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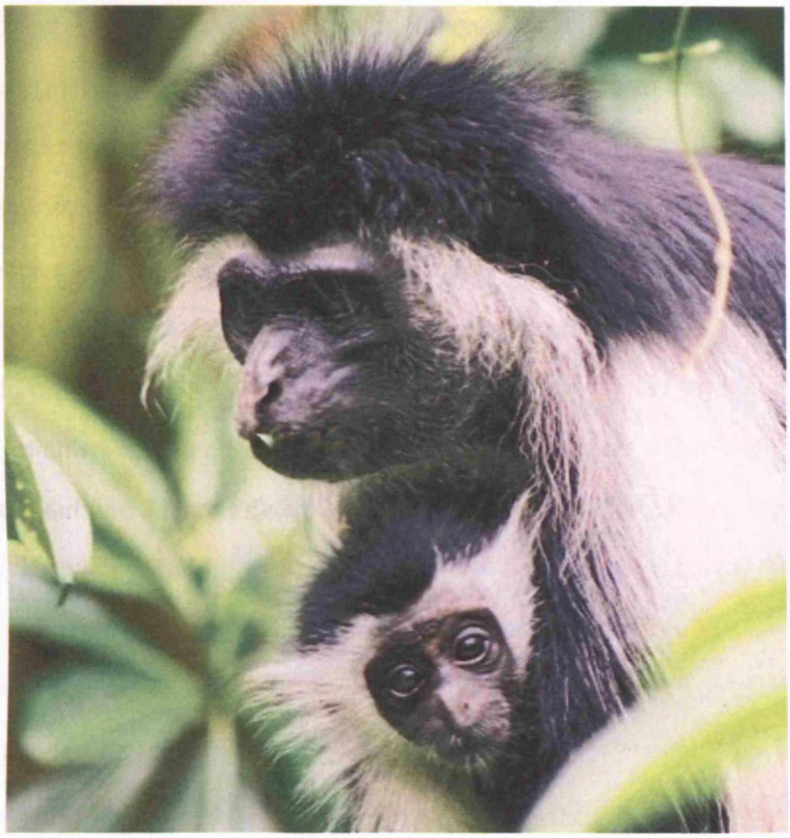
HABITAT FRAGMENTATION AND METAPOPULATION DYNAMICS OF THE ANGOLA BLACK-AND-WHITE COLOBUS (*Colobus angolensis palliatus*) IN COASTAL KENYA

by

Julie Anderson



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GIS has been the bane of my life for the last four years, and without the selfless support of the following people I'd still be lost: Sasha Yumakaev and the Society for Conservation GIS group, Betty Nzoika and Thomas Otieno at the Department of Remote Sensing and Resource Survey, Kenya; Dr. Graham Thackrah at UCL for the crash course in Remote Sensing; Rob Deville and Nick Isaac for sensing remote crashes.

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Finally, my husband Keith, I love him.

Abstract

This study investigates the effects of habitat fragmentation on an Angola black-and-white colobus (*Colobus angolensis palliatus*) metapopulation in southern Kenya. 124 coastal forest fragments were surveyed in 2001. Fifty-five *C. a. palliatus* populations were found during this survey, (44% habitat patch occupancy), with an estimated national population estimate of 3,100 – 5,000 individuals. Colobus occurrence and density in this forest network was significantly linked to the spatial characteristics and quality of habitat patches. The heterogeneous landscape between habitat patches (matrix) was also found to be important, providing additional foraging habitat and connectivity between forest patches. The use of a spatially explicit metapopulation model (the incidence function model) provided a conceptual framework in which to explore future scenarios of habitat change. *C. a. palliatus* metapopulation persistence was found to be dependent upon the five largest forests in the network. Many of the colobus populations inhabiting unprotected forests were found to be on critical limits of population extinction. Population occupancy was also affected by the degradation or enhancement of the surrounding matrix.

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1. Introduction

1.1 The human impact on tropical forests

Human modification of ecosystems is threatening biodiversity on a global scale (Chapman et al., 2003; Cowlishaw, 1999; Cuaron, 2000; Heywood, 1995; Mace & Balmford, 2000; WCMC, 1992). Continued rapid growth of the human population, combined with increasing per capita consumption of resources, has resulted in a global landscape dominated by agriculture, forest plantations, rangelands for livestock, and urban and suburban development (Soule & Orians, 2001). In the process of such large-scale, anthropogenic landscape change, tropical forests have been most severely hit. They are disappearing at a faster rate than any other biome on the planet (Myers, 1988, 1991, 1994), with tropical forest losses amounting to 142,000km^2 annually (FRA, 2000). The ecological impacts of such destruction on a geographic scale are not yet fully understood.

For wildlife communities inhabiting these regions, future population viability can be threatened directly, through human hunting for food, pets and artefacts (Bennett & Robinson, 2000; Cuaron, 2000; Robinson, Redford & Bennett, 1999), or indirectly, through the loss of native habitat. In some cases forest loss is an immediate and drastic event (i.e. outright conversion), but in others forest characteristics are altered gradually, resulting in (1) the reduction of forest area, (2) an increase in the number and isolation, i.e. 'fragmentation', of forest patches, and (3) the modification and degradation of the remaining forest areas (Cuaron, 2000; Fahrig, 2003; Fahrig & Merriam, 1994; Laurance & Vasceoncelos, 2004; Saunders, Hobbs & Margules, 1991). Through these processes, anthropogenic disturbance can alter the behaviour, ecology and population dynamics of forest-dependent species (Bierregaard *et al.*, 2001), resulting in the decline and potential extinction of their populations (Thomas & Kunin, 1999; Wiens, 1989; Wiens *et al.*, 1993b). It is therefore of key importance to identify, study, and understand these processes in order to eliminate or at least mitigate the negative effects of such forest disturbance.

