

available at [www.sciencedirect.com](http://www.sciencedirect.com)

SCIENCE @ DIRECT®

journal homepage: [www.elsevier.com/locate/biocon](http://www.elsevier.com/locate/biocon)

# The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar

Dawn M. Scott\*, Daniel Brown, Simon Mahood, Buck Denton, Anastasia Silburn, Felix Rakotondrapary

Biology Division, University of Brighton, Cockcroft Building, Moulsecoomb, Brighton, East Sussex BN2 4GJ, UK

## ARTICLE INFO

### Article history:

Received: 23 January 2005

Received in revised form

21 June 2005

Accepted: 12 July 2005

### Keywords:

Deforestation

Spiny forest

Madagascar

Vertebrates

Community composition

## ABSTRACT

Madagascar is a global biodiversity hotspot threatened by forest loss, degradation and fragmentation, all of which are detrimental to the future survival of forest-dwelling organisms. For conservation purposes it is essential to determine how species respond to habitat disturbance, specifically deforestation. In this study we investigated the impacts of deforestation on three vertebrate communities, lizards, small mammals and birds, in an area of spiny forest subjected to anthropogenic forest clearance. Spiny forest has high levels of endemism, but conservation in this unique ecosystem is hindered by the lack of research. We undertook standardised trapping, time-constrained and timed species searches to assess species richness, species abundance and community composition of lizards, small mammals and birds in six areas of 'forest' and six 'cleared' areas. From surveys and opportunistic sightings we recorded a total of 70 species of birds, 14 species of mammals and 38 species of reptiles and amphibians. We found forest clearing to have a negative effect on species richness and community structure of all groups and identified loss of canopy cover as a driving factor behind this. However, the response and sensitivity to clearing varied between groups and species. Lizards (50%) and small mammals (40%) had the greatest decline in species richness in response to clearing as compared to birds (26%), although birds showed the greatest shift in community structure. The community in cleared areas contained more generalist and introduced species that have wider geographic ranges and habitat preferences, than those unique to the spiny forest. We found the first suite of species to suffer from forest clearance were those of high conservation priority due to their restricted geographic range. Our findings are discussed in relation to future spiny forest conservation and management.

© 2005 Elsevier Ltd. All rights reserved.

## 1. Introduction

Madagascar has been designated a global biodiversity hotspot, due to its high number of island endemic species (Myers et al., 2000; Ganzhorn et al., 2001), 90% of which

are forest dwelling (Dufils, 2003). Myers et al. (2000) suggests that Madagascar is 'the single highest biodiversity conservation priority in the world'. However, conflict exists between conserving Madagascar's biodiversity and anthropogenic land use. Madagascar has one of the world's highest rates of human population increase (Green and Sussman, 1990),

\* Corresponding author: Tel.: 44 01273 642071; fax: +44 01273 679333.

E-mail address: [dawn.scott@brighton.ac.uk](mailto:dawn.scott@brighton.ac.uk) (D.M. Scott).

0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2005.07.014

resulting in an intensification of forest product exploitation (Jolly and Jolly, 1984; Green and Sussman, 1990; Kull, 2002; Vallan, 2002; Watson et al., 2004a). Due to direct and indirect causes, it is reported that forests have been cleared at an accelerating rate (Green and Sussman, 1990; Casse et al., 2004), although differences in reported estimates and descriptions of the dynamic nature of vegetation change has led to conflicting evidence and more recent attempts at quantification (Ingram and Dawson, 2005). No Malagasy forest escapes anthropogenic pressures (Goodman and Raheerilalao, 2003). Current estimates suggest only 10–20% of Madagascar's natural forests remain largely intact (Du Puy and Moat, 1998; Myers et al., 2000), all of which is under varying degrees of threat (Dufils, 2003).

Deforestation is currently one of the greatest threats to global biodiversity (Primack, 2004). It has been widely demonstrated that deforestation resulting in habitat loss, degradation and fragmentation has detrimental effects on species diversity in Madagascar (Goodman, 1993; Smith et al., 1997; Vallan, 2002; Watson et al., 2004b). The impact of deforestation on communities depends on the forest type, the size and shape of the deforested patch (Goodman and Rakotondravony, 2000; Ramanamanjato and Ganzhorn, 2001; Vallan, 2002; Watson et al., 2004b), the type of clearance (Stephenson, 1993) and the landscape context (Saunders et al., 1991; Watson et al., 2004a). The impact of deforestation is not uniform across species (Vallan, 2002; Watson et al., 2004a). The ability of species to tolerate or exploit modified conditions, or to disperse to alternative sites, will determine their persistence and future survival. To attempt to mitigate the effects of deforestation it is essential for conservation purposes to identify susceptible species. Additionally we need to understand the processes behind how different species and communities respond to different levels and types of forest use (Goodman and Raheerilalao, 2003). This information will help to determine species for conservation priority and to develop and implement potentially effective land use and management practices to aid a resolution to conflict between conservation and anthropogenic needs.

Many studies on the impacts of deforestation on animal communities in Madagascar have focused on tropical rainforest (Stephenson, 1993, 1994b; Raxworthy and Nussbaum, 1994; Vallan, 2000) or littoral forests (Lehtinen et al., 2003; Watson et al., 2005), and until recently have mainly focused on protected areas, such as in eastern and highland forests (Stephenson, 1993; Goodman and Rakotondravony, 2000; Vallan, 2000). In comparison there is relatively little research undertaken in the dry spiny forests, and as a result they are recognised as a high research priority (Goodman and Raheerilalao, 2003; Ganzhorn et al., 2003). Additionally, research tends to focus on a single taxonomic group, such as vegetation (Cadotte et al., 2002; Brown and Gurevitch, 2004), birds (Goodman and Raheerilalao, 2003; Watson et al., 2004a), reptiles (Lehtinen et al., 2003), amphibians (Vallan, 2000), invertebrates (Benstead et al., 2003), large mammals (Smith et al., 1997) and/or small mammals (Stephenson, 1993; Goodman and Rakotondravony, 2000; Ganzhorn et al., 2003), but few have looked across communities to investigate patterns of response (Hawkins et al., 1990).

The 'Southern Domain' also known as the arid xerophytic spiny forest or 'spiny thicket', (Gautier and Goodman, 2003) extends across the extreme south and southwest area of Madagascar covering approximately five million hectares (Wells, 2003). It is restricted to elevations under 400 m and runs southwards from Morombe along the coast to the western slopes of the Anosyennes Mountains in the southeast (Gautier and Goodman, 2003). It is the oldest biome of Madagascar (Wells, 2003) and most arid (Gautier and Goodman, 2003), with an average annual rainfall of approximately 300 mm. The spiny forest is subjected to 'slash and burn' agriculture for cultivation and livestock grazing, charcoal making, selective logging, collection of wood for construction and fuel, and collection of food and medicinal plants (Fenn, 2003).

The Southern Domain has the highest proportion of endemic plants on Madagascar; between 90% and 95% of the documented 336 plant species are endemic (Philipson, 1996; Gautier and Goodman, 2003). Plant families characteristic of this region include the xerophytic Didiereaceae, Euphorbiaceae and baobabs (*Adansonia* spp.). Nine species of birds are restricted solely to spiny forest (Sinclair and Langrand, 1998), two are classified as 'Vulnerable' and two 'Near-threatened' (Birdlife International, 2000). Consequentially, spiny forest is classified as an 'Endemic Bird Area' (Stattersfield et al., 1988). It is also home to three endemic rodent species and six endemic species of tenrec (Goodman, pers. commun.). All nine lemur species occurring in spiny forest are threatened (IUCN, 2003). Reptile fauna is relatively diverse in the spiny forest (Nussbaum et al., 1999) with several habitat specialists (Henkel and Schmidt, 2000). Due to high endemism and species conservation status it is essential to incorporate this unique ecosystem in any National and International biodiversity conservation efforts.

In this paper we investigate the impact of spiny forest deforestation on three selected vertebrate communities commonly used as bio-indicators; small mammals, reptiles and birds (Raxworthy and Nussbaum, 1994; Watson et al., 2004a). We compared species presence and abundance in six 'forested' sites of low-level forest exploitation, and six heavily exploited 'cleared' areas. We hypothesized that anthropogenic forest 'clearance' will have a detrimental effect on species richness, however the impact will be species specific and not all communities will respond in the same manner. To test this our study comprised three aims: (i) assess the impacts of forest clearance on community composition by comparing changes in species presence and abundance; (ii) determine which environmental factors are affecting community shifts in different vertebrate groups; and (iii) within each group assess the sensitivity of each species to deforestation. Findings can then be discussed in relation to current and future spiny forest conservation and management.

---

## 2. Methods

### 2.1. Study area

The study was undertaken between September and December 2003, during the austral summer when most species are active

(Goodman, 1999). Studies were conducted around the village of Bevia in the Behara commune (24°50'S, 46°27'E; Fig. 1). The site is situated on dry sandy soils to the west of the Anosyennes Mountains near the south-eastern limit of the spiny forest range (Goodman et al., 1997). Altitudinal range varied between 0 and 100 m. Average annual rainfall of the region is less than 700 mm with mean annual minimum and maximum temperature range between 15 and 21 °C and 30 and 33 °C, respectively (Donque, 1972). The 'Tandroy' villagers of Bevia are traditional herders and rely on local forest resources, collecting termites as feed for domestic poultry, collecting and harvesting construction and fuel wood, food and medicinal plants, therefore the forest surrounding the village is subjected to continual low-level exploitation. Heavy exploitation of the forest is in the form of 'clearing', where >90% of trees in an area are cut down and subsequently burnt or cleared. This 'slash and burn' agriculture enables the growth of numerous crops and provides a place to graze livestock.

## 2.2. Site selection

Twelve study sites were selected (5 km) 500 m from Bevia village to standardise the level of disturbance. Six sites in continuous forest with low-level exploitation (F1–F6) and six sites that had previously been 'cleared' (>90% of trees felled)

and used for either agriculture or grazing (C1–C6, Table 1). To prevent potential edge effects forest sites were positioned at least 500 m from a cleared area. All sites were spaced at a minimum of 500 m apart to attempt to maximise spatial independence given the boundary limits of the study area. Size of area cleared (Ganzhorn et al., 2000), time since clearing and land use after clearing can confound results from retrospective investigations into the impacts of forest clearance (Langrand and Wilmé, 1997; Rhind, 2004). Therefore all 'cleared' sites were >6500 m<sup>2</sup> in size, <5 years old and had >90% of trees removed, with the exception of one site (C4) was that was 60 years old. This was selected to enable comparisons of the impacts of short and long term clearance.

