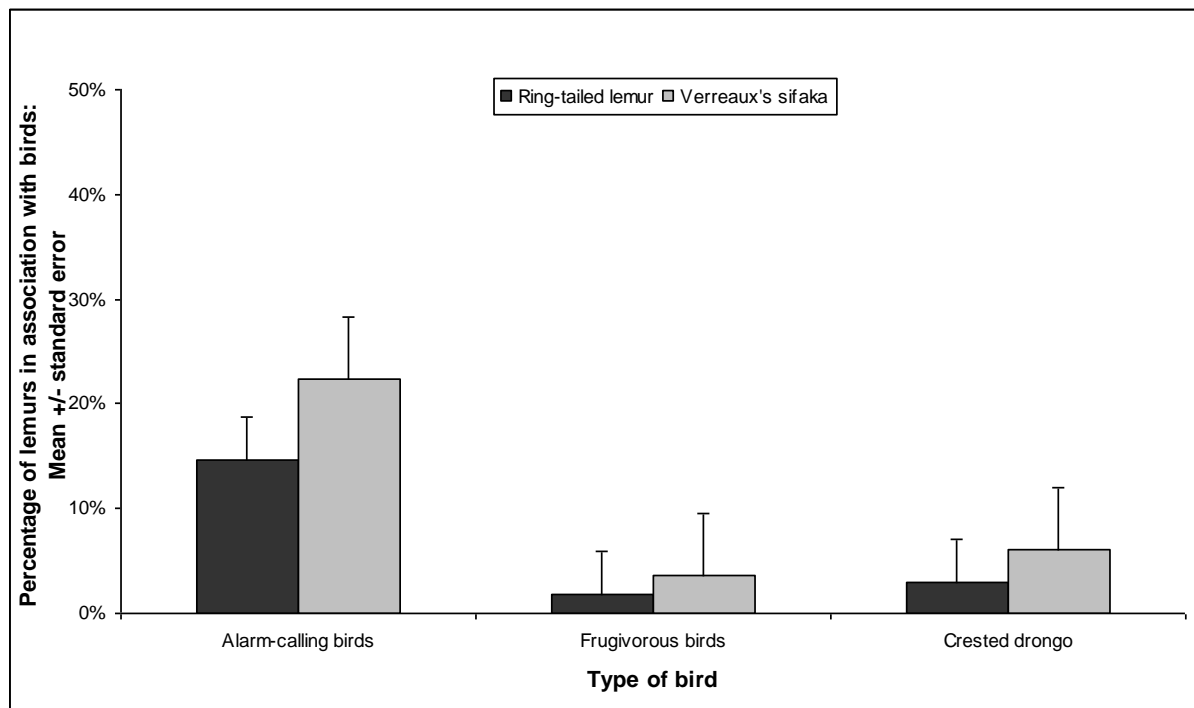
During this research, the birds shown in table 14 were found in association with either ring-tailed lemur or Verreaux's sifaka troops, or with both lemur species.

**Table 14: List of birds found in association with ring-tailed lemurs and Verreaux's sifakas. Number of focal samples where birds found in association shown.**

Bird group	Bird species	Ring-tailed lemur	Verreaux's sifaka
<b>Frugivorous birds</b>	Vasa parrots (lesser & greater) <i>Coracopsis nigra</i> and <i>C. vasa</i>	5	12
<b>Insectivorous birds</b>	Common jery ( <i>Neomixis tenella</i> )	11	26
	Common newtonia ( <i>Newtonia brunneicauda</i> )	11	6
	*Crested coua ( <i>Coua cristata</i> )	12	8
	*Crested drongo ( <i>Dicrurus forficatus</i> )	8	20
	Giant coua ( <i>Coua gigas</i> )	0	2
	Hook-billed vanga ( <i>Vanga curvirostris</i> )	4	9
	Madagascar bee-eater ( <i>Merops superciliosus</i> )	0	2
	*Madagascar paradise flycatcher ( <i>Terpsiphone mutata</i> )	20	44
	*Madagascar magpie robin ( <i>Copsychus albospectularis</i> )	6	16
<b>Omnivorous/other</b>	Common myna ( <i>Acridotheres tristis</i> )	0	2
	Grey-headed lovebird ( <i>Agapornis canus</i> )	2	16
	Madagascar bulbul ( <i>Hypsipetes madagascariensis</i> )	8	10
	Madagascar coucal ( <i>Centropus toulou</i> )	0	4
	Madagascar turtle dove ( <i>Nesoenas picturata</i> )	4	0
	Madagascar white eye ( <i>Zosterops maderaspatanus</i> )	3	4
	Namaqua dove ( <i>Oena capensis</i> )	2	0
	Pied crow ( <i>Corvus albus</i> )	4	10
	Sakalava weaver ( <i>Ploceus sakalava</i> )	0	2
	Souimanga sunbird ( <i>Nectarinia souimanga</i> )	1	0

\* additionally defined as alarm-calling birds (see Methods section)

There was no significant difference between ring-tailed lemurs and Verreaux's sifakas in the amount of time spent in association with alarm-calling birds (Mann-Whitney U test:  $U = 128.5$ ,  $n_1 = 25$ ,  $n_2 = 25$ ,  $P = 0.434$ ) or in association with just drongos (Mann-Whitney U test:  $U = 132.45$ ,  $n_1 = 25$ ,  $n_2 = 25$ ,  $P = 0.572$ ). There was no significant difference between ring-tailed lemurs and Verreaux's sifakas in their time spent in association with frugivorous birds. However it should be noted that the sample size for either lemur species being in association with frugivorous birds was too small for meaningful statistics to be carried out (figure 27 and table 14). Therefore the following graphs include the frugivorous birds for reference but statistics have not been included.