Primates are one component of tropical forest ecosystems that are most threatened by habitat loss and fragmentation. Almost 90% of all worldwide primate species are found within this biome (Mittermeier & Cheney, 1987), and more than half of the 250 existing species are considered to be of conservation concern by the Primate Specialist Group of the World Conservation Union (IUCN). One in four is either Endangered or Critically Endangered in the IUCN Red List of Threatened Species and without better protection these species may be extinct in the next 20 years (IUCN, 2005; Mittermeier, 1996). Some of the most unusual threatened primate communities can be found surviving within highly fragmented forest habitat (Cowlishaw & Dunbar, 2000b; Marsh, 2003b). It is therefore important to understand the ecological flexibility or limits of such communities and species in order to implement effective management strategies for their future conservation (Cowlishaw & Dunbar, 2000b; Hacker, Cowlishaw & Williams, 1998; Harcourt, 1998; 2002; Harcourt & Parks, 2003; Lindenmayer, 1999).

When tackling the practical issue of how to protect species that are at risk from forest loss and fragmentation, there are critical gaps in our knowledge that still need to be addressed. Research priorities include:

1. The widening of tropical forest field studies from the individual patch-specific (population-specific) focus towards a greater understanding of regional, landscape-scale processes which encompass the geographical range of threatened taxon.

2. The development of novel ways to assess the future of fragmented forest landscapes that tackle not only their inherent biological processes, but also the dynamic interaction between these processes and the human populations that exist in them.

3. A more focused attempt at designing tropical forest field research which is both biologically meaningful to wildlife managers and easily synthesized into practical conservation measures.

Each of these priorities will now be discussed in relation to primate conservation.

1.1.1 The regional landscape scale

Traditionally, primate field research has focused on the behavioural ecology of species within protected areas (Chapman & Peres, 2001). Most forest fragments however, lie outside protected areas (Chapman & Peres, 2001; Marsh, 2003b) and vary greatly in the extent of fragment size, isolation and quality (Fahrig, 2003; Fahrig & Merriam, 1994). Wildlife managers need to be able to predict which species will survive in such fragments in order to identify which species are most threatened by habitat loss. Generalisations drawn from single-population studies, often in optimal habitat, may fail to identify critical resources within such fragments that are required for population persistence. Studies focusing on forest fragment comparisons would allow researchers to test the generality of the results obtained from one site (Chapman & Peres, 2001), whilst providing new insights into ecological processes operating at the *within-fragment* scale.

Knowledge of primate population-level processes may also benefit from analyses which incorporate the regional network of forest fragments and thus *between-fragment* processes (Davies, Gascon & Margules, 2001). Over the past two decades metapopulation ecology has provided a theoretical framework in which to explore such processes (Hanski, 1994b; Hanski & Gilpin, 1997; Levins, 1969b). Species survival at a regional 'metapopulation' scale can be viewed as the total number of populations persisting within a fragmented forest network over time. Within this network, discrete populations may persist, become extinct, or narrowly escape extinction through the 'rescue effect' of immigrating individuals from other forest fragments (Brown & Kodric-Brown, 1977). Previously extinct populations may also reappear through the re-colonization of empty habitat patches from the same dispersal process. In this theoretical approach, both the size and isolation of habitat patches, as well as the spatial distribution of existing populations in these patches, are critical to understanding future population dynamics (Hanski, 1994a, b; Hanski, Moilanen & Gyllenberg, 1996a; Hanski & Simberloff, 1997; Hanski & Gilpin, 1997). Metapopulation theory has focused ecological thinking towards the spatial, landscape level of both population processes and habitat management (Hanski & Simberloff, 1997; Hanski, 2004; Ovaskainen & Hanski, 2003b; Wiens, 1997), and may provide a useful framework in which to explore the relative importance of individual forest fragments in a conservation management context (Cabeza & Moilanen, 2003; Hanski & Simberloff, 1997; Hanski, 2004; Ovaskainen & Hanski, 2003b).

Furthermore, the nature of the matrix, i.e. the non-forest, land cover between forest fragments, can be important in determining the use of fragments by primates or other wildlife (e.g. Bonte *et al.*, 2003; Gascon *et al.*, 1999; Marsh, 2003b; Pardini *et al.*, 2005; Ricketts, 2001; Vandermeer & Carvajal, 2001; Wethered & Lawes, 2003). Some species readily move between forest patches, using habitat corridors, while others do not (Beier & Noss, 1998; Bennett, 1998; Laurance & Laurance, 1999; Laurance, 2004). Identifying which species can use corridors, or which existing matrix types are useful for inter-patch dispersal, will permit wildlife managers to predict future extinction rates in increasingly isolated forest fragments (Chapman & Peres, 2001) and to implement matrix enrichment schemes to buffer such negative effects (Fahrig & Merriam, 1994; Hess & Fischer, 2001; Laurance, 2004). The significance of matrix heterogeneity has yet to be incorporated into theoretical metapopulation models (Ricketts, 2001) and future model development could test the influence of the matrix on metapopulation dynamics and provide an additional degree of realism to model simulations (Ricketts, 2001; Vandermeer & Carvajal, 2001).

1.1.2 The future of forest fragments

To date, the human use of tropical forest landscapes and the resulting ecological impacts have largely been ignored by primatologists (Marsh *et al.*, 2003). In these landscapes, most fragments have no protection status, and forest structure and composition may change due to the land-use practices of local communities (Chapman *et al.*, 2003; Chapman & Peres, 2001; Cowlishaw & Dunbar, 2000b; Marsh *et al.*, 2003; Struhsaker, 1981b). Any analysis of population viability which assumes a static, unchanging environment does not provide a sufficient basis for practical species management (Balmford, Mace & Ginsberg, 1998a; Smith, Bruford & Wayne, 1993). Ecological research is required that integrates the effects of further deterioration of forest habitat and landscape change into future population projections. Within such modelling exercises, populations, habitat patches and regions that are particularly significant to long-term species survival may be identified

(Fahrig, 2001; Fahrig & Merriam, 1994; Janzen, 1986; Mace & Baillie, 2001; Wahlberg, Moilanen & Hanski, 1996)

1.1.3 The practicalities of conservation

Conservation biologists must do more than generate theories and principles. In effect, they must deliver effective, science-based information, decision-making tools and reliable monitoring programs for wildlife managers (Marsh *et al.*, 2003; Possingham *et al.*, 2001; Sutherland, 1998). It is currently recognised that most conservation practice is based upon anecdotal sources, with very little use of direct scientific evidence (Sutherland, 1998; Sutherland *et al.*, 2004). Similarly, *ex-situ*, long-term conservation projects rarely use baseline (or ongoing) scientific data to provide a systematic check of the effectiveness of the conservation management actions themselves (Possingham *et al.*, 2001; Sutherland *et al.*, 2004).