## 2.3. Habitat assessment

Longitude and latitude, altitude (m), slope angle (°), predominant soil substrate, distance from standing water (m), distance from nearest track (m), size of patch (m<sup>2</sup>) and type of management were noted for each site. Tree and shrub species were identified and abundance scored on a DAFOR scale (Kent and Coker, 1992). Habitat structure was separated into three distinct vegetation layers, ground (<1 m), shrub (>1 <3 m) and canopy (>3 m). Five random 10 × 10 m (shrub and canopy) and 2 × 2 m (ground layer) quadrats were undertaken in each

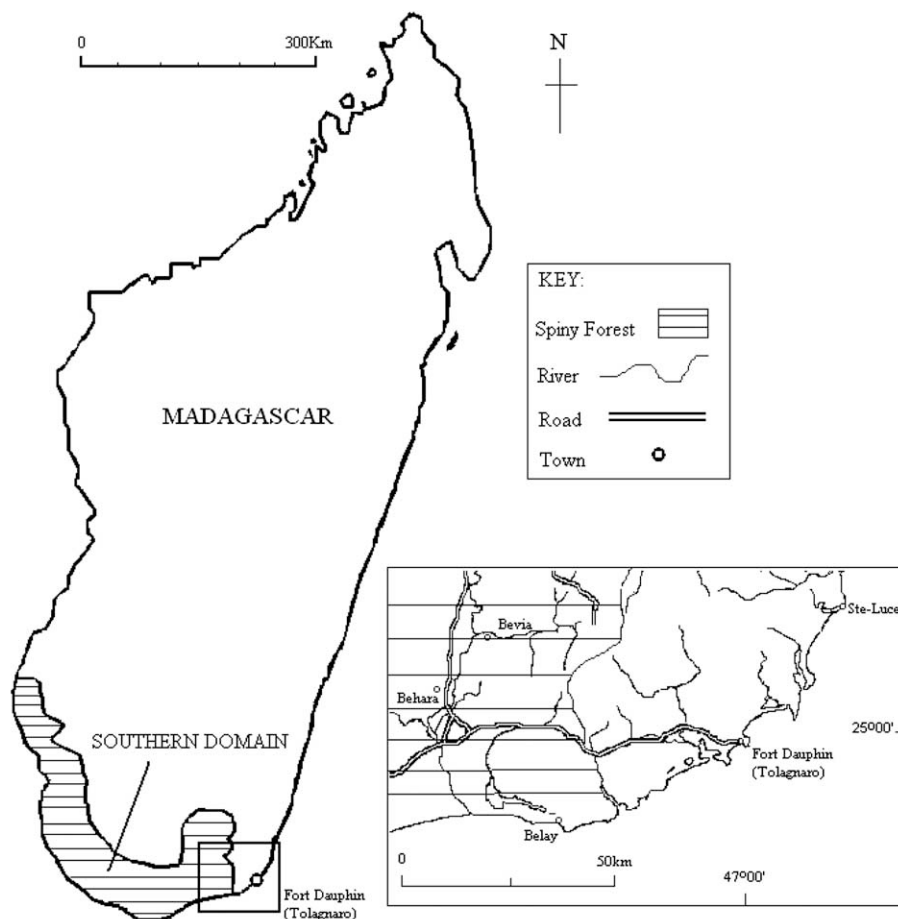


Fig. 1 – Map of Madagascar showing the distribution on the Southern Domain and inset map showing location of the study area, Bevia Village.

**Table 1 – Site descriptions for the 12 study sites indicating location, area of clearance, slope and aspect. Use of site, clearing type and time since clearing is also shown. S&B means 'slash and burn' clearance.**

Habitat	Code	South	East	Area (m <sup>2</sup> )	Slope (°)	Aspect	Clearing type	Year's since clearing	Use
Cleared	C1	24° 50,914	046° 27,541	20,000	10	WNW	S&B; all trees removed	5	Grazing and crop growing
	C2	24° 51,245	046° 28,198	6500	0		S&B; all trees removed	2	Agriculture planned
	C3	24° 50,670	046° 27,677	13,000	6	S	S&B; some trees left	3	Agriculture and grazing planned
	C4	24° 51,520	046° 27,053	14,000	5	SW	Cleared	60	Grazing, seasonally flooded for rice paddies
	C5	24° 50,811	046° 26,929	30,000	2	SW	S&B; all trees removed	< 1	Agriculture planned
	C6	24° 50,546	046° 27,375	7500	1	SW	S&B; some trees left	2	Agriculture planned
Forest	F1	24° 50,598	046° 27,426		4	W		0	Grazing cattle and goats (low); wood cutting (low)
	F2	24° 50,221	046° 27,494		5	N		0	Grazing cattle and goats (low); wood cutting (low)
	F3	24° 51,308	046° 27,136		6	SSW		0	Grazing cattle and goats (low); wood cutting (low)
	F4	24° 51,126	046° 26,553		18	NE		0	Grazing cattle and goats (low); wood cutting (low)
	F5	24° 51,040	046° 26,553		15	NNE		0	Grazing cattle and goats (high); fuel wood collection (low)
	F6	24° 51,058	046° 27,412		4	NNE		0	Grazing cattle and goats (low); wood cutting (low)

area. Table 2 details the parameters recorded. For measurements of height and depth a minimum of five measurements were taken per quadrat.

#### 2.4. Lizard surveys

Species presence and relative abundance of lizards (suborder Lacertilia) in each 'forested' and 'cleared' sites were estimated using two methods, drift lines with pitfall trapping and time-

constrained searches (O'Shea, 1992; Sutherland, 1996; Bennett, 1999; Ryan et al., 2002). A pitfall trapping line consisting of ten, 30 cm deep × 30 cm diameter buckets at 10 m intervals with a drift fence (50 cm height, 100 m in length and buried to 5 cm depth) was established for five consecutive days (adapted from Goodman, 1999). In 'cleared' sites, trap lines were set in the middle of the patch, as far from the edge as possible. Leaf litter was provided for shelter. Buckets were checked twice daily at dawn and dusk. Individuals caught

**Table 2 – Description and mean values (standard deviations in parentheses) for environmental variables recorded in 'forested' (n = 6) and 'cleared' sites (n = 6). The results of independent t tests comparing the means are also displayed (P < 0.05).**

Variable	Description	'Forest' (n = 6)	'Cleared' (n = 6)	t value	P
Distance to water	Mean distance to standing water (m)	60.00 (51.38)	12.50 (20.92)	-0.13	0.903
Distance to track	Mean distance to track (m)	330.00 (169.12)	360.83 (581.45)	2.10	0.062
10 × 10 m					
Tree canopy cover	Percentage crown cover of trees >3 m in height	30.90 (12.27)	0.57 (0.98)	9.00	0.000*
Shrub cover	Percentage cover of shrubs 1–3 m high	25.13 (4.75)	10.75 (10.49)	7.00	0.000*
Cut stumps	Mean number of cut stumps	1.73 (1.57)	17.57 (11.78)	-2.90	0.009*
Fallen logs	Mean number of fallen logs	7.37 (5.73)	4.57 (4.79)	0.90	0.380
Termite mounds	Number of mounds intact	0.67 (0.41)	0.17 (0.20)	6.03	0.000*
Termite use	Number of mounds broken	0.13 (0.24)	0.33 (0.45)	4.22	0.002*
Termite activity	Other activity	1.80 (0.78)	0.90 (1.02)	16.68	0.000*
2 × 2 m					
Vegetation cover	Percentage cover of vegetation <1 m	9.77 (2.52)	8.57 (4.14)	0.73	0.483
Vegetation height	Mean height (cm) of vegetation <1 m	25.20 (11.69)	26.42 (20.92)	-0.12	0.903
Litter cover	Percentage cover of ground litter/dead vegetation	14.00 (2.88)	7.33 (7.64)	2.16	0.057
Litter depth	Mean depth of litter (cm)	1.17 (0.59)	0.68 (0.57)	1.40	0.181
Rock cover	Percentage cover of rocks >10 cm	21.90 (12.45)	15.00 (10.81)	1.20	0.257
Rock height	Mean height of rocks (cm)	23.77 (20.03)	11.75 (7.61)	1.40	0.200
Bare ground	Percentage cover of bare ground	25.47 (12.46)	39.90 (21.94)	-1.21	0.253
Dead wood	Percentage cover of dead wood	28.13 (11.55)	21.93 (12.61)	0.95	0.365

were identified to species when possible, aged and sexed, and head-body and tail length (mm) measured. Individuals were uniquely marked with a temporary non-toxic marker for individual identification. The second survey consisted of a single half-hour active random search for lizards within 6000 m<sup>2</sup> of each site. Surveys were carried out between 11:00 and 13:00 h and were conducted by the same team. All species sighted during the survey period were identified and the number of sightings recorded. Night time-constrained searches were piloted, however these proved unsuccessful therefore data were restricted to diurnal counts.

### 2.5. Small mammal surveys

Pitfall and Sherman trapping have both been used effectively to survey small mammals in Madagascar (Stephenson et al., 1994; Goodman and Rakotondravony, 2000), however the success of the two techniques varies. Consequentially, in addition to the pitfall traps 30 Sherman live traps (9 × 8 × 23 cm, H.B. Sherman Traps Inc., Orlando, Florida) were employed for five consecutive nights within each study site. Three parallel transects of Sherman traps, 10 traps per transect spaced at 10 m intervals and one trap per station (Stephenson, 1995), were placed at 10 m from pitfall traps. The first line and last line of traps was placed at ground level and the middle line was arboreal >1 < 2 m from the ground (Stephenson et al., 1994). Traps were placed within 1 m of the trap station in suitable microhabitat and covered with vegetation to protect them (Gurnell and Flowerdew, 1990). Traps were baited with dried shrimps (Stephenson, 1993), cooked rice, peanut butter, oats and fruit (Barnett and Dutton, 1995). All traps were checked twice a day, at dawn and dusk, and re-baited daily. All mammals caught were identified, weighed, aged, sexed, had their external reproductive status determined and biometrics recorded (Scott and Dunstone, 2000), then released within 5 m of their point of capture. Animals were marked with a unique hair clip or non-toxic marker for individual identification (Gurnell and Flowerdew, 1990). In total 2400 trap nights were undertaken, 200 in each study site, equivalent to 1200 trap nights for both 'forest' and 'cleared' areas.