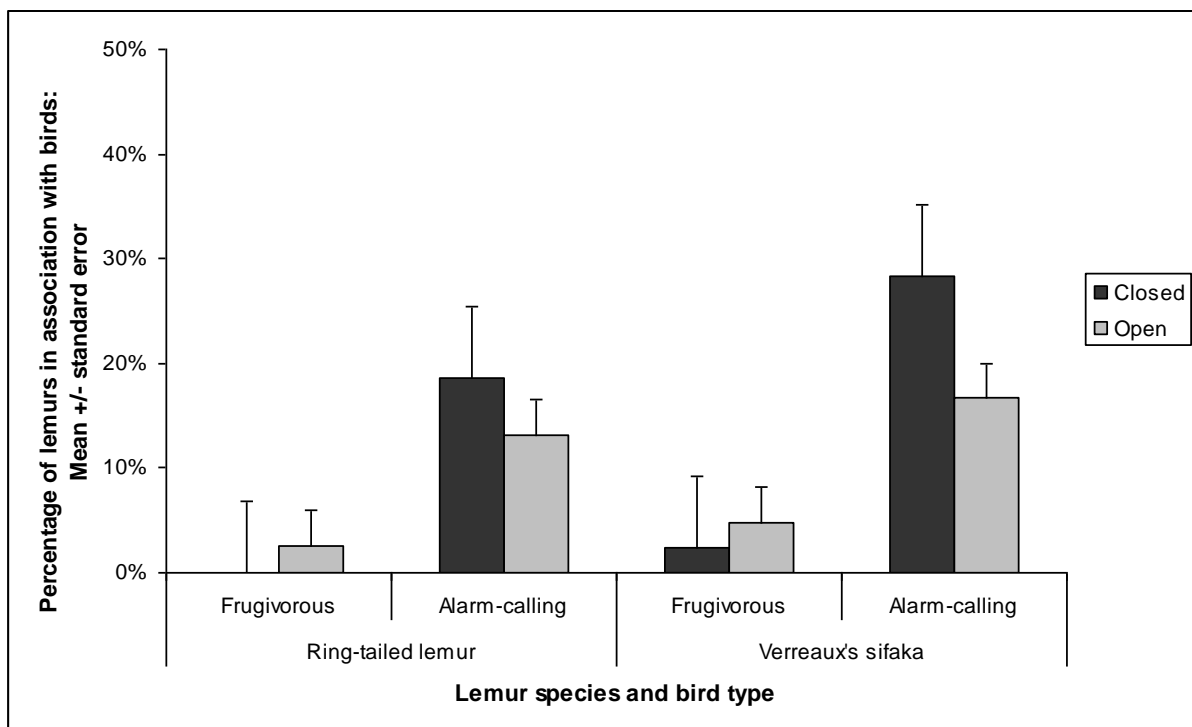


**Figure 27: Mean percentage of ring-tailed lemurs and Verreaux's sifakas in association with alarm-calling birds, frugivorous birds and crested drongos. Focal sampling. SE shown.**

The habitat context (open or closed) did not have a significant impact on the time either lemur species spent in association with alarm-calling birds although both spent more time in association with alarm-calling birds when in a closed habitat (table 15 and figure 28).

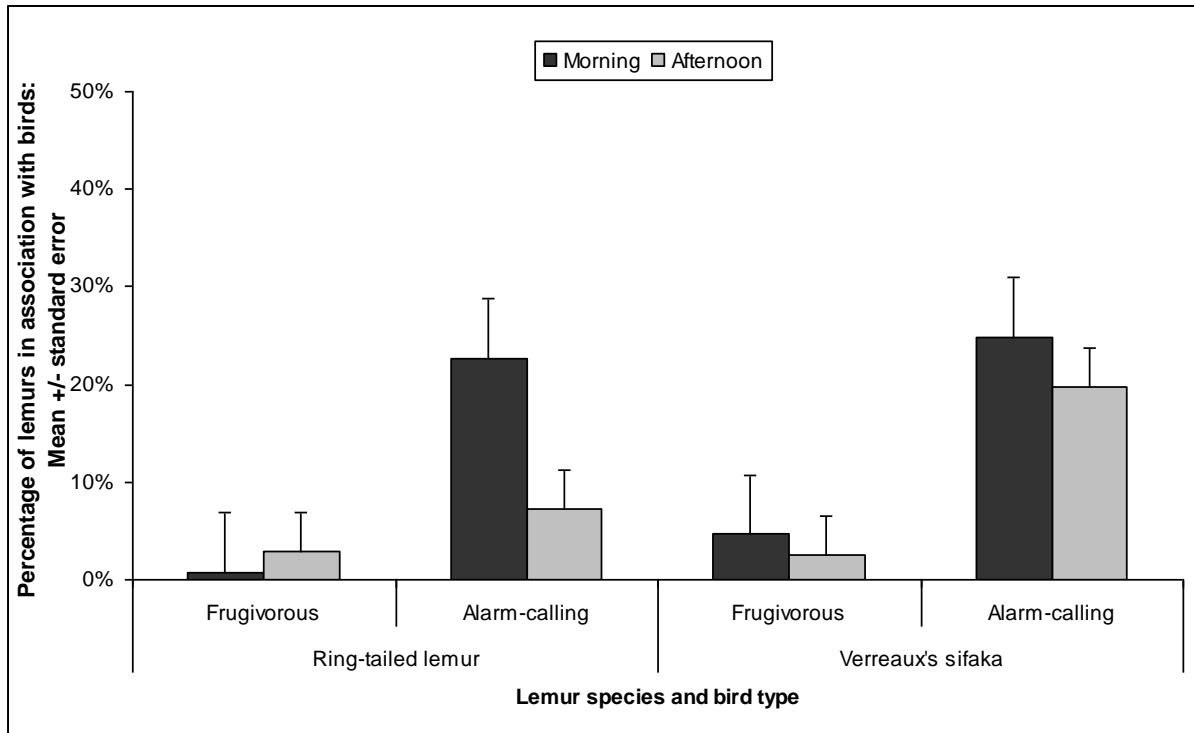
**Table 15: Impact of different factors on the association of lemurs with alarm-calling birds using Wilcoxon signed-rank test.**

Factor	Lemur species	T	N/n	P	Result
Habitat context	Ring-tailed lemur	6	11	0.109	Not significant
	Verreaux's sifaka	8	14	0.893	Not significant
Time of day	Ring-tailed lemur	31	11	0.069	Not significant
	Verreaux's sifaka	53	14	0.272	Not significant