The primate conservation community has been very proactive in implementing specialist groups, tools and models for the monitoring of global primate species status and the formulation of viable conservation strategies (Cowlishaw & Dunbar, 2000a; Ellis, 1997). With conservation action guided largely by the IUCN Species Survival Commission Primate Specialist Group (PSG), regional strategies or 'Action Plans' are published (e.g. Asia: Eudey, 1987; Madagascar: Mittermeier *et al.*, 1992; Africa: Oates, 1996a), whilst specialist workshops are instigated which compile status, threat details and strategic guidance for the application of intensive management. These workshops can either take the form of conservation assessment management plans (CAMPs) or population and habitat viability assessments (PHVAs) (Cowlishaw & Dunbar, 2000a; Ellis, 1997; Rylands, Rodriguez-Luna & Cortés-Ortiz, 1997).

Nevertheless, the success of these policy-level conservation strategies, and the efficacy of wildlife managers when implementing appropriate management-level conservation action on the ground, both depend on the quality of information about species abundance that is available. For most primate species, we have relatively little knowledge of the extent of occurrence within the species geographic range, and where information on local population density is available it only comes from a handful of sites (e.g. Cowlishaw &

Dunbar 2000). The problem is a particularly difficult one for wildlife managers, who in the absence of detailed data on local species abundance, must use either population density data drawn from other sites (which may be totally inapplicable) or else make do with presence/absence data to (1) prioritise the conservation management of the local populations, forest fragments and/or regions, (2) pinpoint the external factors that are influencing the dynamic changes in their forest network, and (3) monitor primate populations and the effects of conservation efforts in the future.

1.2 The Angola black-and-white colobus in Kenya's coastal forests

The coastal forests of southern Kenya are part of the Northern Zanzibar-Inhambane Coastal Forest Mosaic (Burgess *et al.*, 2000; White, 1976, 1983). International interest in the coastal forests (which include the Eastern Arc Mountains and coastal forests of Tanzania, and coastal forests of northern Kenya) has increased over the last three decades due to the realization of the global biodiversity value of these forests, and the threat of human modification of this important eco-region (CEPF, 2003; Schipper & Burgess, 2004). Presently, these coastal forests are listed as one of 25 global diversity hotspots (Myers *et al.*, 2000) and one of 11 'priority' regions for international conservation investment (Brooks *et al.*, 2002).

The forests are extremely diverse, and include many strictly endemic flora and fauna, including: 400 plant, 10 bird, 34 reptile, 14 amphibian, 75 butterfly and 8 mammal species (Burgess, 2000; Schipper & Burgess, 2004; WWF-US, 2003). The patterns of endemism in this eco-region are complex, with a high degree of turnover of local species between adjacent forest patches and many disjunct distributions (Burgess, 2000; WWF-US, 2003). This makes it extremely difficult to prioritise the forest patches in terms of their biodiversity (CEPF, 2003).

Much of the East African coastal forest has been destroyed with remaining natural habitats becoming more fragmented as agriculture and other human activities spread with increasing population (CEPF, 2003; Schipper & Burgess, 2004; Struhsaker, 1981b). Protected coastal forest areas in Kenya include the Tana River Primate Reserve, Arabuko-Sokoke National Park and Shimba Hills National Reserve (the latter forest is found in southern Kenya). Some of the remaining forest areas are protected as government-controlled Forest Reserves, however small fragments of coastal forest are found throughout this region, and are largely unprotected.

The Angola black-and-white colobus *Colobus angolensis palliatus* Peters 1868 is a large, distinctive, and well-known primate that is endemic to the coastal forests of East Africa. In light of the threats facing the unique ecological communities that comprise this global biodiversity hotspot, and in particular the paucity of information about the status of *C. a. palliatus* (Oates 1996a), the purpose of this study is to investigate the population ecology and future conservation management of this colobine monkey. Whilst the topic of whether to conserve biodiversity at the species level is hotly debated (Bowen-Jones & Entwistle, 2002; Caro, 2003; Caro *et al.*, 2004; Franklin, 1993, 1994; Lindenmayer, 1999; Olden, 2003; Towns & Williams, 1993; Walpole & Leader-Williams, 2002), the impossibility of managing the wide array of taxa that inhabit the coastal forests of this region make the approach potentially important in southern Kenya. If a species such as *C. a. palliatus* can be integrally linked to (1) the quality and regional (spatial) characteristics of coastal forest fragments, and (2) the surrounding (human-dominated) landscape and its associated pressures, it may further augment local and national interest towards the preservation of remaining coastal forest fragments in the region (Bowen-Jones & Entwistle, 2002; Towns & Williams, 1993; Walpole & Leader-Williams, 2002).

Ecologically, *C. a. palliatus* is largely a folivorous primate (Moreno-Black & Maples, 1977) dependant upon forest foliage for its survival. It's arboreal nature (Oates & Davies, 1994) also compounds its dependency on canopy forest and poses important questions regarding the species response to forest degradation and fragmentation, and the use (if any) of non-forest 'matrix' between adjacent patches of coastal forest. Kenyan *C. a. palliatus* populations are documented as being highly vulnerable to extinction due to ongoing human land use practices in the region (Struhsaker, 1981). Recent African primate conservation action plans have also recommended that the status of *C. angolensis palliatus* needs to be assessed in Kenya, with a stringent management plan to conserve remaining forest areas (Oates 1996).