### 2.6. Bird surveys

The presence and relative abundance of bird species in 'cleared' and 'forested' areas was quantified using timed species counts (Bibby et al., 1998). A total 160 min observation time was conducted in each site (four replicates of 40 min observation time), giving a total of sixteen hours of observation for both 'forest' and 'cleared' areas. To prevent temporal bias counts were restricted between 05:00 and 07:00. All surveys were undertaken within a one month period to reduce seasonal bias. To reduce observer bias, all surveys were conducted by the same two observers with prior training and experience. All surveys were undertaken on days without rain or strong wind (Watson et al., 2004a). Visibility varied between 'forest' and 'cleared' areas, therefore to ensure coverage of the site and maximize detection, a random slow walk was conducted with intermittent stops. To prevent edge species being documented only individuals utilizing the core of the 'cleared' were recorded >50 m from edge.

Average relative abundance scores for each species at each site were calculated based on when they were sighted within the 40-min timed species count. If a species was sighted in the first 10 min they were assigned a score of '4', in the next 10 min a score of '3', and so on. If a species wasn't sighted within 40 min it was assigned a score of '0'. The average score was then calculated over the four replicates. To enable analysis of species rank shift between 'forest' and 'cleared' areas, sites were pooled and each species assigned a rank based on their relative abundance, highest score assigned a rank of one, the next highest scoring rank of two, etc. (Bibby et al., 1998). Rank shift was then calculated as the percentage shift in rank, for example if a species drops by 10 ranks out of a possible 40 ranks, this is expressed as a -25% rank shift.

### 2.7. Species characteristics

Species sensitivity to forest clearance was based on the magnitude of change in abundance between forest and cleared habitats, expressed as either positive or negative response to clearing. To enable comparisons between ecological characteristics, reptile, small mammal and bird species status, distribution, diet and habitat specialism were compiled based on species accounts in the literature; Glaw and Vences (1994), Morris and Hawkins (1998), Garbutt (1999), Henkel and Schmidt (2000) and Goodman and Benstead (2003).

### 2.8. Statistical analysis

To verify that we undertook sufficient trapping effort, species accumulation curves for small mammals and lizards were plotted against the number of trap nights for Sherman and pitfall trapping, and bird counts, in two 'forest' sites. 'Forest' sites were compared for similarity of vegetation using a Jaccard index as a similarity coefficient (Waite, 2000). All data were tested for normality prior to analysis. Redundant variables were removed from the data by checking for inter-correlations (Pearson product moment correlation) (Waite, 2000). Percentage data were arcsine transformed before analysis. Mann-Whitney U tests were conducted on data not normally distributed and independent sample t tests on normally distributed. Levenes' test for equal variance was used before independent t tests were conducted. Rank abundance curves were produced for small mammal and lizard data by plotting species ranks against log abundance in 'forest' and 'cleared' areas (Waite, 2000). Changes in bird species ranks between 'forest' and 'cleared' habitats were compared using a Pearson product moment correlation. To investigate relationships between species and habitat structure, species abundance was correlated with environmental variables representative of habitat structure. Pearson product moment correlation was undertaken on normal data and Spearman rank correlation on other data. SPSS version 12 was used for all univariate analysis (Dytham, 1999).

Non-metric multidimensional scaling (NMS) (Kruskal, 1964) was used to graphically represent the vegetation structure, lizard, small mammal and bird community relationships between 'forest' and 'cleared' study areas. PC-ORD package was used which uses Kruskal (1964) and Mather (1976) methods for NMS analysis (McCune and Grace, 2002). Settings were

Sørensen's similarities as a distance measure, two axes and 100 iterations with random starting co-ordinates (McCune and Grace, 2002).

### 3. Results

#### 3.1. Changes in habitat structure in relation to clearing

'Forest' habitats appeared to be relatively homogenous, although all 'forest' sites had low similarity in tree and shrub species composition using a Jaccard index (0.53–0.62). Sixty-four species of trees, shrubs and lianas were recorded. The dominant trees included Euphorbiaceae (e.g., *Acalypha* sp., *Securinega* sp. and *Euphorbia* spp.), Didiereaceae (e.g., *Alluaudia procera*, *A. dumosa*, *A. humberti* and *A. ascendens*), Burseraceae (e.g., *Commiphora* spp.), Hernandiaceae (e.g., *Gyrocarpus* sp.), Fabaceae (e.g., *Dicrostachys* sp., *Dolichos* sp., *Baudouinia* sp. and *Tetrapterocarpon* sp.) and Ebenaceae (e.g., *Diospyros* sp.). All environmental variables had normal distributions. As expected, analysis showed that forest clearance caused changes in upper storey vegetation structure with a statistically significant decrease in tree cover and shrub cover (Table 2). Unexpectedly there was no significant difference in ground level characteristics between 'forest' and 'cleared' habitats (Table 2). Termite activity in the form of the number of mounds and 'other' observed activity were significantly lower in cleared areas than forested areas. Forest clearance appears to have a greater impact on the three-dimensional habitat structure and canopy cover than ground-level parameters. Clearance also appears to be associated with increased anthropogenic exploitation of resources, for example there was a higher incidence of broken termite mounds on 'cleared' sites compared to 'forested' sites.

#### 3.2. Community responses to forest clearance

Species accumulation curves reached asymptotes indicating a trapping period of five days was sufficient time to rapidly assess representative small mammal and lizard species pres-

ence within a site, given the employed survey techniques. 160 min of observation time in both 'cleared' and 'forest' was deemed sufficient to sample bird communities from species accumulation plots (Fig. 2). In total 70 bird species, 14 mammal species and 38 species of reptiles and amphibians were recorded during both opportunistic and standardised surveys. The abundance of 43 bird species, five small mammal and 14 lizards were compared quantitatively between 'forest' and 'cleared' sites. Overall, 41% of lizard species, 60% of small mammal species and 77% of bird species were found in 'cleared' patches (see Tables 3–5).

Overall 116 individuals of 12 species of lizards were trapping during 600 pitfall trap nights (19% trap success). Species richness and abundance differed between the two survey methods. *Oplurus* spp., *Phelsuma* sp. and *Geckolepis* sp. were more frequently sighted than caught in pitfalls, whereas *Pareodura* spp., *Amphiglossus* sp. and *Androngo* sp. were only recorded during trapping. Seven species found in 'forest' habitat were absent from 'cleared' areas with only one species (*Geckolepis* sp.) present only in 'cleared' areas (Table 3). Three species (*Mabuya aureopunctata*, *O. cyclurus* and *Tracheloptychus madagascariensis*) showed a statistically greater abundance in 'forest' areas.

Small mammals were caught in pitfall traps and in terrestrial and arboreal Sherman traps, although trapping methods varied in trap success (66% of all captures were in pitfalls). Overall trap success was low (1.4%), with only 35 individuals of five small mammal species captured (Table 4). Two species of endemic small mammal present in 'forested' sites were absent from 'cleared' areas. *Geogale aurita* was significantly more abundant in 'forest' than 'cleared' areas.

Overall species richness and abundance (number of individuals) of lizards and small mammals followed normal distributions. Tables 3 and 4 show the mean and standard deviation of lizard and small mammal species in 'forest' and 'cleared' habitats. In comparison to 'forested' sites, 'cleared' sites showed a significant decrease in overall lizard abundance ( $t = 2.77$ , d.f. = 10,  $p < 0.05$ ) and lizard species richness ( $t = 7.98$ , d.f. = 10 and  $p < 0.01$ ). There was no significant difference in either species richness ( $t = 0.44$ , d.f. = 10 and  $p = 0.67$ ) or overall abundance ( $t = 0.50$ , d.f. = 10 and  $p = 0.63$ ) for small

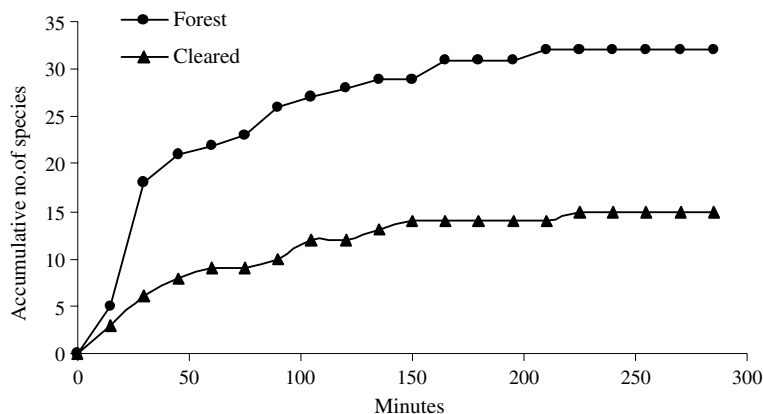


Fig. 2 – Bird species accumulation plots with increased sampling effort, for both forest and cleared habitats to determine appropriate sampling effort.

**Table 3 – Mean and standard deviation of the total number of lizards (suborder Lacertilia) recorded during surveys at each site within the ‘forest’ and ‘cleared’ habitats, in decreasing order of ‘sensitivity’ to clearance**

Response	Family	Species	Code	E/I	Distribution	Habit	‘Forest’ (n = 6)		‘Cleared’ (n = 6)		P	
							Mean	S.D.	Mean	S.D.		
–ve	Opluridae	<i>Oplurus saxicola</i>	OS	E	S	T	2.50	6.12	–	–	0.317	
	Opluridae	<i>Oplurus quadrimaculatus</i>	OQ	E	SW	T	0.67	1.03	–	–	0.138	
	Gekkonidae	<i>Hemidactylus</i> sp.	H	E	W	A	0.67	1.21	–	–	0.140	
	Scincidae	<i>Mabuya aureopunctata</i>	MA	E	S*	T	0.67	0.52	–	–	0.019*	
	Gekkonidae	<i>Phelsuma</i> sp.	P	E	Wide	A	0.17	0.41	–	–	0.317	
	Scincidae	<i>Amphiglossus igneocaudatus</i>	AI	E	SW	T	0.17	0.41	–	–	0.317	
	Scincidae	<i>Androngo trivittatus</i>	AT	E	S	T	0.17	0.41	–	–	0.317	
	Scincidae	<i>Mabuya gravenhorstii</i>	MG	E	Wide	T	1.33	1.21	0.17	0.41	0.060	
	Gekkonidae	<i>Pareodura androyensis</i>	PA	E	SE*	T	1.17	1.47	0.17	0.41	0.083	
	Opluridae	<i>Oplurus cyclurus</i>	OC	E	S-SW*	A	2.50	1.64	0.83	2.04	0.037*	
	Gerrhosauridae	<i>Tracheloptychus madagascariensis</i>	TM	E	S	T	13.33	7.12	4.50	3.51	0.016*	
	Scincidae	<i>Mabuya elegans</i>	ME	E	Wide	T	7.83	4.58	4.50	5.58	0.199	
	+ve	Gekkonidae	<i>Pareodura pictus</i>	PP	E	S-SW*	T	1.83	1.47	3.83	2.64	0.145
		Gekkonidae	<i>Geckolepis</i> sp.	G	E	Wide	A	–	–	0.50	0.55	0.056
		Mean no. of individuals					33.00	11.47	14.50	11.64	0.025*	
		Mean no. of species					7.17	0.75	3.5	0.84	0.003*	
		Total no. of individuals	285				198		87			
		Total no. of species	14				13		7			

Response indicates direction of change in abundance between ‘forest’ and ‘cleared’ habitats, negative (–ve) or positive (+ve). Status (endemic (E) or introduced (I)), distribution (Wide = widespread, S = restricted to south (or SW, southwest Madagascar)) and habits (T = Terrestrial, or A = Arboreal) are also noted.