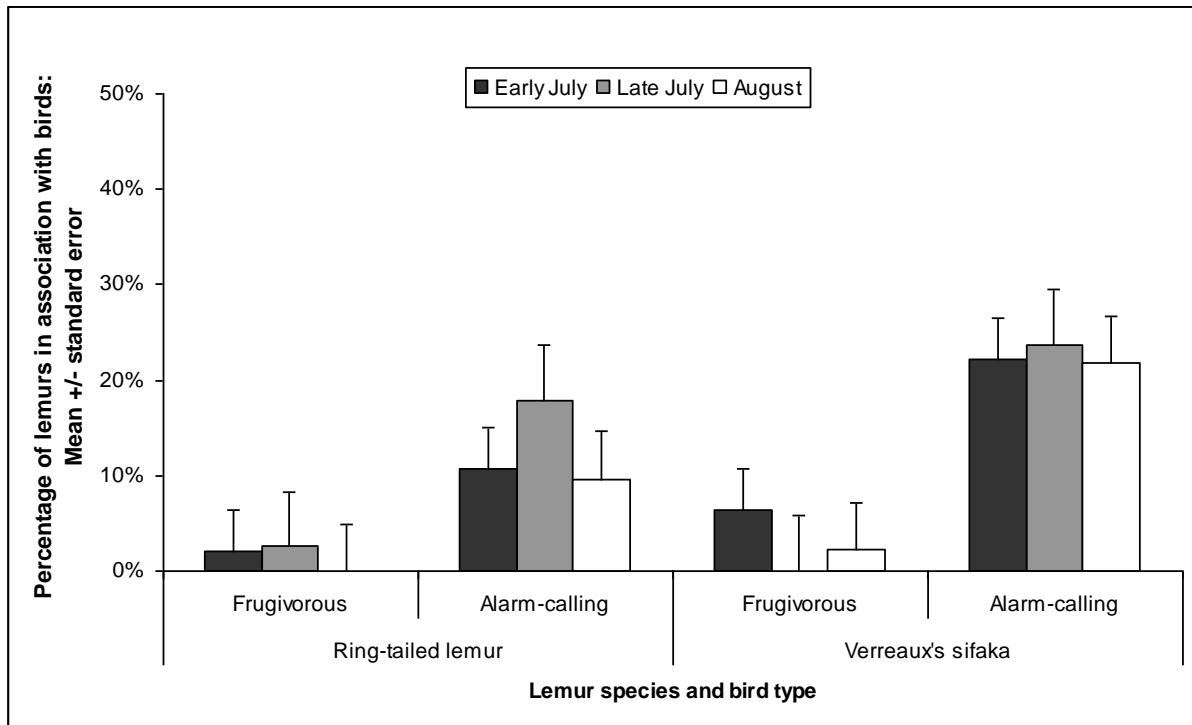
**Figure 28: Comparison of the mean percentage of ring-tailed lemurs and Verreaux's sifakas in association with alarm-calling and frugivorous birds in different habitat contexts. Focal sampling. SE shown.**

The time of day (morning or afternoon) did not have a significant impact on the time spent by ring-tailed lemurs in association with alarm-calling birds. The same was true of Verreaux's sifakas although both lemur species spent more time in association with alarm-calling birds in the morning (table 15 and figure 29).



**Figure 29: Comparison of the mean percentage of ring-tailed lemurs and Verreaux's sifakas in association with alarm-calling and frugivorous birds at different times of day. Focal sampling. SE shown.**

The month did not have a significant impact on the time either lemur species spent in association with alarm-calling birds. Both species spent most time in association with alarm-calling birds in late July but this was not significant (figure 30 and table 16).

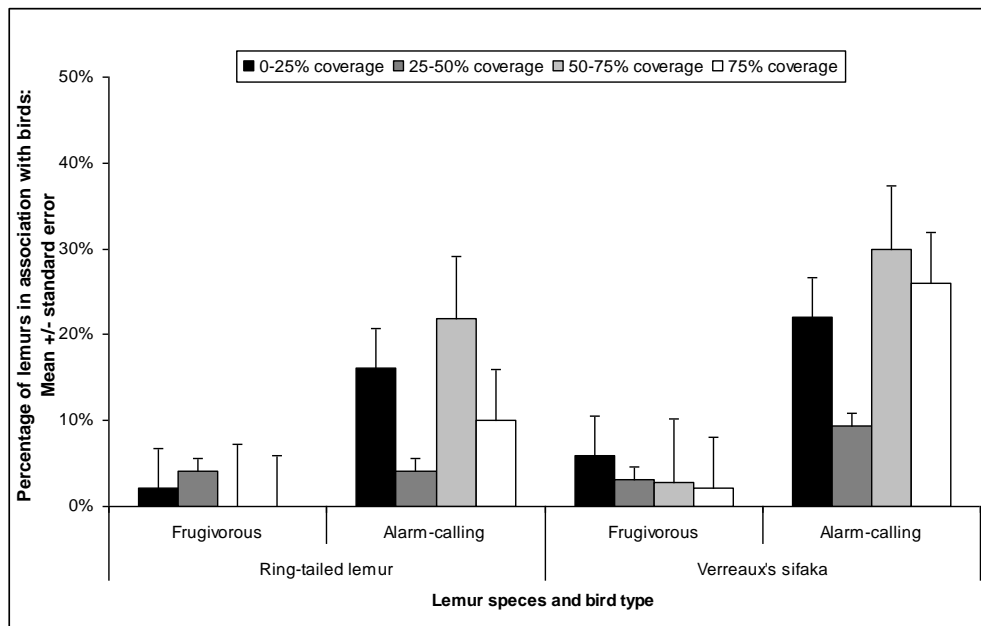


**Figure 30: Comparison of the mean percentage of ring-tailed lemurs and Verreaux's sifakas in association with alarm-calling and frugivorous birds in different months. Focal sampling. SE shown.**

**Table 16: Impact of different factors on the association of lemurs with alarm-calling birds using Friedman test. As none of the results were significant, post hoc tests were not conducted.**