The Angola black-and-white colobus also presents a useful case study in how colobine monkey populations respond to anthropogenic habitat change. Humans are influencing the population status of arboreal, folivorous primates throughout Africa (Oates, 1996b). While in West and Central Africa the predominant threat is from bushmeat hunting (Davies, 1987; Lahm, 1993; Martin & Asibey, 1979; Oates, 1996b), habitat loss remains the most significant threat to future colobus population survival in the more densely populated parts of East Africa and elsewhere (Oates, 1996b; Rodgers & Homewood, 1982; Struhsaker, 1981b; Struhsaker & Siex, 1998). A detailed understanding of how fragmented colobus populations can be affected by habitat disturbance would therefore be timely and may provide useful lessons for the conservation of other colobine and primate taxa.

A local conservation organisation, "Wakuluzu, Friends of the Colobus Trust" (http://www.colobustrust.org), has also been based within the coastal forest region of Kenya for the past nine years. Its aim is to promote, in close co-operation with other organisations and local communities, the conservation of primates, in particular the Angola black-and-white colobus and its associated coastal forest habitat. It is hoped that this study will form a baseline upon which to: (1) implement future colobus population/coastal forest conservation initiatives, and (2) measure the effectiveness of the organisation's research, monitoring and education programs (Cunneyworth & Rhys-Hurn, 2004).

1.3 Study chapters

By integrating field research, remote sensing techniques, geographical information systems (GIS) and theoretical modelling approaches, this study successively builds, through each chapter, a greater level of knowledge concerning the study species and its surrounding environment. Knowledge that can influence the conservation management of the species and increase our understanding of primates in fragments.

Chapter 1 has provided an overview of the human impact on primates in tropical forest systems, and background to the coastal forests of East Africa and the endemic Angola black-and-white monkey *C.a. palliatus* in those forests.

Chapter 2 will investigate the current extent and protection status of remnant coastal forest patches in southern Kenya, and provide population status and distribution information on *C. a. palliatus* populations inhabiting these fragments. This chapter will also include research into the historic distribution of *C. angolensis* in Kenya and the current anthropogenic threats facing the species.

Chapter 3 will provide a more detailed ecological analysis of the effects of habitat fragmentation on the study species. This chapter will identify the significant habitat attributes (i.e. spatial, structural, resource and disturbance) that determine *C. a. palliatus* occupancy and abundance patterns within coastal forest fragments.

Chapter 4 will adopt a wider, more landscape-based approach to colobus research, investigating the occurrence and behaviour of *C. a. palliatus* in the matrix occurring between forest patches. The study will investigate whether there are particular habitat attributes that determine colobus usage of the matrix, whilst the current extent of important matrix habitat will be determined via remotely-sensed mapping of land cover in the study site.

Chapter 5 will explore how the spatial geometry of the fragmented forest network may influence the metapopulation dynamics of *C. a. palliatus.* Using Hanski's incidence function model (Hanski, 1994b), parameterised from data collected during this study, this chapter will explore the theoretical persistence of *C. a. palliatus* populations, under both present conditions and alternative scenarios of future habitat destruction.

Chapter 6 will develop the incidence function model to incorporate matrix quality, and use this extended model to investigate its importance on future *C. a. palliatus* metapopulation dynamics, under both present matrix conditions and alternative scenarios of future matrix quality.

Chapter 7 will present a synopsis of the study findings and assess their implications for conservation management. Recommendations for future *C. a. palliatus* research and conservation initiatives in Kenya will also be discussed.

2. Status, distribution and conservation of the Angola black-and-white colobus (*Colobus angolensis palliatus*) in coastal Kenya.

2.1 Abstract

The status of the Angola black-and-white colobus (*Colobus angolensis palliatus*) is unknown in East Africa. This study provides the first evaluation of colobus distribution, status and current threats within the Kenyan extent of the subspecies' range; the southern coastal District of Kwale. Line transect and sweep count surveys were carried out between July – November 2001, covering 25,514ha of coastal forest within 124 forest fragments. Fifty-five colobus populations were discovered, with total Kenyan *C. a. palliatus* population estimates ranging between 3,100 – 4,900 individuals (560 – 900 groups). The Shimba Hills National Reserve protects both the largest forest and largest colobus population in the District. Local semi-structured interviews and archival research into the possible historical distribution of the subspecies in north coast Kenya confirmed the occurrence of the subspecies in Kilifi District, with the last sightings of the subspecies occurring in Arabuko Sokoke Forest in 1979. Differences in the settlement distribution, associated habitat loss and hunting preferences of the nine coastal tribes (Mijikenda) are thought to explain the loss of colobus from north coast. Unprotected forests were found to be under the greatest pressure of further habitat loss, fragmentation and degradation, while holding over 17% of the national population of colobus. The study found no difference between Forest Reserves and unprotected forests in the rate of forest loss or tree extraction densities, highlighting the need for increased law enforcement and management of the Reserves. However, Kaya (sacred) forests were significantly better at minimising threat, illustrating the critical role of community involvement in the successful future management of the Kwale District coastal forests.

2.2 Introduction

The Angola black-and-white colobus *Colobus angolensis palliatus* Peters 1868 is a folivorous primate (Moreno-Black & Maples, 1977) confined to the Eastern Arc Mountains and coastal forests of northern Tanzania and southern Kenya (Kingdon, 1997). Like most East African forest-dependent primates, habitat loss is a major threat to *C. a. palliatus* survival (Oates, 1996b; Struhsaker, 1981b). Their coastal habitat is remnant of a once continuous mosaic of unique forest, thicket, woodland, bushland and grassland (Hawthorne, 1993) which stretched from the Kenya-Somalia border to the border of Tanzania and Mozambique (Clarke, 2000), often referred to as the 'Northern Zanzibar-Inhambane floristic region' (White, 1976). These forests are one of 25 global diversity hotspots (Myers et al., 2000) and are listed as one of 11 'priority' regions for international conservation investment (Brooks et al., 2002) due to the significant rate of habitat destruction, linked to massive human population growth, agricultural expansion and tourist development in the region (CEPF, 2003; UNEP, 1982).