\* Indicates specialist to dry or spiny forests.

**Table 4 – Mean and standard deviation of the total number of small mammals caught at each site within the ‘forest’ and ‘cleared’ habitats, in decreasing order of ‘sensitivity’ to clearance**

Response	Family	Species	Code	E/I	Distribution	Diet	‘Forest’ (n = 6)		‘Cleared’ (n = 6)		P
							Mean	S.D.	Mean	S.D.	
–ve	Tenrecidae	<i>Geogale aurita</i>	GA	E	SW*	In	1.33	1.37	–	–	0.006*
	Tenrecidae	<i>Setifer setosus</i>	SS	E	Wide	O	0.17	0.41	–	–	0.317
Neg.	Muridae	<i>Mus musculus</i>	MM	I	Wide	O	0.17	0.41	0.17	0.41	1.000
+ve	Soricidae	<i>Suncus madagascariensis</i>	SE	E	Wide	In	0.50	0.55	0.67	0.82	0.789
	Tenrecidae	<i>Echinops telfairi</i>	ET	E	SW*	O	1.00	1.10	1.83	1.72	0.452
		Mean no. of individuals					3.17	3.83	2.67	2.95	0.63
		Mean no. of species					2.33	1.21	1.33	1.03	0.67
		Total no. of individuals	35				19		16		
		Total no. of species	5				5		3		

Response indicates direction of change in abundance between ‘forest’ and ‘cleared’ habitats, negative (–ve), positive (+ve) or negligible (Neg.). Status (endemic (E) or introduced (I)), distribution (Wide = widespread, SW = restricted to southwest Madagascar) and diet (In = insectivorous, O = omnivorous) and \* indicates specialist of dry or spiny forests.

mammals. Rank abundance plots for lizards (Fig. 3(a)) showed the species rank order remained relatively consistent between ‘forest’ and ‘cleared’ sites, with the exception of *Pareodura pictus*, which was higher ranking in cleared than forest. However, abundance was generally lower in cleared areas, especially in the lower ranking species. Small mammal species abundance was similar between cleared and forested sites. Rank order was consistent (Fig. 3(b)) with the exception

of *Echinops telfairi* which was in greater abundance in cleared areas.

Multiple zeros within our data-set limit the ability to find solutions with NMS ordination. Fig. 4(a)–(d), show the relationships of study areas in relation to environmental variables, lizard, small mammal and bird data, respectively. There were poor levels of fit and high stress in both axes for environmental variables (axis 1 = 42.75, axis 2 = 19.46,

**Table 5 – Bird species presence and abundance in ‘forest’ and ‘cleared’ areas**

‘Forest’ species	E/I	Rank shift (%)	‘Cleared’ species	E/I	Rank shift (%)
Madagascar harrier hawk ( <i>Polyboroides radiatus</i> )	E	–	Yellow-billed kite ( <i>Milvus aegyptius</i> )**	M	–
Banded kestrel ( <i>Falco zoniventris</i> )	E	–	Madagascar kestrel ( <i>Falco newtoni</i> )	E	–
Lesser vasa parrot ( <i>Coracopsis nigra</i> )	E	–	Madagascar sandgrouse ( <i>Pterocles personatus</i> )**	E	–
Madagascar lesser cuckoo ( <i>Cuculus rochii</i> )	EM	–	Greater vasa parrot ( <i>Coracopsis vasa</i> )	E	–
Giant coua ( <i>Coua gigas</i> )*	E	–	Madagascar bee-eater ( <i>Merops superciliosus</i> )**	EM	–
Running coua ( <i>C. cursor</i> )*	E	–	Madagascar spinetail ( <i>Zoonavena grandidieri</i> )	E	–
Olive-capped coua ( <i>C. olivaceiceps</i> )*	E	–	Long-billed sunbird ( <i>Nectarinia notata</i> )	E	–
Broad-billed roller ( <i>Eurystomus glaucurus</i> )	EM	–	Common mynah ( <i>Acridotheres tristis</i> )	I	–
Archbolds’ newtonia ( <i>Newtonia archboldi</i> )*	E	–	Gray-headed lovebird ( <i>Agapornis cana</i> )**	E	61
Thamnornis warbler ( <i>Thamnornis chloropetoides</i> )*	E	–	Chabert’s vanga ( <i>Leptopterus chabert</i> )	E	58
Lafresnays’ vanga ( <i>Xenopirostris xenopirostris</i> )*	E	–	Madagascar fody ( <i>Foudia madagascariensis</i> )**	B	55
Common newtonia ( <i>Newtonia brunneicauda</i> )	E	–71	Helmeted guineafowl ( <i>Numida meleagris</i> )	I ?	39
Madagascar coucal ( <i>Centropus toulou</i> )	B	–45	Sakalava weaver ( <i>Ploceus sakalava</i> )	E	39
Madagascar magpie-robin ( <i>Copsychus albospectularis</i> )	E	–42	Pied crow ( <i>Corvus albus</i> )	B	36
Striped-throated jery ( <i>Neomixis striatigula</i> )	E	–36	Madagascar buzzard ( <i>Buteo brachypterus</i> )	E	32
Madagascar paradise fly-catcher ( <i>Terpsiphone mutata</i> )	B	–23	Namaqua dove ( <i>Oena capensis</i> )	B	32
Madagascar turtle dove ( <i>Streptopelia picturata</i> )	B	–19	White-headed vanga ( <i>Artamella viridis</i> )	E	19
Sickle-billed vanga ( <i>Falcula palliata</i> )	E	–16	Madagascar buttonquail ( <i>Turnix nigricollis</i> )	E	16
Madagascar bulbul ( <i>Hypsipetes madagascariensis</i> )	B	–16	Madagascar white eye ( <i>Zosterops maderaspatana</i> )	B	16
Souimanga sunbird ( <i>Nectarinia souimanga</i> )	B	–13	Common jery ( <i>Neomixis tenella</i> )	E	6
Crested coua ( <i>Coua cristata</i> )	E	–10			
Madagascar hoopoe ( <i>Upupa marginata</i> )	E	–10			
Hook-billed vanga ( <i>Vanga curvirostris</i> )	E	–10			
Crested drongo ( <i>Dicrurus forficatus</i> )	B	–3			

Species with values are listed in order of ‘sensitivity to clearing’ based on rank shift (%). This is calculated as the change in abundance rank from ‘forest’ to ‘cleared’ areas expressed as a percentage of the overall number of ranks. Table also shows if the species is endemic (E), migratory (M) or introduced (I), \*indicates specialist to dry or spiny forests and \*\*indicates specialist to open habitats. (–) means there was no shift in rank due to absence in other habitat.

$p > 0.05$  for first axis, Monte Carlo test) and small mammals (axis 1 = 53.91, axis 2 = 15.65,  $p > 0.05$ ) resulting in potentially misleading interpretations of these ordinations. However, for lizard data, NMS resulted in a fair level of stress (categories based on Kruskal’s rule of thumb, Kruskal, 1964) in axis one (12.29,  $p < 0.05$ ) and good to fair stress in axis two (7.9). A fair level of stress in axis 1 (16.05) for the bird data ( $p < 0.05$ ) and good level of stress in axis 2 (8.52), meaning these ordinations (Fig. 4(c) and (d)) can be more useful at drawing inferences.

It can be seen from Fig. 4(a) that ‘forest’ sites tend to group in relation to environmental variables, whereas ‘cleared’ areas were more scattered in the ordination. The clearing process in forests does not appear to cause a uniform single-directional shift in environmental parameters (Fig. 4(a)). F3 did not cluster with other ‘forest’ sites, whereas C3 clustered with ‘forest’ sites. Inspection of the environmental data show F3 has the lowest shrub density and highest dead wood of all ‘forest’ sites, whereas C3 has highest shrub cover and tree density of all the ‘cleared’ sites. Time since clearing and type of clearance did not appear to separate the sites by their environmental variables.

Lizard species community composition also appeared to cluster in NMS ordination (Fig. 4(b)). C3 again showed similarities with a distinct ‘forest’ cluster and ‘cleared’ areas appeared to cluster with the exception of an outlier C4. This is the oldest ‘cleared’ site and possesses the lowest number of individuals and species recorded. Similarities in small mammal communities in relation to habitat were less evident in the ordination analysis (Fig. 4(c)). Overall there was an axis-two separation in

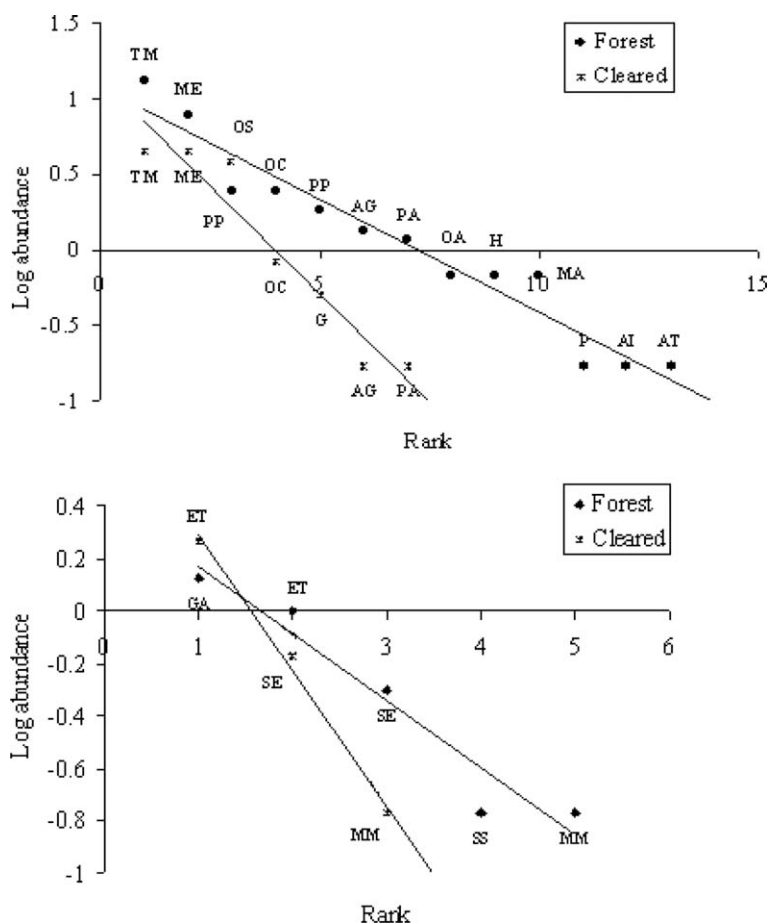
the data above and below axis-one, although F4 appeared to be more closely associated with ‘cleared’ areas, having an identical community composition as C4. Again, time since clearing and type of clearance did not appear to be separating the sites in the small mammal NMS ordination.