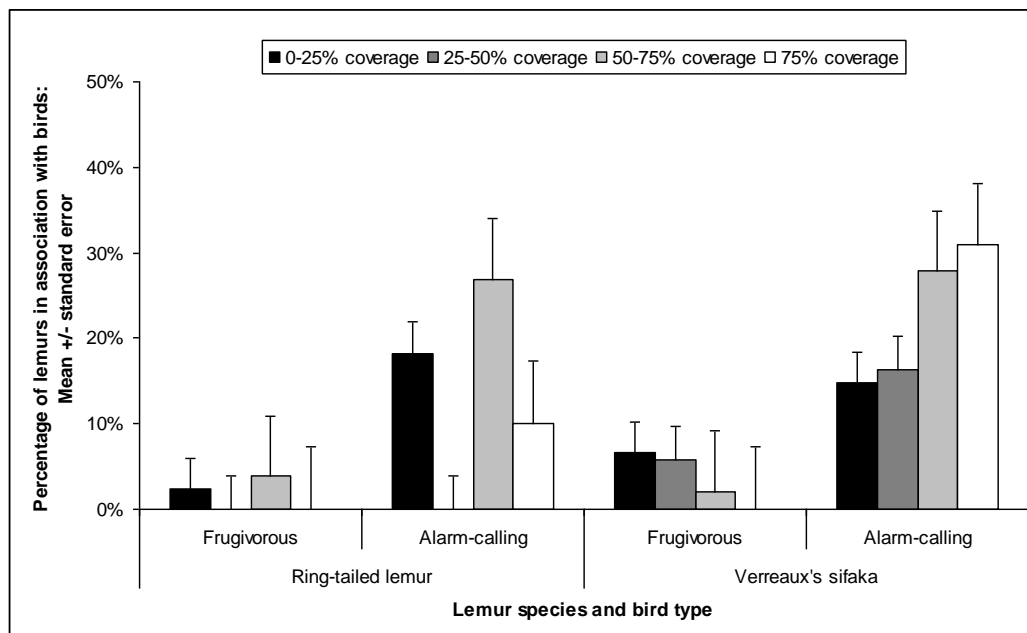
Factor	Lemur species	X <sup>2</sup>	df	N	P	Result
Time of season	Ring-tailed lemur	3.250	2	11	0.197	Not significant
	Verreaux's sifaka	3.500	2	14	0.174	Not significant
Upper canopy density	Ring-tailed lemur	5.056	3	11	0.168	Not significant
	Verreaux's sifaka	2.310	3	14	0.511	Not significant
Lower canopy density	Ring-tailed lemur	6.529	3	11	0.089	Not significant
	Verreaux's sifaka	1.000	3	14	0.801	Not significant

The upper canopy density did not have a significant impact on the time either lemur species spent in association with alarm-calling birds. Both species spent most time in association where there was 50-75% coverage but this was not significant (table 16 and figure 31).



**Figure 31: Comparison of the percentage of ring-tailed lemurs and Verreaux's sifakas in association with alarm-calling/frugivorous birds at different upper canopy densities. SE shown.**

The lower canopy density did not have a significant impact on the time either lemur species spent in association with alarm-calling birds (table 16 and figure 32).



**Figure 32: Comparison of the percentage of ring-tailed lemurs and Verreaux's sifakas in association with alarm-calling/frugivorous birds at different lower canopy densities. SE shown.**

## Chapter 4: Discussion

### 4.1 Interspecific recognition of calls

#### 4.1.1 Key findings

The responses of ring-tailed lemurs and Verreaux's sifakas to the playbacks of four different bird calls suggest that they are able to differentiate between the calls of different bird species, which supports prediction 1. As predicted, the crested drongo alarm call elicited a greater vigilant response from both lemur species (prediction 2). Contrary to prediction 3, Verreaux's sifakas responded more than ring-tailed lemurs to the calls of frugivorous birds. Habitat context in general, open or closed, did not have a significant effect on either species of lemurs' response to the crested drongo alarm calls, although the density of the lower canopy did affect the response of the ring-tailed lemurs. This contradicts prediction 4, which suggested that lemurs would respond more vigilantly in open habitat.

#### 4.1.2 Using calls to avoid predation

It is clear from the results that both ring-tailed lemurs and Verreaux's sifakas can distinguish between the calls of different bird species, and like many other primates, could benefit from eavesdropping on the alarm calls of other species, including birds (Seyfarth & Cheney, 1990; Kitchen *et al.*, 2010; Heymann & Hsia, 2015). Recent research showed that the nocturnal Sahamalaza sportive lemur responded vigilantly to the alarm calls of the crested coua and the Madagascar magpie robin (Seiler *et al.*, 2013). This study extends our understanding by showing that diurnal lemurs also respond vigilantly to alarm calls. Whilst ring-tailed lemurs and Verreaux's sifakas are already known to recognise each others' alarm calls and the calls of aerial predators (Sauther, 1989; Oda, 1998; Fichtel, 2004), this is the first time that an experiment has been conducted to test their responses to non-predator bird alarm calls. The scan which took place between 10 and 15 minutes after playback showed a small increase in vigilance but this was not significant. This suggests that whilst both species of lemur increased their vigilance immediately following the crested drongo alarm call, the increased vigilance was not prolonged for more than a few minutes.

It was predicted that lemurs would respond more vigilantly to crested drongo alarm calls in open habitats as the risk of predation is thought to be greater, particularly during terrestrial travel, as the ground is a preferred striking location for the Madagascar harrier hawk (Sauther, 1989; 2002). Whilst the more terrestrial ring-tailed lemurs (Sauther, 1994) were significantly more vigilant in general when in open canopy, their response to drongo alarm

calls did not differ between closed and open areas. Interestingly the greatest vigilant response to the alarm call came when they were in 50-75% lower canopy density rather than when they were in a more open environment. This could be related to visibility: the lemurs were able to scan effectively in more open canopy but when the visibility was not as good in denser canopy they were more reliant on other cues, such as alarm calls. These results support the findings of Boinski *et al.* (2003), who found that in squirrel monkeys, pre-emptive vigilance occurs in open habitats with little canopy; but reactive vigilance (for example, in response to alarm calls) tends to happen more in denser foliage. Like ring-tailed lemurs, Verreaux's sifakas showed no difference in their response to the crested drongo alarm call in open or closed areas, but unlike the ring-tailed lemurs they did not differ significantly in their general vigilance between these two habitat contexts.