C. a. palliatus is currently listed as 'Data Deficient' in IUCN red listings (IUCN, 2004), with Rodgers (1981) providing the only published record of distribution for the subspecies in Tanzanian forests. Current IUCN/SSC African primate conservation action plans recommend that *C. a. palliatus* status needs to be established in Kenya, along with a stringent management plan to conserve remaining forest areas in the region (Oates, 1996a).

C. a. palliatus range in East Africa is thought to extend from the northern banks of the Rufiji River in Tanzania (7° 50' S, 38˚ 10' E) (Rodgers, 1981) to the border between Kwale District and Mombasa town in Kenya (3 59' S, 39 33'E) (Kahumbu, 1997). The distribution and subsequent taxonomic distinction of *C. a. palliatus* from other *C. angolensis* populations in north-east Angola, Democratic Republic of Congo (DRC), Rwanda, Uganda and Burundi, originates from a southern ancestral radiation of colobus from the montane forests of the Congo basin, and geographic isolation of the East African coastal forests during the last ice age, 1.8 million years ago (Kingdon, 1981; Rahm, 1970; Rodgers, Owen & Homewood, 1982). Today, these Kenyan coastal forest fragments persist in the north, beyond current *C. a. palliatus* range (Burgess, Clarke & Rodgers, 1998; Robertson & Luke,

1993) and a previous publication (Tarara, 1986) and anecdotal reports mention *C. a. palliatus* existing in some of these forests, but no study has verified, nor systematically investigated these claims.

Given this deficiency of knowledge concerning *C. a. palliatus* status in Kenya, this study investigates (1) the present population status and distribution of *C. a. palliatus* in Kenya, (2) the current extent and protection status of remnant coastal forest fragments within this distribution, (3) information on the historical incidence of colobus in the northerly forests within this region and (4) a discussion of the current threats facing the subspecies, highlighting possible conservation initiatives to ensure its continued survival in Kenya.

2.3 Methods

2.3.1 Study species

The Angola black-and-white colobus *Colobus angolensis* Sclater 1860 is one of four species of black-and-white colobus found in sub-Sahara Africa (Groves, 2001; Grubb *et al.*, 2003). Seven Angola black-and-white colobus subspecies have been described to date, based on distinguishing differences in pelage coloration pattern, habitat type and geographical distribution. Five subspecies exist within the Congo (Zaire) basin (*cottoni, angolensis, cordieri, prigoginei and ruwenzorii*) (Colyn, 1991); a sixth, isolated subspecies, the 'Nkungwe's Angolan Colobus' (Nishida *et al.*, 1981), is presently unnamed (Groves, 2001) and exists on Mount Nkungwe and the Mahale mountains in western Tanzanian. The final, seventh subspecies *palliatus* Peters, 1868 is the focus of this study. Often referred to as Peters' Angola colobus (Grubb *et al.*, 2003); with previous synonyms of *C. a. sharpei* Thomas, 1902 and *C. a. langheldi* Matschie, 1914; the subspecies has a discontinuous distribution through the southern highland (Eastern Arc Mountains), coastal, and gallery forests of southern and eastern Tanzania into south-eastern Kenya (Groves, 2001; Kingdon, 1997).

2.3.2 Study site

The Coastal Province of Kenya encompasses six main administrative Districts: Kilifi, Kwale, Lamu, Mombasa, Taita and Tana River. Three of these Districts were the focus of this study: the Kwale District, i.e. 'south coast' (which included the present-day distribution of the study species), and the Mombasa and Kilifi Districts, i.e. 'north coast' (which incorporated the possible historical distribution of the study species).

Kwale District lies between Mombasa and the border of North Eastern Tanzania (3°30', 4°45'S; 38°31' and 39°31'E) (Fig. 2.1). The District comprises approximately 8,322km^2, and contains a heterogeneous mix of grassland, woodland, swamp, shrubland, forestry plantation, mangrove and agricultural land (commercial and subsistence crops). Kwale District is also home to the study species, which inhabit the isolated, fragmented and largely threatened coastal forests within this region. Average temperature is 26°C for the District, with highest mean temperatures of 33°C reached between November and April. Altitude varies from sea level along the Indian Ocean shore, to slightly over 1000m, as one travels further inland (HSEDCO, 1998). The rainfall pattern is bimodal (long rains between March and July, short rains occur in October to December), with the initial 36km from the sea, the 'coastal forest belt' (Clarke, 2000), receiving 900-1500mm of rainfall annually (Jaetzold & Schmidt, 1983). It is within this coastal belt that most forest patches are distributed as a mix of lowland rain forest, swamp forest, scrub forest and undifferentiated forest types (Clarke, 2000).

Protection status of forest patches within Kwale District varies considerably. The largest of the District's forest reserves is the Shimba Hills National Reserve (>15,000 ha), which is double-gazetted by the Forest Department (FD) and Kenya Wildlife Service (KWS) (Robertson & Luke, 1993). The remaining forest patches in the District, in order of declining protection status, are either (1) gazetted Forest Reserves and community sanctuaries (i.e. the Mwaluganje Elephant Sanctuary), (2) sacred Kayas (some of which are gazetted as national monuments) or (3) unprotected forests on private or county council owned land. The Kayas owe their existence to the beliefs, culture and history of the coastal Mijikenda people (Digo, Duruma and seven groups of Giriama) who historically established fortified villages within these forests (Githitho, 1998; Spear, 1978). Today, they are jointly protected by the

National Museums of Kenya (Coastal Forest Conservation Unit) and the local Mijikenda, with some communities still actively using the Kayas as ceremonial or burial grounds. The Digo and Duruma protect Kayas within the boundaries of the Kwale District, whilst Kayas occurring in the Mombasa and Kilifi Districts are protected by the Giriama (Robertson & Luke, 1993). Kayas also exist in the north coast region of the study area (see *2.3.8* below).