NMS revealed bird community composition was similar between forest sites with forest sites clumping in the ordination in comparison to the cleared sites which were widely scattered in the ordination. The site most recently cleared (<1 year old) was closest to forest sites in terms of community composition. C4 and C6 were positioned close together. A 2 year old site (with some trees remaining) was close in term of community composition with an old site (60 years) with no trees present, indicating that factors other than age and remaining tree cover, may be determining bird community composition.

Bird species richness was similar in ‘forest’ and ‘cleared’ habitats. Nineteen species appeared habitat specific and were recorded in either ‘forest’ or ‘cleared’ areas (Table 5). Bird species ranks (based on presence and abundance) were normally distributed and showed no correlation between ‘forest’ and ‘cleared’ habitats ( $r = -0.160$ ,  $n = 44$ ,  $p = 0.30$ ), indicating marked shifts in communities.

### 3.3. Species sensitivity to forest clearance

Overall our analysis showed that forest clearance does have a marked effect on community composition and species richness, although the response varied (Tables 3–5). Lizard (50%



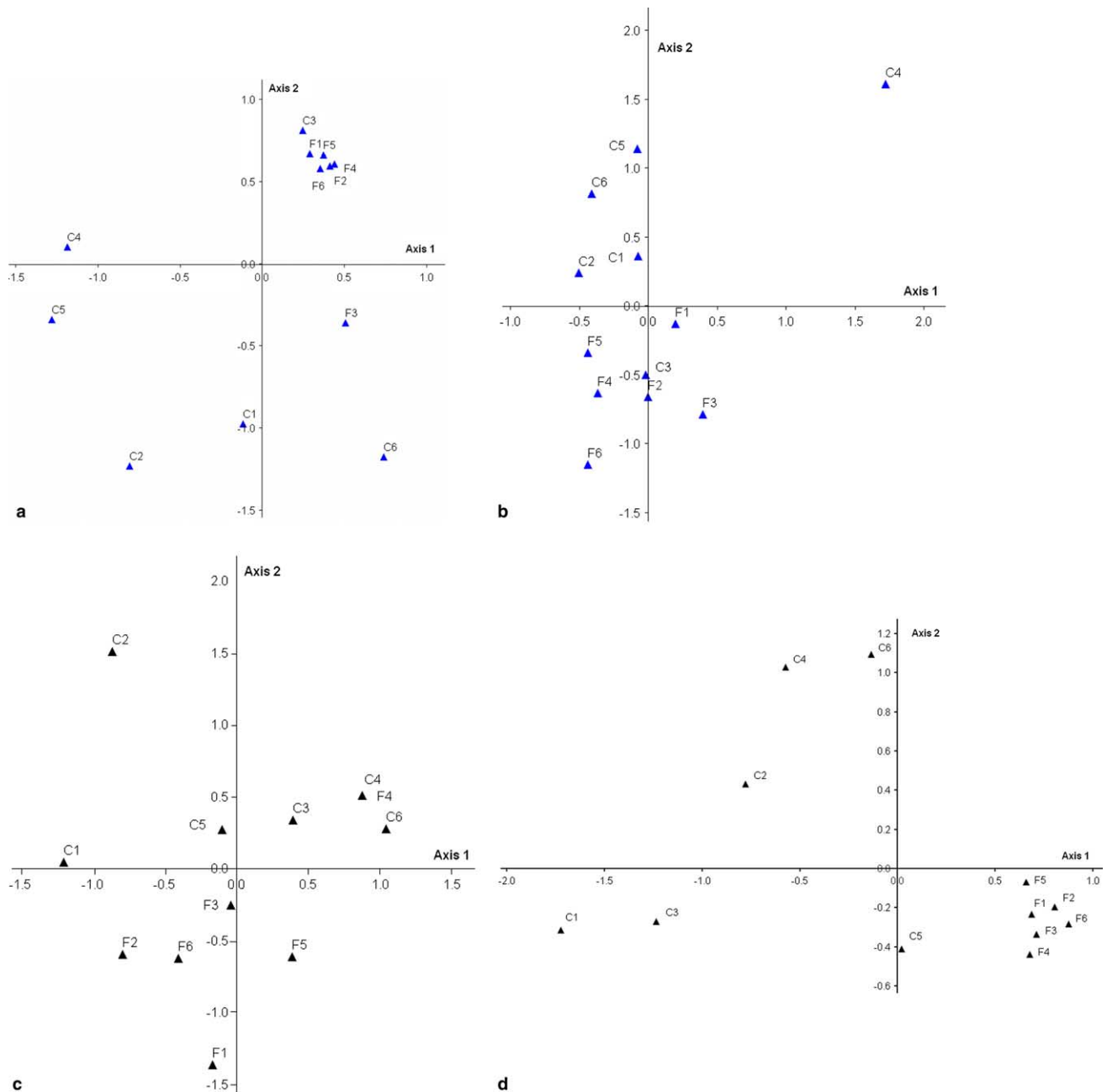
**Fig. 3** – Rank abundance curves in ‘forest’ and ‘cleared’ habitats for (a) lizards and (b) small mammals. Plotted lines are linear trend-lines and abbreviations are species names (see Tables 3 and 4).

decline) and small mammal (40% decline) species richness had the greatest overall negative response to clearing compared to birds (26%). For reptiles, both arboreal and ground species demonstrated positive and negative responses to forest clearance (Table 3). In the small mammal community, two of the three species of endemic tenrecs were not found in ‘cleared’ areas. However, the third tenrec, *Echinops telfairi*, showed a positive response to clearing and was nearly twice as abundant in ‘cleared’ areas compared to ‘forested’ areas. Eleven species of birds were classified as ‘forest species’ as they were not found in ‘cleared’ areas, of these 11, six are classified as dry or spiny forest specialists (Table 5). Species were listed in order of ‘sensitivity to clearing’ based on rank shift (%). This was calculated as the change in abundance rank from ‘forest’ to ‘cleared’ areas expressed as a percentage of the overall number of ranks. Three species showed a large negative rank shift (>40%) in ‘cleared’ habitats: *Newtonia brunneicauda*, *Centropus toulou* and *Copsychus albospectularis*. Eight bird species were only present in ‘cleared’ areas and an additional three species showed a relatively strong positive increase in abundance in ‘cleared’ habitats (>40% rank shift); *Agapornis canus*, *Leptopterus chabert*, *Foudia madagascariensis*. Of the eight species found only in ‘cleared’ areas, three were open area specialists; *Milvus aegyptius*, *Pterocles personatus*, and *Merops superciliosus*, and one was introduced species, *Acri-*

*dothores tristis*. Nineteen species were ‘ubiquitous’ (Watson et al., 2004a) as they were found in both ‘forest’ and ‘cleared’ areas and did not show a marked response to clearing.

#### 3.4. Relationships between species and specific habitat variables

Tables 6 and 7 detail significant correlation coefficients between individual species and descriptors of habitat structure. It can be seen from the results that 36% of lizard species surveyed showed a positive correlation with one or more features. Not all species demonstrating a negative association with clearing showed relationships with a specific habitat variable. There was no one variable that was correlated with all species, although it was evident that increased tree and shrub cover was positively correlated with four species. Rock cover, dead wood cover, fallen logs and termite mounds were also important for several species. The number of termite mounds was significantly correlated with the abundance of the small mammal *Geogale aurita*. No other small mammals showed relationships with habitat variables. It is clear from Table 7 that habitat structure is also important for many bird species. Shrub and/or tree cover was significantly positively correlated with 17 bird species, all of which were classified as ‘forest’ species and showed a negative association with cleared areas. The avail-



**Fig. 4 – Two-dimensional non-metric multidimensional scaling ordination diagrams to show the relationship between ‘forest’ and ‘cleared’ areas in relation to: (a) environmental variables; (b) lizard communities; (c) small mammal communities; (d) bird communities.**

ability of termite mounds, and (to a much lesser extent) litter cover also appeared to be important to some species of bird.

## 4. Discussion

### 4.1. Changes in habitat structure and complexity

Overall, forest clearance reduces the complexity of habitat structure, reducing the availability of three-dimensional

structure, resources and niches especially within the canopy and shrub layers, but also rock and litter layers. Changes in canopy cover will affect environmental conditions of the site, which consequentially influence the under-storey vegetation structure and composition (Saunders et al., 1991). In our study, forest and cleared sites had similar under-storey cover, which may be due to sparse herbaceous cover (<10%) of the forest floor. The forest edge left bordering ‘cleared’ patches will be subject to different environmental effects compared to core forest, which can effect community composition (Watson et al., 2004a,b). Habitat disturbance can aid the establish-

**Table 6 – Correlation coefficients between lizard and small mammal species and descriptors of habitat structure, where \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.0001**

Species	Environmental variable						
	Tree cover %	Shrub cover %	Litter cover %	Rock cover%	Dead wood %	# Termite mounds	# Fallen logs
Lizards							
<i>Geckolepis</i> sp.			–0.585*				
<i>Mabuya aureopunctata</i>		0.768**					
<i>Mabuya gravenhorstii</i> <sup>a</sup>		0.641*					
<i>Oplurus cyclurus</i> <sup>a</sup>						0.739**	0.728**
<i>Pareodura androyensis</i> <sup>a</sup>	0.707*			0.590*			
<i>Tracheloptychus madagascariensis</i> <sup>a</sup>	0.695*	0.631**			0.595*		
Mammals							
<i>Geogale aurita</i> <sup>a</sup>						0.792**	

Pearson product correlations denoted by <sup>a</sup>, all other correlations were Spearman rank.