Position in canopy wasn't a significant factor in either lemur species' response to the crested drongo alarm call. It was interesting to note that Verreaux's sifakas were, in general, most vigilant when in the middle of the canopy, and although this wasn't significant, they responded least to the alarm call playback when they were in the top third of the canopy. The potential predators specific to this site should be considered, although a co-evolved response would reflect the history of predation on the lemur populations at Berenty as well as the current situation (Morse, 1970). Fossas, which are known to predate lemurs at other sites, such as Ranomafana (Karpanty & Wright, 2007), are not present at Berenty. Some domestic dogs and cats are known to predate lemurs at Berenty, alongside larger raptors such as the Madagascar harrier hawk and the Madagascar buzzard (Jolly *et al.*, 2006). The assumption would be that Verreaux's sifakas would be most visible, and therefore most vulnerable to predation by raptors, when at the top of the canopy, and in this context the reduced vigilant response was perhaps surprising. However, these results are in line with other studies that have shown that some primate species decrease their vigilance as they get higher in the canopy (Steenbeek *et al.*, 1999; Hirsch, 2002, Smith *et al.*, 2004). It is reported that many raptors soar over the canopy in search of prey; however, some raptors adopt a 'sit and wait' strategy, ambushing their prey from within the canopy, so that lemurs may be more at risk lower in the canopy (Shultz, 2001; Smith *et al.*, 2004).

The results could also partly be explained by the lemurs' ability to see predators. At the top of the canopy, the sifakas had a clear view of the surrounding environment which allowed them to spend less time scanning, and be less reliant on cues from other species. Conversely, in the middle of the canopy, there is diminishing light and often denser foliage, and whilst the



risk of predation isn't necessarily higher, other studies have shown that primates may have to devote more effort to vigilance to spot any potential predators (Wright, 1998; Treves, 2002).

Ring-tailed lemurs responded vigilantly to the crested drongo alarm call most when on the ground, and it was only when they were on the ground that they fled as opposed to scanning or looking up. This is perhaps not surprising as they are particularly vulnerable to aerial and terrestrial attack by predators when on the ground (Sauther, 1989). In terms of overall vigilance, like the sifakas, they were significantly more vigilant in the middle of the canopy. The most likely explanation for this is discussed above.

Time of day was found to significantly affect the response of ring-tailed lemurs to the crested drongo alarm calls; the vigilant response was greater in the afternoon than in the morning. This cannot be explained by their pattern of vigilant behaviour in general as there was no significant difference between their level of vigilance in the morning and afternoon. Time of day did not have an impact on Verreaux's sifakas' response to the crested drongo alarm calls, and there was no significant difference in their general level of vigilance in the morning and afternoon. Raptors tend to hunt at different times of day, and this may influence lemurs' behaviour, including response to heterospecific calls. Raptors that predate lemurs primarily hunt at dawn and in the late afternoon; it is thought that they may be exploiting early morning or late afternoon movements to and from the sleeping sites of both diurnal and nocturnal species (Karpanty, 2006). However, the sample size was too small to analyse the playback response for these smaller time periods.

Raptor predation on lemurs varies seasonally, with peak encounters happening during the birth and weaning seasons (Sauther, 2002; Karpanty, 2006; Karpanty & Wright, 2007). It was not possible to investigate the impact on ring-tailed lemurs of having an infant in the group as at Berenty they usually give birth during September (although it can be as early as August and occasionally as late as December) and the fieldwork was carried out in July and early August. (Jolly, 1966; Jolly *et al.*, 2002; Gemmill & Gould, 2008; Simmen *et al.*, 2010). Some Verreaux's sifaka females, however, gave birth during the research period. The presence of an infant was surprisingly not a significant factor in the response to the crested drongo alarm call; and although it was not significant, groups with an infant actually responded less vigilantly than those without. However, the sifaka troops had highest levels of vigilance to the crested drongo alarm calls in early July which was when some troops started to have infants present. In addition to this they had highest levels of vigilance in early July. Not all Verreaux's sifaka females give birth every year, and as such, may invest more time in vigilance to

protect their young when they are particularly vulnerable (Richard *et al.*, 1991; Richard *et al.*, 2002; Karpanty & Wright, 2007).

Both lemur species showed a variety of vigilant responses to the crested drongo alarm call; looking up, scanning, and on occasion, fleeing. When flight occurred it was away from the speaker, and either across or upwards. As previously mentioned, it was only when they were on the ground that the ring-tailed lemurs fled as opposed to scanning or looking up. Flight never took place when either lemur species was in the top half of the canopy. This suggests that both lemur species may have felt more vulnerable to predation when lower down, which is supported by studies suggesting that lemurs are particularly vulnerable to aerial and terrestrial attack when on the ground (Sauther, 1989). It should be noted that it was not clear as to whether the crested drongo alarm call was a general, aerial or terrestrial alarm call, and this may have influenced the response. Both lemur species are known to exhibit a mixed alarm call system with functionally referential alarm calls for different types of predators, and recognises these different calls in other species of lemur (Oda, 1998; Fichtel, 2004). It therefore seems likely that they could similarly evolve the ability to differentiate signals in non-primates.

Mixed species flocks of birds are observed all year round in the Malagasy forests, and the crested drongo is a regular participant in such flocks (Eguchi *et al.*, 1993; Hino, 1998). For the crested drongo, the benefits of mixed species flocks are mainly improved foraging success; they capture prey significantly more when participating in mixed species flocks (Hino, 1998; 2009). However, other species, for example, the blue vanga, join flocks for increased protection from predators (Hino, 1998) and may rely on alarm-calling birds such as the crested drongo. The response of the two lemur species to the crested drongo alarm calls suggest that this diffuse co-evolution may extend beyond mixed species flocks of birds.