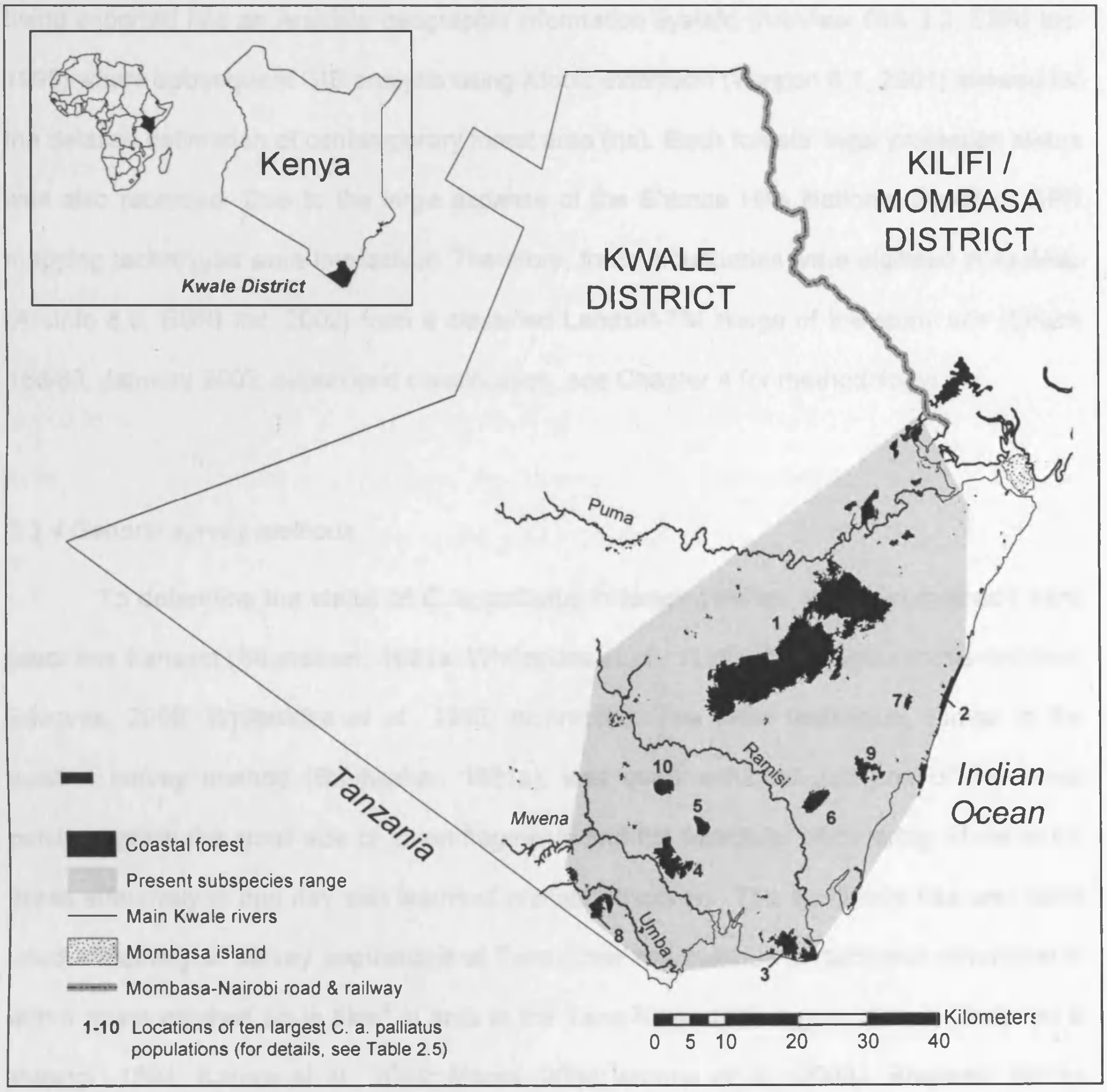


Fig. 2.1. Map of forest distribution and *C. a. palliatus* population occurrence within the Kwale District, Kenya.

2.3.3 Forest cover

To establish the present status of forest cover in the Kwale District, eight current 1:50,000 topographical maps covering the entire coastal forest belt of Kwale District (Survey of Kenya 1991, Edition 4, Series Y731, Sheets 200/1, 200/2, 201/1, 200/3, 200/4, 201/3, 201/1, 202/2) were initially used to establish the location and present-day (2001) existence of forest cover for the District. During the period between July and November 2001, all forest patch boundaries within a 4,258km^2 survey area were mapped by two field assistants traversing each patch perimeter on foot, recording positional data at 10-second intervals using a Garmin 12XL global positioning systems (GPS). These GPS data were then downloaded into MapSource software (MapSource 5.3, Garmin Corporation 1999), before being imported into an ArcView geographic information system (ArcView GIS 3.2, ESRI Inc. 1999) where subsequent GIS analysis using Xtools extension (Version 6.1, 2001) allowed for the detailed estimation of contemporary forest area (ha). Each forests' legal protection status was also recorded. Due to the large expanse of the Shimba Hills National Reserve, GPS mapping techniques were impractical. Therefore, forest boundaries were digitised in ArcMap (ArcInfo 8.3, ESRI Inc. 2002) from a classified Landsat-TM image of the study site (Scene 166/63, January 2003; supervised classification, see Chapter 4 for methodology).