**Table 7 – Correlation coefficients between bird species and descriptors of habitat structure, where \* P < 0.05, \*\* P < 0.01, \*\*\*P < 0.0001**

Species	Environmental variable			
	Tree cover %	Shrub cover %	Litter cover %	# Termite mounds
<i>Centropus toulou</i> <sup>a</sup>		0.639*	0.806**	
<i>Copsychus albospectularis</i> <sup>a</sup>	0.827**	0.741**		0.643*
<i>Coracopsis nigra</i>	0.636*			
<i>Coua cristata</i> <sup>a</sup>	0.775**		0.795**	
<i>Coua cursor</i> <sup>a</sup>		0.806**		0.639 <sup>a</sup>
<i>Coua olivaceiceps</i> <sup>a</sup>		0.864***		0.609*
<i>Cuculus rochii</i> <sup>a</sup>	0.837***	0.884***		0.594*
<i>Dicrurus forficatus</i> <sup>a</sup>	0.593*	0.723**		
<i>Falco newtoni</i>				–0.591*
<i>Foudia madagascariensis</i>				–0.630*
<i>Falcula palliata</i>	0.649*	0.663*		
<i>Hypsipetes madagascariensis</i>	0.627*	0.634*		
<i>Nectarinia souimanga</i>	0.598*	0.617*		
<i>Neomixis striatigula</i>	0.743**	0.756**		
<i>Newtonia archboldi</i>	0.815**	0.671*		0.750**
<i>Newtonia brunneicauda</i> <sup>a</sup>	0.908***	0.866**		0.674*
<i>Terpsiphone mutata</i> <sup>a</sup>		0.581*	0.585*	
<i>Vanga curvirostris</i> <sup>a</sup>		0.621*		
<i>Xenopirostris xenopirostris</i> <sup>a</sup>		0.609*		0.864***

Pearson Product correlations denoted by <sup>a</sup>, all other correlations were Spearman rank.

ment of non-native plants, which may lead to additional changes in abiotic conditions and biotic interactions (Brown and Gurevitch, 2004).

#### 4.2. Effects of clearing on species richness and community composition

Previous studies in Madagascar have shown that species richness declines in response to forest clearance (Stephenson, 1993; Smith et al., 1997; Watson et al., 2004a,b). We hypothesized spiny forest clearance would have a detrimental effect on species richness. Within the limitations of our study, we can accept this hypothesis statistically for lizards, but our bird and small mammal data showed similar species richness in both ‘forest’ and ‘cleared’ areas, however species composition and relative abundance varied between the two habitat types.

These results allow us to support our caveat that the impact of clearance is species-specific and not all communities respond in the same way. Watson et al. (2004a) in tropical coastal Malagasy forests also reported species-specific responses to forest fragmentation for birds and Lehtinen et al. (2003) demonstrated this response within herpetofauna.

#### 4.3. Reptile community shift

Lizard species richness and abundance was significantly lower in ‘cleared’ areas, with only 41% of the ‘forest’ diversity recorded. This shift in lizard species occurrence suggests that this group may be the most sensitive to habitat modification, which has previously been noted in highland forests of Madagascar by Vallan (2003). Community shift may be a result of direct mortality during clearing, or possibly a reduction in

available niches, as the structural complexity of the habitat is reduced so is the availability of perch sites, shelter and protection from adverse conditions (Bauer, 2003), refuges from predators, reproductive sites (Meier, 1993) and food resources. Several ground dwelling (*Mabuya* spp.), rock dwelling (*Oplurus* spp.) and arboreal species (*Phelsuma* spp., *Oplurus cyclurus*) were absent in cleared areas. Termite mounds and dead wood may be important in supporting food sources, whereas rock cover, leaf litter and fallen logs may also provide essential camouflage, microclimate and microhabitats (Henkel and Schmidt, 2000). Increase in ground temperature and radiation due to removal of canopy cover and litter depth may also affect thermal regimes important in determining distribution, dispersal, activity patterns, nesting sites and the demography of reptiles (Shine et al., 2002). Reduced resources, cover and protection would also influence biotic interactions, resulting in increased inter and intra specific competition and increase susceptibility to predation.

The only species to show an increase in abundance in 'cleared' areas was the nocturnal, terrestrial *P. pictus*, which prefers open sandy substrate (Henkel and Schmidt, 2000). Some *Geckolepis* sp. are widely distributed and adaptable to urban environments (Henkel and Schmidt, 2000) which may account for this species being found only in cleared areas, albeit in low abundance. *Mabuya elegans* is a widely distributed generalist, which may explain its occurrence in both habitats.

The two methods used to survey reptiles produced different results. Pitfall buckets were less successful at recording arboreal (*O. cyclurus*) or rock dwelling species (*O. saxicola*) than ground dwelling species (*P. pictus*). Reptile species composition from our study was similar to that recorded in southeastern forest habitats of parcel 2 of the Andohahela National Park (Nussbaum et al., 1999) and in Malahelo Forest (Ramamanjato et al., 2002). However, to provide more comprehensive evaluation of species composition and abundance further methods could be employed, for example, night searches, canopy traps and cover boards (O'Shea, 1992). Not all reptile genera could be identified to the species level, therefore species diversity is likely to be an under-estimate and further survey work on each group is required to provide a comprehensive species inventory.

#### 4.4. Small mammal community shift

Small mammal species richness did not differ significantly between 'forest' and 'cleared' areas, however this was possibly due to the overall low number of species recorded. Whilst most species showed similar abundance levels in 'cleared' and 'forested' areas, two species of tenrec showed distinct differences. The endemic *Geogale aurita*, found almost exclusively in spiny forest (Garbutt, 1999), was not recorded in cleared areas (Table 3). This species is nocturnal and terrestrial, resting during the day inside fallen dead logs (Stephenson, 2003). It is strictly insectivorous with a preference for termites and ants (Nicoll and Rathbun, 1990; Stephenson et al., 1994). This species showed a positive correlation with availability of termite mounds (Table 6) and the loss of termites as a result of clearing, along with a reduction in potential resting sites, may be the cause of loss of this species. In contrast, *Echinops telfairi* was positively associated with clear-

ing, which may be a consequence of competitive release or an increase in availability of alternative food resources. This species is more generalist in diet than *G. aurita*, although it is also restricted in range to dry deciduous, gallery and spiny forest (Garbutt, 1999). To enable us to investigate these hypotheses, dietary habits and resource availability within 'cleared' and 'forested' areas would need to be assessed in detail as current information is limited (Soarimalala and Goodman, 2003). *Setifer setosus* a nocturnal, predominantly ground dwelling omnivore found throughout Madagascar was only trapped once in a 'forested' area, therefore we cannot draw conclusions on its sensitivity to forest clearance. *Suncus madagascariensis* and *Mus musculus* had similarly low capture rates in both 'forest' and 'cleared' areas. Both species are widely distributed having a wide habitat tolerance (Garbutt, 1999).

Small mammal capture rates in this study were lower than studies in other forest habitats (Stephenson et al., 1994; Goodman and Rakotondravony, 2000), but similar to those undertaken in spiny forest (Goodman, 1999). Low recapture rates suggest longer trapping periods would be required to draw substantial conclusions (Goodman, pers. commun.). Several species of spiny forest small mammals were not trapped during our surveys, including the arboreal *Eliurus myoxinus* and *Macrotarsomys bastardi* (Goodman, 1999). This suggests a wider range of survey methods, (e.g., arboreal or hair tube traps) may be required to further assess community composition. Whilst surveying the spiny forest of Andohahela N.P., Goodman (1999) recorded *Rattus rattus* and *Rattus norvegicus*. These introduced species are of conservation concern as it is suggested that they may be replacing the endemic Nesomyinae rodents (Goodman, 1995).

#### 4.5. Bird community shift

The bird community showed significant changes following land clearance. Forest species were predominantly positively correlated with tree and shrub cover. This was consistent with previous findings by Watson et al. (2004a) who demonstrated vegetation structure, especially canopy cover, was one of the primary driving forces behind community shifts in littoral forests in Madagascar. Though the avifauna of both 'cleared' and 'forest' areas in our study was dominated by Malagasy endemics none of the spiny forest endemic species were recorded using 'cleared' areas. As with other taxonomic groups, loss of habitat structure and complexity from tree and shrub removal, along with the resources associated with them, is suggested to be the primary cause of species loss. Arboreal insectivorous birds, which gain their food by leaf gleaning (e.g., *Newtonia* spp. and *Neomixis* spp.), were distinctly scarcer or absent in 'cleared' areas. This may be a result of the loss in canopy cover but also the loss in prey availability. Species which hunt for concealed insects under bark, dead twigs or detritus, e.g., *Xenopirostris xenopirostris* (Yamagishi and Eguchi, 1996), were also affected by forest clearance. Bird species that either showed a large negative response to clearing or were exclusive to 'forest' were generally canopy dwellers (e.g., *Cuculus rochii* and *Coracopsis nigra*), species which require dense vegetation cover (e.g., *Centropus toulou*), or arboreal nesters. *Polyboroides radiatus* considered to be at low densities throughout its range (Thorstrom et al., 2003)

was absent from cleared areas, although it can often be seen moving between forest parcels (Goodman, pers. commun.). *Falco zoniventris* has a preference for forest edge habitats (Thorstrom et al., 2003) and was also only sighted in 'forest' habitats. Unexpectedly the typical woodland species, *Leptopterus chabert* had a higher occurrence in cleared areas than forest. This species is an aerial insectivore and was regularly sighted using cut tree stumps as vantage points for foraging. It has been indicated that this species is tolerant to forest disturbance being found in secondary re-growth and scrub (Morris and Hawkins, 1998). In our study site it appeared to take advantage of open areas and may be less susceptible to forest clearance in spiny forest than in other forest types.

Species which occurred in cleared areas included aerial feeders (e.g., *Merops superciliosus*), terrestrial granivores (e.g., *Oena capensis*), open area specialists (e.g., *Pterocles personatus*) and widespread generalist species (e.g., *Foudia madagascariensis*). Introduced generalists with wide habitat ranges also occurred in 'cleared' areas (e.g., *Acridotheres tristis* and *Milvus aegyptius*). *Falco newtoni* has been suggested to be one of the few raptors to benefit from deforestation (Thorstrom et al., 2003). Agricultural development also provides new resource opportunities: the nectarivorous *Nectarinia notata*, were observed to be regular visitors to the flowers of the introduced prickly pear, planted in the 'cleared' areas (pers. obs.).