#### **4.1.3 Calls as a cue to food**

It was predicted that if either lemur species responded to the frugivorous green pigeon song it would be ring-tailed lemurs since they are by far the more frugivorous of the two species (Jolly *et al.*, 2002; Simmen *et al.*, 2006; Gemmill & Gould, 2008), and other primates have been found to use interspecific calls as a cue to finding food (Cords, 1990; Olupot *et al.*, 1998; Haugaasen & Peres, 2008). It might also be expected that this response would increase later in the season as fruit became more sparse (Gemmill & Gould, 2008).

However, there was not a significant response by ring-tailed lemurs to the pigeon song, and there was not a single occasion where a ring-tailed lemur advanced towards the microphone

on hearing the call, a response that might be expected if they were using the pigeon song as a cue. It should be noted that whilst not an alarm call, the exact function of the green pigeon song used was not known. It is possible that the function of the song may have been an influencing factor in the response by the lemurs, although pigeons do not have the same range of vocalisations as Passeriformes (Baptista & Trail, 1992). Whilst time of season was not an explanatory variable, there are seasonal events that may explain the territorial ring-tailed lemurs' (Pride, 2005) lack of response to green pigeon calls. Green pigeons were mainly sighted in a solitary remaining fruiting fig tree, located in the territory of one of the groups of lemurs. Although the troops tested were still eating nearly 60% fruit in August, most of this was tamarind since all troops had access to tamarind trees, and it is known to produce fruit and flowers in July and August (Simmen *et al.*, 2006). Thus the lemurs would not need to use bird calls to help find food.

Contrary to predictions, Verreaux's sifakas *did* respond to the green pigeon call. Sifakas are primarily folivorous (Lewis & Kappeller, 2005; Howarth *et al.*, 1986; Wright, 1998) and so it is unlikely the green pigeon song was being used as a cue for food. The vigilant response observed to this call may have been a general startle response. Unfortunately a pigeon call/song recorded in Berenty could not be sourced, and so this is a confounding variable that could possibly have affected the results. It is possible that Verreaux's sifakas are more sensitive to noises that they are not familiar with, although there is a paucity of published literature on this subject. Sifakas were found to be no more vigilant than ring-tailed lemurs overall, and there does not appear to be a correlation between those troops who were most vigilant and those troops who responded vigilantly to the calls (the sample size was too small to test this significantly).

## **4.2 Interspecific associations**

### **4.2.1 Key findings**

Some of the results for bird – lemur associations ran contrary to predictions. Ring-tailed lemurs did not form associations with frugivorous birds more than Verreaux's sifakas (prediction 5) and habitat context did not have a significant effect on the associations formed by either lemur species with alarm-calling birds (prediction 7). However, it was predicted (prediction 6) that there would not be a significant difference between lemur species in their time spent in association with alarm-calling birds (see table 16 for definition) and this was the case.

#### 4.2.2 Associations with frugivorous birds

The prediction was that if either lemur species formed an association with frugivorous birds, it would be ring-tailed lemurs as they have a greater reliance on fruit in their diet (Jolly *et al.*, 2002; Simmen *et al.*, 2006; Gemmill & Gould, 2008); however, there was little evidence of either species forming associations. Previous studies have shown that frugivorous primates and non-primates do form associations (Robinson & Eisenberg, 1985; Olupot *et al.*, 1998; Haugaasen & Peres, 2008). There is also evidence of a seasonal influence of mixed species associations: the association of collared peccaries with weeper capuchin is strongest during the six months of lowest fruit availability (Robinson & Eisenberg, 1985; Haugaasen & Peres, 2008). It was assumed that an association might be more prevalent at the time of the research, as this was undertaken in the dry season when the fruit resource is scarcer (Gemmill & Gould, 2008).

There are only three frugivorous bird species at Berenty: the green pigeon and the two vasa parrots. During fieldwork, green pigeons were only ever sighted in a solitary fruiting fig tree. A troop of ring-tailed lemurs was seen in this tree on a different day but neither species of lemur was seen in association with green pigeons at any point. Vasa parrots were more widespread and seen in a number of different locations. However, they were found in association with ring-tailed lemurs just 2% of the time, and with Verreaux's sifakas only 4% of the time. There was no significant difference between the two lemur species' associations. There has been no previous evidence of lemurs forming associations with fruit-eating birds (Heymann & Hsia, 2015) and this research seems to support this.

Heymann & Hsia (2015) hypothesise that the lack of diurnal frugivorous mammals in Madagascar also limits the probability of non-primate led associations forming. However, they do not consider the benefits that lemurs may bring to frugivorous birds. Primates are considered to be 'wasteful feeders', and frugivorous primates drop large amounts of fruit pulp and seeds (Howe, 1980). It is more common for these to be eaten by terrestrial herbivores/frugivores, for example, collared peccaries (Robinson & Eisenberg, 1985), chital deer, *Axis axis* (Newton, 1989) and South American coatis, *Nasua nasua* (Haugaasen & Peres, 2008). However, the two Madagascan vasa parrots do eat fruit and seeds from the ground as well as in the canopy (Morris & Hawkins, 1998), and so could benefit from an association with the more frugivorous ring-tailed lemurs. Whilst this research focused on focal sampling of lemurs, the very small percentage of occasions where they

were found in association suggests that deliberate associations were not being formed. However, research involving focal sampling of frugivorous birds would need to be conducted to draw firmer conclusions.

#### **4.2.3 Associations with insectivorous/alarm-calling birds**

It was predicted that lemurs would associate more with alarm-calling birds in open canopy areas, given the risk of predation by the Madagascar harrier hawk in open habitats, particularly during terrestrial travel (Sauther, 1989; 2002). However, the association results mirror that of the lemurs' responses to alarm calls; whilst habitat context did not have a significant effect on the associations of either lemur species, both spent more time in association with alarm-calling birds when in closed habitat. In addition to this, ring-tailed lemurs spent more time in association with alarm-calling birds when they were in 50-75% lower canopy density. This was not a significant result but with a  $P$  value of 0.089, it may have proved significant with a larger sample size. As previously discussed, studies have shown that the lack of visibility in closed canopy or denser foliage may lead to an increased need for vigilance (a real or perceived need); this could lead to lemurs forming associations with alarm-calling birds (Wright, 1998; Treves, 2002; Smith *et al.*, 2004).