2.3.4 General survey methods

To determine the status of *C. a. palliatus* in forest patches two main methods were used: line transect (Struhsaker, 1981a; Whitesides et al., 1988) and sweep sample (White & Edwards, 2000; Whitesides *et al.*, 1988) techniques. The latter technique, similar to the quadrat survey method (Struhsaker, 1981a), was used within all but one of the forest patches, given the small size of forest fragments and the feasibility of covering whole forest areas effectively in one day with teams of primate observers. This technique has also been used effectively to survey populations of Tana River red colobus (*Procolobus rufomitratus*) within forest patches up to 5km^2 in area in the Tana River delta region, Kenya (Butynski & Mwangi, 1994; Karere *et al.*, 2004; Mbora, 2004; Muoria *et al.*, 2003). However, sweep samples were impractical in the Shimba Hills National Reserve (>150km^2), therefore line transect sampling was used exclusively in this forest.

Prior to the census period of July till November 2001, all field researchers took part in a two-week pre-survey training course led by the author, to standardise recordings of colobus group counts, demographics, group spread and sighting heights (Peres, 1999). Sweep survey and line transect techniques were also practiced within three forests of known colobus density to check for observer bias and recording errors. Since most distance measurements were obtained through pacing, every researcher's average pace length (m) was calculated by counting the number of paces walked within a 15m transect (this procedure was repeated ten times). The resultant transect lengths used in analyses were in meters, calibrated from the transect-pacer's average pace length. Leading census participants were field researchers from Wakuluzu, Friends of the Colobus Trust, Diani Beach, Kenya, who were proficient at identifying colobus age and sex classes.

2.3.5 Line transect and Distance sampling

A one-month, line transect survey was conducted throughout the Shimba Hills National Reserve between October and November 2001. Four census teams were used, each comprised of two observers and one KWS ranger. Due to the logistical and time constraints of the survey period, it was decided that transects would be walked only once, covering a large representative area of the Reserve. A 1:50,000 topographical map assisted in the planning of transect entrance routes and courses. By utilising the 1x1km reference grid within the map, it was possible to maximise transect coverage that would sample the greatest number of forested grids within the reserve (81% of grid cells sampled). In most instances, daily transects were walked in parallel, $\geq$ 500m apart. Independent sampling was assumed, as colobus generally do not flee over such distances, frequently 'freezing' in trees in response to observers (Brugiere & Fleury, 2000; Mbora & McGrew, 2003). Colobus sighting times and group demography records were also checked after each daily survey, to rule out the possibility of double-counts between neighbouring transects. Census walks were undertaken between 06.30 and 15.00, omitting days when it rained. Observers travelled quietly at an average pace of 1-1.5km/hr, briefly stopping every 100m to watch and listen for primates (White & Edwards, 2000). Transect lengths were estimated by pacing, recording major physical features, vegetation changes and general primate locations by pace number. When primate groups were encountered the time, animal-observer distance, sighting angle and perpendicular distance (paced) to first animal seen were recorded (Buckland et al., 2001). No more than 10 minutes were spent with each group, gathering data on species, sighting height, behaviour (at time of sighting, and response to observers), polyspecific association, group count, spread and composition. Additional primates encountered within the National Reserve included the yellow baboon (*Papio hamadryas cynocephalus*) Syke's monkey (*Cercopethicus mitus albogularis*) and vervet monkey (*Chlorocebus aethiops*).

A total of 169 transects totalling 450.7km in length were surveyed within the Shimba Hills National Reserve (mean 1.8km ± 0.1km SE; range 0.1-13.5 km). Transect sampling predominantly concentrated on closed canopy forest (313.9km). However, 37.1km wooded shrubland, 26.9km wooded grassland, 31.9km shrub grassland, 27.3km grassland, 10.1km conifer plantation and 3.5km of swampland were also sampled.

Absolute colobus density estimates were calculated using the program DISTANCE 4.0 (Thomas et al., 2002) and the primate sightings from the 313.9km closed canopy forest transects. Perpendicular distances were calibrated from first animal seen to the centre of colobus groups by adapting Whitesides' method (Whitesides et al., 1988): instead of using a standard correction measure of mean group spread for all sightings, individual group spreads were used. The size of detected groups (see below) was independent of sighting distance, even when correcting for polyspecific group size, thus eliminating this relationship as a possible source of bias in density estimation (Buckland *et al.*, 2001). During model fitting, outliers in the distribution of perpendicular distances were ignored by truncating the furthest 5% of sightings. A half-normal function with cosine series expansion was selected according to Akaike's information criteria (AIC) in DISTANCE 4.0. To calculate colobus group density estimates and encounter rates that would be comparable with other colobine surveys, sightings of solitary individuals were excluded from the analysis (Chapman *et al.*, 2000; Fashing & Cords, 2000; Marshall *et al.*, 2005). However solitaries were included in a second analysis to give an estimate of individual density and total population estimate for the National Reserve. In this latter analysis, solitaries were treated as additional groups, whereby group size equalled one.

The resultant *C. a. palliatus* encounter rates, individual and group density estimates via DISTANCE 4.0 were also compared with other known studies of *C. angolensis* for a between-subspecies comparison, whilst results were also compared with *C. guereza* study sites for a between-species comparison.

2.3.6 Forest sweep surveys

During the period of July till November 2001, all other forest patches within the Kwale District (*n* = 123) were systematically censused by one-day sweep surveys (Whitesides et al., 1988). Four or more census teams, each comprised of three trained observers and a local guide, began surveys between 06.30 and 07.00am each day. Teams walked parallel transects 100m apart, starting at the same time and travelling at the same speed, along pre-determined routes (Struhsaker, 1981a) until an entire forest patch had been effectively covered (total survey time being a function of patch area and the number of census teams). Sweep sample accuracy was facilitated by (1) the maintenance of compass bearings throughout transect walks, and (2) re-grouping of survey teams after each forest transect sweep to re-synchronise movements. Data gathered during primate encounters were similar to those detailed in the Shimba Hills National Reserve, however locations were referenced by transect distance and sighting angle only. Time and direction of primate group departures were also recorded. All teams discussed and enumerated results immediately after the completion of each survey and 'double-counts' were removed by comparing similarities in team observations, based on primate sighting times, departure directions and group compositions. All primate encounters (including the National Reserve) were ranked on a four-point scale in accordance with observation quality: 0, primate vocalisation detected but no individuals observed; 1, primate group detected but group count incomplete; 2, primate group detected and counted but age-sex composition incomplete; and 3, primate group detected with complete count and age-sex composition. These codes were used to guide the subsequent allocation of group size to each group encountered, as follows: 0, data discarded (no confirmed group encounter), 1, group size based on mean group size (calculated from the entire census' rank 3 group counts, see *3.2 Results*), 2 and 3, group size taken from the actual count. Once group size had been established for all groups, the population estimate for each patch (*n* = 123) was calculated from the sum of individuals in each group plus all solitary animals recorded.