#### 4.6. Sensitivity to forest clearance across various vertebrate groups

We found similar patterns in sensitivity in relation to forest clearance with previous studies. Vallan (2000), summarizing work in Madagascar noted that different vertebrate groups showed differing levels of sensitivity to forest fragmentation, with reptiles being more sensitive than lipotyphlans or birds. Goodman and Rakotondravony (2000) also working in Madagascar on the central high plateau, suggested that forest dwelling birds may be more sensitive to the effects of fragmentation and isolation than lipotyphlans. Forest clearance also influences other vertebrate groups. For amphibians, the main consequence of rain forest disturbance and anthropogenic change is a decrease in species number and individual density with loss in structural complexity and absence of water bodies (Vallan, 2000). Lemur species are reliant on canopy for food and shelter, Smith et al. (1997) found that lemur diversity in western dry deciduous forests of Madagascar was most strongly influenced by habitat clearing and human disturbance (harvesting, grazing and hunting). Andrianarimisa et al. (2000) noted that habitat fragmentation may also lead to genetic consequences within populations.

#### 4.7. Limitations to the study

Species composition of the theoretically protected spiny forest of Parcel 2 of the Andohahela National Park (Goodman, 1999) was similar to our study, although we found fewer plant species (64 compared to 85) and slightly higher species richness of reptiles (38 compared to 34). Our 'forest' sites were subjected to low-level exploitation and this may have resulted in a lower species richness and abundance compared to primary unexploited forests. However,

in dry deciduous forest, bird species richness and density did not significantly differ between un-logged and selectively logged forests (Hawkins and Wilmé, 1996). The timing of the survey period will affect the recorded species richness and abundance (Stephenson, 1994a). Small mammal presence and abundance will vary seasonally (Eisenberg and Gould, 1970; Stephenson, 1994a,b), therefore seasonal replication should also be considered. Our sample size is relatively low and geographically restricted. To provide more accurate estimates of relative abundance and to enable generalisations of vertebrate responses to spiny forest clearance, more spatial and temporal replicates over a larger geographic area are recommended. Additionally spatial independence for all groups cannot be assumed, 500 m may be adequate distance to independently sample lizards and some of the small mammals with small home ranges, but is probably insufficient for many bird species. Hence, it is also recommended that future studies also attempt to ensure spatial independence between replicates. The size of the 'cleared' area and the size of the remnant forest patch will affect the remaining species composition (Ramanamanjato and Ganzhorn, 2001; Watson et al., 2004b). On the central high plateau of Madagascar, Goodman and Rakotondravony (2000) showed that lipotyphlan species richness declined progressively with diminishing forest patch size and suggested that this was related to the ability of species to disperse across open areas. Langrand and Wilmé (1997) showed a negative relationship between forest size and bird species diversity and Ganzhorn et al. (2000) demonstrated the number of both lipotyphlan and amphibian species declined with declining forest fragment size. Studies which address patch size, species dispersal ability and habitat hospitability would provide further insights into the responses to forest clearance.

#### 4.8. Implications for conservation

Clearing in the form of slash and burn agriculture is a potential threat to the conservation of many endemic spiny forest species. It appears that species first to suffer from forest clearance are also those of conservation priority due to their restricted geographic distribution within Madagascar. Forest clearance caused communities to shift from one unique to the Southern Domain to one with more prevalence of generalist, widespread or introduced species, typical of degraded land. 'Cleared' areas had fewer endemic spiny forest specialists, and if present, their relative abundance tended to be lower than in forest habitats. This pattern was seen across all taxonomic groups studied, to different extents. Of the three lizards which showed a significant decline in abundance as a result of clearing, two were spiny forest specialists. The only small mammal showing a significant decline in abundance was also a spiny forest specialist and of the 11 bird species only found in forested sites, six were spiny forest specialists. In contrast, species which are wide ranging, flexible in diet and habitat use, and with a high dispersal ability will be more effective at persisting in degraded forests. Identifying general trends in the characteristic of species and of habitats that are more sensitive and susceptible to anthropogenic habitat modification is essen-

tial to target and prioritise effective conservation efforts. However, in many cases, such as in our study, these patterns are difficult to identify due to the lack of basic ecological data on the species and habitats in question.

In low-level utilised forest, outside protected areas, endemic species can still persist, with species diversity in our study being similar to the theoretically protected areas (Goodman, 1999). In this paper, we have shown that forest clearance has a detrimental effect on spiny forest specialists, predominantly as a result of loss of canopy cover, three-dimensional forest structure, niches and food resources. Our data identifies which species may be lost as a result of deforestation and also species that may become more vulnerable in future as a result of population decline in response to deforestation. Conservation of species outside protected areas will rely on activities of local people. Clearly it is important for local villages to be informed of the impacts of clearance on forest species and for all stakeholders to encourage implementation of appropriate clearance practices to minimise species loss. One potential way to mitigate the impacts is to retain some canopy cover. Remaining canopy cover may be suitable when employing cattle grazing but may result in economic loss by potentially reducing agricultural yields or increasing harvesting time. Canopy cover could be improved in utilised areas by increasing the number of trees remaining within the cleared plot, reducing plot size, allowing re-growth in the form of rotation and/or considering the heterogeneity of the surrounding landscape. However it is not known to what extent this needs to be implemented to be effective. Further studies need to be undertaken on the impacts of the size of area cleared, time since clearing, type of clearing, regeneration time and the surrounding landscape mosaic. Ideally experiments should be conducted in which species presence and abundance is assessed pre-, during and post-clearance and followed for many years to look at the direct, short and long term effects of clearance.

### Acknowledgements

The research was funded by B.P. Conservation Program, The Royal Geographical Society (with I.B.G.), University of East Anglia, University of Brighton, Rio Tinto PLC, Gilchrist Educational Trust, Adrian Ashby-Smith Memorial Fund, Albert Reckitt Charitable Trust and Lindeth Charitable Trust. We thank the following for their support and advice in country, Barry Ferguson, The Tandroy Conservation Trust, Sylvain Eboroke, Libanona Ecology Centre, Parc Botanique et Zoologique de Tsimbazaza, Tulear University, Daniel Rakotonravony, Mark Fenn, Mily Velomila, Fabien Génin, Frank Hawkins and Martin Nicoll. Special thanks to Steve Goodman for his encouragement and insightful comments on the manuscript. We are grateful to Daniel Metcalfe and Steve Waite who provided guidance on early manuscripts and two anonymous referees for comments. Finally, thanks to Arsene Indriambelo, Felicien Rafazantsoa and Meta Saroy for field assistance, and all the Bevia community for their support.

### REFERENCES

- Andrianarimisa, A., Bachmann, L., Ganzhorn, J.U., Goodman, S.M., Tomiuk, J., 2000. Effects of forest fragmentation on genetic variation in endemic understory forest birds in Central Madagascar. *Journal für Ornithologie* 141, 152–159.
- Barnett, A., Dutton, J., 1995. Expedition Field Techniques: Small Mammals. Expedition Advisory Centre. Royal Geographical Society with IBG, London.
- Bauer, A.M., 2003. Gekkonidae, Geckos. In: Goodman, S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 973–978.
- Bennett, D., 1999. Expedition Field Techniques: Reptiles and Amphibians. Expedition Advisory Centre, Royal Geographical Society with IBG, London.
- Benstead, J.P., Douglas, M.M., Pringle, C.M., 2003. Relationships of stream invertebrate communities to deforestation in eastern Madagascar. *Ecological Applications* 13 (5), 1473–1490.
- Bibby, C., Jones, M., Marsden, S., 1998. Expedition Field Techniques: Bird Surveys. Expedition Advisory centre, RGS, London.
- Birdlife International, 2000. *Threatened Birds of the World*, Lynx Edicions and Birdlife International, Barcelona and Cambridge, UK.
- Brown, K.A., Gurevitch, J., 2004. Long-term impacts of logging on forest diversity in Madagascar. *Proceedings of the National Academy of Sciences (USA)* 101 (16), 6045–6049.
- Cadotte, M.W., Franck, R., Reza, L., Lovett-Doust, J., 2002. Tree and shrub diversity and abundance in fragmented littoral forest of southeastern Madagascar. *Biodiversity and Conservation* 11 (8), 1417–1436.
- Casse, T., Milhoj, A., Ranaivoson, S., Randriamanarivo, J.R., 2004. Causes of deforestation in southwestern Madagascar: what do we know? *Forest Policy and Economics* 6 (1), 33–48.
- Donque, G., 1972. The climatology of Madagascar. In: Battistini, R., Richard-Vindard, G. (Eds.), *Biogeography and Ecology of Madagascar*. Dr. W. Junk B.V., Publishers, The Hague, pp. 87–143.
- Dytham, C., 1999. *Choosing and Using Statistics: A Biologists Guide*. Blackwell Science Ltd., Oxford, UK.
- Dufils, J.-M., 2003. Remaining forest cover. In: Goodman, S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 88–96.
- Du Puy, D.J., Moat, J., 1998. Vegetation mapping and classification in Madagascar, using GIS: implications and recommendations for the conservation of biodiversity. In: Huxley, C.R., Lovelock, M.J., Cutler, D.F. (Eds.), *Chorology, Taxonomy and Ecology of the Floras of Africa and Madagascar*. Royal Botanic Gardens, Kew, pp. 97–117.
- Eisenberg, J.F., Gould, E., 1970. The tenrecs: a study in mammalian behaviour and evolution. *Smithsonian Contributions to Zoology* 27, 1–137.
- Fenn, M., 2003. Learning conservation strategies: a case study of the Parc National d'Andohahela. In: Goodman, S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 1494–1501.
- Ganzhorn, J.U., Goodman, S.M., Ramanamanjato, J.-B., Rakotonravony, D., Rakotosamimanana, B., Vallan, D., 2000. Vertebrate species in fragmented littoral forests of Madagascar. In: Lourenco, W.R., Goodman, S.M. (Eds.), *Mémoires de la Société de Biogéographie*, Paris, pp. 155–164.
- Ganzhorn, J.B., Lowry, P.P., Schatz, G.E., Sommer, S., 2001. The biodiversity of Madagascar: one of the world's hottest hotspots on its way out. *Oryx* 35, 346–348.
- Ganzhorn, J.U., Goodman, S.M., Dehgan, A., 2003. Effects of forest fragmentation on small mammals and lemurs. In: Goodman,