The habitat preferences of alarm-calling birds should also be considered as an explanation for any associations. The crested coua, magpie robin and paradise flycatcher are predominantly found in the forest rather than in open canopy areas (Morris & Hawkins, 1998). It is therefore logical that they would be more commonly be found in association with lemurs more frequently in these types of habitats. The crested drongo, however, is considered to be a generalist and inhabits a variety of habitats (Morris & Hawkins, 1998; Fuchs *et al.*, 2013) and this should therefore not be an influencing factor in associations with either lemur species.

There is some evidence that time of day can affect the associations between primates and birds (Boinski & Scott, 1988), although this was not supported by this research: time of day was not found to have a significant effect. If primates are benefiting from birds' ability to spot predators and alarm call, it might be expected that they would choose to associate with them at times when they are more at risk from predation, for example, at dawn and late afternoon when raptors are more likely to be hunting them (Karpanty, 2006). In this research, the requirement to find a different troop of lemurs each day resulted in minimal observations at dawn; this is therefore an area that could be explored further.

If lemur – bird associations are motivated by insectivorous birds benefiting from flushed insects, then the associations would be more likely to take place during times of the day when the primates are more active, for example, foraging or travelling. This is the case for rock kestrels, and chacma baboons (King & Cowlshaw, 2009) and various birds that follow South American squirrel monkeys (Boinski & Scott, 1988). Both ring-tailed lemurs and Verreaux's sifakas tend to be more active in the morning and late afternoon, with a rest period during the middle of the day (Jolly, 1966; Jolly *et al.*, 2002; Lewis & Kappeller, 2005; pers.obs., 2012). However, in this research this pattern of activity did not appear to affect the results.

The presence of an infant was not a significant factor in Verreaux's sifakas' association with alarm-calling birds. There were more associations between Verreaux's sifakas and alarm-calling birds in late July, which is when some troops had very young infants. This supports the suggestion that if associations function to decrease the risk of predation, they would associate with other beneficial species when the group had most young infants present (Chapman and Chapman, 2000). However, it has already been reported that their response to the crested drongo alarm call was *not* higher at this time in the season. Given the lack of significance, and the relatively small number of birds in association, it seems likely that any associations observed were random.

#### **4.2.5 Differences between species**

Verreaux's sifakas spent more time in association with alarm-calling birds than ring-tailed lemurs but the results did not show this to be significant. Prior to undertaking fieldwork it had been hypothesised that there would be no difference between the two species, but following the results of the activity surveys, it would have been less surprising to find that Verreaux's sifakas spent more time in association with alarm-calling birds. Primates, and other animals, have to trade-off time spent feeding and time spent vigilant (Brown, 1999; Teichroeb & Sicotte, 2012). Verreaux's sifakas spent significantly more time feeding than ring-tailed lemurs; it may be that they had made the decision to invest time in feeding rather than vigilance, and therefore might be more reliant on other cues such as alarm calls.

In the majority of primate – non-primate associations (PNPAs), it is thought that the non-primate approaches and follows the primate, although there is a paucity of quantitative data on this. There have been just two recorded cases of primates initiating the association; squirrel monkeys following coatis (Haugaasen & Peres, 2008) and tantalus monkeys, *Chlorocebus tantalus*, following West African bushbuck, *Tragelaphus scriptus* (Henshaw,

1972), but none to date reporting primates initiating an association with a bird (Heymann & Hsia, 2015). Therefore, any potential differences between the two lemur species should also be considered in the context of the benefits to birds as well as to lemurs.

Verreaux's sifakas are more arboreal than ring-tailed lemurs (Howarth *et al.*, 1986; Sauther, 1994; Fichtel & Kappeler, 2002; Lewis & Kappeler, 2005) and are therefore more likely to flush insects as they move through the trees. All of the birds defined as alarm-calling are also insectivorous and so could benefit from these flushed insects (Morris & Hawkins, 1998). However, Heymann & Hsia (2015) showed that insectivorous birds are more likely to associate with insectivorous primates, rather than frugivorous and folivorous primates such as the two lemur species studied (Sauther, 1994; Simmen *et al.*, 2003, Lewis & Kappeler, 2005; Gould *et al.*, 2011). This is because the foraging manoeuvres of insectivorous primates are more likely to flush prey that can be captured by insectivorous birds on the wing (Boinski & Scott, 1988). It has also been suggested that smaller groups of primates provide less prey flushing and thus little benefit to insectivorous birds – however, this hypothesis was not supported in the 2014 review by Heymann & Hsia (2015).

### **4.3 Evaluation of methods and research limitations**

The control, the song of the magpie robin, was well chosen for the Verreaux's sifakas tested, with only 4% responding vigilantly to this playback. The ring-tailed lemurs had a higher vigilant response to the control (12%) but the response was always to look up rather than to scan or flee (with the exception of one juvenile who fled once). This was significantly different to the response of the crested drongo alarm calls (70%), but was very close to their responses to the white-headed vanga (11%) and the green pigeon (13%) which also only elicited a look up response rather than scanning. This suggests that ring-tailed lemurs may respond in a similar way to calls that are less relevant to them, regardless of the bird species, i.e. grouping non-alarm calls into the same category. The results showed that the call sequence did have an effect on the ring-tailed lemur response to the crested drongo call and the Verreaux's sifaka response to the green pigeon. To mitigate this potential effect in future experiments, the different bird calls should be played at least 30 minutes apart.

The need to minimise disturbance and pseudoreplication meant that a variety of troops were followed for playback, activity and association data. This limited the ability to identify individuals within each troop over a period of time which resulted in data for each troop only being used once. The need to search for troops most mornings also reduced the time

available to collect activity and association data. A longer study period would have enabled activity and association data to be collected separately to the playback data, thus enabling better identification of individuals, and a larger data set for activity and association.