- S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 1228–1235.
- Garbutt, N., 1999. *The Mammals of Madagascar*. Pica Press, Sussex.
- Gautier, L., Goodman, S.M., 2003. Introduction to the flora of Madagascar. In: Goodman, S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 229–250.
- Glaw, F., Vences, M., 1994. *A Field Guide to the Amphibians and Reptiles of Madagascar*. Verlags, Köln.
- Goodman, S.M., 1993. A reconnaissance of Ile Sainte-Marie, Madagascar – The status of the forest, avifauna, lemurs and fruit bats. *Biological Conservation* 65 (3), 205–212.
- Goodman, S.M., 1995. *Rattus* on Madagascar and the dilemma of protecting endemic rodent fauna. *Conservation Biology* 9 (2), 450–453.
- Goodman, S.M., 1999. A flora and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, with reference to elevational variation. *Fieldiana: Zoology*, new series, No. 94.
- Goodman, S.M., Rakotondravony, D., 2000. The effects of forest fragmentation and isolation on insectivorous small mammals (Lipotyphla) on the Central High Plateau of Madagascar. *Journal of Zoology* 250, 193–200.
- Goodman, S.M., Benstead, J.P., 2003. *The Natural History of Madagascar*. The University of Chicago Press.
- Goodman, S.M., Raherilalao, M.J., 2003. Effects of forest fragmentation on bird communities. In: Goodman, S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 1064–1067.
- Goodman, S.M., Pigeon, M., Hawkins, A.F.A., Schulenberg, T.S., 1997. The birds of southeastern Madagascar. *Fieldiana Zoology*, new series, No. 87, 1–132.
- Green, G.M., Sussman, R.W., 1990. Deforestation history of the eastern rainforests of Madagascar. *Science* 248, 212–215.
- Gurnell, J., Flowerdew, J.R., 1990. Live trapping small mammals: a practical guide. *Mammal Society Occasional Publication* No. 3.
- Hawkins, A.F.A., Wilmé, L., 1996. Effects of logging on forest birds. In Ganzhorn, J.U., and Sorg, J.-P. (Eds.), *Ecology and Economy of a Topical Dry Forest in Madagascar*, pp. 203–213. *Primate Report*, special Issue 46(1), 1–382.
- Hawkins, A.F.A., Chapman, P., Ganzhorn, J.U., Bloxam, Q.M.C., Barlow, S.C., Tonge, S.J., 1990. Vertebrate conservation in Ankarana Special Reserve, Northern Madagascar. *Biological Conservation* 54 (2), 83–110.
- Henkel, F.W., Schmidt, W., 2000. *Amphibians and Reptiles of Madagascar and the Mascarene, Seychelles and Comoro Islands*. Krieger Publishing Company, Florida.
- Ingram, J.C., Dawson, T.P., 2005. Inter-annual analysis of deforestation hotspots in Madagascar from high temporal resolution satellite observations. *International Journal of Remote Sensing* 26 (7), 1447–1461.
- IUCN, 2003. 2003 IUCN Red List of Threatened Species. <[www.redlist.org](http://www.redlist.org)> (accessed 8.08.2004).
- Jolly, A., Jolly, R., 1984. Malagasy economics and conservation: a tragedy without villains. In: Jolly, A., Oberlé, P., Albignac, R. (Eds.), *Key Environments: Madagascar*. Pergamon Press, Oxford.
- Kent, M., Coker, P., 1992. *Vegetation Description and Analysis: A Practical Approach*. Belhaven Press, London.
- Kruskal, J.B., 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29, 1–27.
- Kull, C.A., 2002. Madagascar's burning issue: The persistent conflict over fire. *Environment* 44 (3), 8–19.
- Langrand, O., Wilmé, L., 1997. Effects of forest fragmentation on extinction patterns of the endemic avifauna on the Central High Plateau of Madagascar. In: Goodman, S.M., Patterson, B.D. (Eds.), *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington and London, pp. 280–305.
- Lehtinen, R.M., Ramanamanjato, J.B., Raveloarison, J.G., 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar. *Biodiversity and Conservation* 12 (7), 1357–1370.
- Mather, P.M., 1976. *Computational Methods of Multivariate Analysis in Physical Geography*. J. Wiley and Sons, London. 532pp.
- McCune, B., Grace, J., 2002. *Analysis of Ecological Communities*. MjM Software Design, USA.
- Meier, H., 1993. Neues über einige Taxa der Gattung *Phelsuma* auf Madagascar, mit Beschreibung zweier neuer Formen. *Salamandra* 29, 119–132.
- Morris, P., Hawkins, F., 1998. *Birds of Madagascar: A photographic Guide*. Pica Press, Robertsbridge, East Sussex.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403 (6772), 853–858.
- Nicoll, M.E., Rathbun, G.B., 1990. African Insectivora and Elephant Shrews: An Action Plan for Their Conservation. Gland, IUCN.
- Nussbaum, R.A., Raxworthy, C.J., Raselimanana, A.P., Ramanamanjato, J.B., 1999. Amphibians and reptiles of the reserve naturelle integrale d'Andohahela, Madagascar. *Fieldiana* 94, 155–173.
- O' Shea, M., 1992. *Reptiles and Amphibians: Expedition and Techniques Expedition Advisory Centre*. Royal Geographical Society, London.
- Philipson, P.B., 1996. Endemism and non-endemism in the flora of Southwestern Madagascar. In: Lourenco, W.R. (Ed.), *Biogeographie de Madagascar*. Paris Editions, ORSTOM, pp. 125–136.
- Primack, R.B., 2004. *A Primer for Conservation Biology*, third ed. Sinauer Associates Inc., Massachusetts, USA.
- Ramanamanjato, J.-B., Ganzhorn, J.U., 2001. Effects of forest fragmentation, introduced *Rattus rattus* and the role of exotic tree plantations and secondary vegetation for the conservation of an endemic rodent and a small lemur in littoral forests of southeastern Madagascar. *Animal Conservation* 4, 175–183.
- Ramanamanjato, J.-B., McIntyre, P.B., Nussbaum, R.A., 2002. Reptile, amphibian and lemur diversity of the Malahelo Forest, a biogeographical transition zone in southeastern Madagascar. *Biodiversity and Conservation* 11, 1791–1807.
- Raxworthy, C.J., Nussbaum, R.A., 1994. A rain-forest survey of amphibians, reptiles and small mammals at Montagne d'Ambre Madagascar. *Biological Conservation* 69 (1), 65–73.
- Rhind, S.G., 2004. Direct impacts of logging and forest management on the bush-tailed phascogale *Phascogale tapoatafa* and other arboreal marsupials in a jarrah forest in Western Australia. In: Lunney, D. (Ed.), *Conservation of Australia's Forest Fauna*. Royal Zoological Society of New South Wales, Sydney, pp. 639–655.
- Ryan, T.J., Philippi, T., Leiden, Y.A., Dorcas, M.E., Bently Wigely, T., Whitfield Gibbons, J., 2002. Monitoring herpetofauna in a managed forest landscape: effects of habitat types and census techniques. *Forest Ecology and Management* 167, 83–90.
- Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5, 18–32.
- Scott, D.M., Dunstone, N., 2000. Environmental determinants of desert-living rodent community structure in the north-east Badia region of Jordan. *Journal of Zoology* 251, 481–494.
- Shine, R., Barrott, E.G., Elphik, M.J., 2002. Some like it hot: effects of forest clearing on nest temperatures of montane reptiles. *Ecology* 83 (10), 2808–2815.
- Sinclair, I., Langrand, O., 1998. *Birds of the Indian Ocean Islands*. Struik Publishers Ltd.
- Smith, A.P., Horning, N., Moore, D., 1997. Regional biodiversity planning and lemur conservation with GIS in western Madagascar. *Conservation Biology* 11 (2), 498–512.

- Soarimalala, V., Goodman, S.M., 2003. The food habits of Lipotyphla. In: Goodman, S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 1203–1205.
- Stattersfield, A.J., Crosby, M.J., Long, A.J., Wege, D.C., 1988. *Endemic Bird Areas of the World: Priorities for Biodiversity Conservation*. BirdLife Conservation Series, 7. BirdLife International.
- Stephenson, P.J., 1993. The small mammal fauna of Reserve Speciale d'Analamazaotra, Madagascar – The effects of human disturbance on endemic species diversity. *Biodiversity and Conservation* 2 (6), 603–615.
- Stephenson, P.J., 1994a. Seasonality effects on small mammal trap success in Madagascar. *Journal of Tropical Ecology* 10, 439–444.
- Stephenson, P.J., 1994b. Small mammal species richness in a Madagascar rain forest. *African Journal of Ecology* 32 (3), 255–258.
- Stephenson, P.J., Randriamahazo, H., Rakotoarison, N., Racey, P.A., 1994. Conservation of mammalian species diversity in Ambohitantely Special Reserve, Madagascar. *Biological Conservation* 69 (2), 213–218.
- Stephenson, P.J., 1995. Small mammal microhabitat use in lowland rain forest of north-east Madagascar. *Acta Theriologica* 40 (4), 425–438.
- Stephenson, P.J., 2003. *Geogale aurita*, large-eared Tenrec. In: Goodman, S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 1265–1267.
- Sutherland, W.J., 1996. *Ecological Census Techniques: A Handbook*. Cambridge University Press, Cambridge.
- Thorstrom, R., Rene de Roland, L.-A., Watson, R.T., 2003. Falconiformes and Strigiformes: ecology and status of raptors. In: Goodman, S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 1080–1085.
- Vallan, D., 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar. *Biological Conservation* 96, 31–43.
- Vallan, D., 2002. Effects of anthropogenic environmental changes on amphibian diversity in the rain forests of eastern Madagascar. *Journal of Tropical Ecology* 18, 725–742.
- Vallan, D., 2003. Consequences of rain forest fragmentation for herpetofauna: a case study from Ambohitantely. In: Goodman, S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 899–908.
- Waite, S., 2000. *Statistical Ecology in Practice: A guide to the Analysis of Environmental and Ecological Field Data*. Prentice Hall, 414 pp.
- Watson, J.E.M., Whittaker, R.J., Dawson, T.P., 2004a. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependant birds in tropical coastal forests in southeastern Madagascar. *Biological Conservation* 120 (3), 311–327.
- Watson, J.E.M., Whittaker, R.J., Dawson, T.P., 2004b. Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. *Journal of Biogeography* 31 (11), 1791–1807.
- Watson, J.E.M., Whittaker, R.J., Dawson, T.P., 2005. The importance of littoral forest remnants for indigenous bird conservation in southeastern Madagascar. *Biodiversity and Conservation* 14 (3), 523–545.
- Wells, N.A., 2003. Some hypotheses on the Mesozoic and Cenozoic paleoenvironmental history of Madagascar. In: Goodman, S.M., Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, pp. 16–34.
- Yamagishi, S., Eguchi, K., 1996. Comparative foraging ecology of Madagascar vangids (Vangidae). *Ibis* 138, 283–290.