The short length of the study resulted in two main limitations: small sample size and lack of seasonal variation. The small sample size limited the conclusions that could be drawn in relation to lemurs and their associations with frugivorous birds. As the study took place in July and August (dry season), it was not possible to compare playback response, activity and associations in the dry and wet seasons. The seasons have an impact on the food resource available; fruit is sparse in Madagascar between June and September (particularly the dry southern part of the country) (Yamashita, 2002; Gemmill & Gould, 2008), and therefore responses to and associations with frugivorous birds may vary according to the season.

The time of year also influences the vulnerability of lemurs to predation, and therefore potentially to the response to playback and to the types of associations formed. Previous studies have shown that monthly predator encounters by groups of ring-tailed lemurs and Verreaux's sifakas, peak annually during the lemurs' birth and weaning seasons (Sauther, 2002; Karpanty, 2006). The different breeding seasons of ring-tailed lemurs (usually September at Berenty) and Verreaux's sifakas (July/August at Berenty) (Jolly *et al.*, 2002; Gemmill & Gould, 2008; Simmen *et al.*, 2010; pers. obs., 2012) eliminated the possibility of comparing between species the impact that having an infant in the group might have had on the playback response and associations. Whilst this study didn't show a difference in response to the crested drongo alarm calls when an infant is present by Verreaux's sifakas, it did show an increase in general vigilance at the time when the infants were at their youngest. It would be interesting to investigate whether this is also the case for ring-tailed lemurs.

The research was only carried out on one site: Berenty is a small site with habituated lemurs. This made it possible to collect data in a short period of time, but the responses may not be typical and may vary at other sites where lemurs are less habituated. With a longer period of time it may have been possible to compare lemur responses to playback at tourist front (the most habituated lemurs) with those further away from the tourist area, or compare to responses at another site.

Only one bird call per species was tested; whilst the control and crested drongo alarm calls were recorded at Berenty, the white-headed vanga and green pigeon calls were recorded at different sites. Given that there is some evidence of birds having different dialects in different



parts of the country (van Dongen & Mulder, 2006) the robustness of the research could have been improved by testing either calls only from Berenty and/or two or three different recordings of the same bird species.

#### **4.4 Direction for future research**

Future studies would benefit from conducting the playback experiments and collation of association data over a longer time period: this would enable a greater sample size as well as testing the seasonal variation more comprehensively. Whilst this study was able to compare different periods in the dry season, it would benefit from comparison to playback responses and associations in the wet season. The study period did not include that of the ring-tailed lemur breeding period – it would be interesting to compare the playback responses and time spent vigilant between Verreaux's sifaka and ring-tailed lemur troops when they had an infant present.

Another interesting comparison would be that of gender. The males of some primate species are known to spend more time vigilant than the females. In some cases this is related to monitoring for rival males (Cheney and Seyfarth, 1981; Boinski, 1988; Cords, 1990; Buchanan-Smith 1999) but in others it may be related to their visual ability to detect predators (Smith *et al.*, 2004). However, both ring-tailed lemur and Verreaux sifakas troops are led by alpha females rather than males (Brockman, 1999; Gould *et al.*, 1997). Gould *et al.* (1997) found that the dominant female ring-tailed lemur was significantly more vigilant than other lemurs in the group. It would therefore be interesting to not only compare levels of vigilance between the sexes in both lemur species, but also see if this affected their response to crested drongo alarm calls. This would be achievable with a larger sample size and the ability to identify individuals in the troops more easily.

A longer study period would also allow data collection in a different protected area so that data could be compared to that at Berenty. This would also allow the study to be extended to different species of lemur. In a fragile ecosystem such as Madagascar, where habitat fragmentation threatens the survival of many lemurs, as well as many other animals and birds (Bollen & Donati, 2006; Mittermeier *et al.*, 2005), it is crucial to identify any reliance on birds by lemurs for foraging or predation avoidance. The results of this study have shown that both lemur species clearly respond vigilantly to drongo alarm calls, and therefore there may be potential knock on effects for them if the dynamics of their ecosystem changes, e.g. if drongos or other alarm calling birds were no longer present in the area (Laland & Boorgert, 2010; Harrison & Whitehouse, 2011). Understanding whether other lemur species rely on

birds to avoid predation is clearly important to conservation, and this is perhaps particularly true of the rarer lemur species who are only present in isolated forests. The finding that two different lemur species appear to be sensitive to drongo vigilance suggests the finding is likely to be transferable to other lemur species, including rare species which are conservation priorities.

This research only tested lemur responses to four different species of bird, and only one alarm call (the crested drongo). It would be interesting to trial alarm calls from different birds so see if the vigilant response was as high as that for the crested drongo. Future research would also benefit from testing different crested drongo alarm calls to see if there are different responses from the two lemurs species to functionally different (for example, terrestrial or aerial) alarm calls. The use of different bird species' calls may also provide some insight on the apparent sensitivity of the sifakas to the green pigeon call.

Another direction for future research would be to use the birds as the focal study subject rather than the lemurs. The methods used for this research did not test whether insectivorous birds associated with lemur troops in order to benefit from flushed insects as they moved through the trees. Evidence suggests that insectivorous bird species in the Neotropics and main-land Africa do follow primate groups to obtain flushed prey (Heymann, 1992; Boinski & Scott, 1998; Hankerson *et al.*, 2006; Haugaasen & Peres, 2008; King & Cowlishaw, 2009). Heymann & Hsia (2015) suggest that in the majority of PNPAs, the non-primate is the main beneficiary and therefore initiates the association, so there is further merit in undertaking this research with birds as the focus.

## **4.5 Summary**

This research certainly supports the suggestion that species in co-evolved communities may rely on others to avoid predation or access resources. It seems likely from the results of this study that the primary reason for these two diurnal lemur species listening to bird communication is predation avoidance rather than to help them access food resources. The lemurs studied both clearly responded vigilantly to bird alarm calls and whilst they did not appear to seek out associations with alarm calling birds, there are potential knock on effects for them if the dynamics of the ecosystem changes. Understanding these relationships is clearly important to conservation, including the expansion of this type of research to rarer species.

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