2.3.7 River intercept transects

Within the same survey period, sweeps were also made along the banks of the Mwena, Umba, Ramisi and Puma rivers (the four major rivers within the Kwale District). Both banks of each river were traversed in tandem by survey teams aiming to cover as much of the river's main tributary length as possible. Changes in vegetation cover were recorded by line intercept method (Bullock, 1996; Grieg-Smith, 1983). In this survey method, observers walked line transects within 5-10m of the river bank, continuously noting changes in the vegetation cover by the number of paces taken (White & Edwards, 2000). Vegetation was classified as either indigenous riverine vegetation (Clarke, 2000), wooded grassland, shrub grassland, grassland, shrubland, mangrove, annual cropland (e.g. maize, sugarcane, bananas, root vegetables), perennial plantation (mango, coconut and cashewnut) or human development (e.g. settlements). The total length (km) of each vegetation type encountered along each of the four rivers gave a course vegetation profile of the riverbanks in the District. Colobus sightings along riverbanks were summarised as: (1) the total number of groups and individuals observed, and (2) encounter rates (groups/km), for each riverbank vegetation type.

2.3.8 Historical incidence

To determine the historical incidence of *C. a. palliatus* in the 'north coast' forests we used two main methods: local interviews and archive research. During November 2001 and April 2003 sites were visited within the Kilifi and Mombasa Districts, to carry out semi-structured interviews (Bernard, 2002) with local community members. The sampling effort was deliberately selective, targeting individuals over 60 years of age, who could provide historical information regarding the Kilifi and Mombasa District forests and the cultural use of wildlife in the region. Initially, key informants were interviewed from the Coastal Forest Conservation Unit (CFCU) and Kenya Forestry Research Institute (KEFRI), Kilifi, who provided ethnographic information for the region and lists of suitable interview participants. These included: Kaya chairmen and elders of the Chonyi, Jibana, Kambe, Kauma, Rabai and Ribe tribes; medicine men, dancers and village elders of the Giriama and Waata (Wasanyi/Walungulu) communities surrounding Arabuko Sokoke Forest; and Mazrui clan elders from the villages of Roka and Takaungu, on the coastline of Kilifi District. Detailed interviews quantified each participant's exposure to local forests within their lifetime. A total of 51 'north coast' elders, medicine men and dancers were interviewed. The average age of participants was 73 years of age (SE = 1.7, mode = 80yrs, range 49 – 97 years). During interviews, historical knowledge of forest wildlife and hunting practices, direct and indirect accounts of colobus occurrence in the area, local uses of colobus skin and body parts, and the possible reasons for colobus disappearance were recorded (for a detailed interview guide, see *Appendix I*).

Expedition reports, Kenya game department annual reports (1909-1957), Kilifi District and Coast Provincial administrative documents, Kenya forest department reports and pre-1950s travel literature from the region were also examined for documented evidence of *C. a. palliatus* sightings in the Kilifi District. Documents were held at: Fort Jesus Museum, Mombasa; KEFRI library, Arabuko Sokoke Forest, Kilifi; Kenya National Archives and Kenya Wildlife Service Archives, Nairobi; The School of African and Oriental Studies Library, Royal Geographic Society, Zoological Society of London and the British Natural History Museum, London. In addition, the following museum mammal collections were checked for the occurrence of north coast *C. a. palliatus* specimens: National Museum of Kenya, Nairobi; American Museum of Natural History, New York; Smithsonian Institute NMNH, Washington DC; Museum fur Naturkunde, East Berlin; Powell-Cotton Museum, Kent; and the British Natural History Museum, London.

2.3.9 Threats

During the population census, both qualitative and quantitative measures of human disturbance were recorded for each forest. Notes were taken on the nature and threat of both forest utilisation and local activities that encroached upon forest boundaries. Presence and absence of three main indicators of recent disturbance were also noted for all 124 forest patches. These were: (1) logging (recent logging activity, pitsaws in forest, presence of loggers during survey period, chainsaws heard), hunting (evidence of recent snares, traps or hunters in forest during survey period with bows, arrows and dogs), and (3) charcoal (evidence of charcoal pit construction and recent use). Additional local interviews on an *ad lib* basis helped to determine the relative incidence of primate crop-raiding.

A sub-sample of 46 randomly selected forest patches were chosen for a more quantitative comparison of disturbance within the Forest Reserves, Kayas and unprotected forests. Firstly, four botanical survey teams, each comprising two researchers, carried out 4m belt transects (Grieg-Smith, 1983) to quantify the extent of tree damage, in particular logging, within each of these forests. Between 3-26 transects were carried out in each patch, depending on the patch area. Transect lengths also varied between patches with longer transects used in larger patches (n = 314, mean length = 1.4 km ± 0.7 S.E., range = 0.1 - 3km). The systematic placement of transects throughout each forest also ensured an accurate representation of each patch. All tree damage within 4m of transects were enumerated, stump/stem diameters (cm) were estimated, the type of damage (natural death, animal damage, logging or debarking) was recorded, as well as the approximate age of damage (recent, old, very old). Patch disturbance was thus summarised as the absolute density of logging and debarking tree damage (basal area m^2/ha) per forest. Patch disturbance data were also collected during the one-month survey in the Shimba Hills National Reserve, however for the results of this study only qualitative details are given for this forest patch, as a future, more extensive analysis is planned due to the uniqueness and size of this forest.

Secondly, the same 46 patches were also used in a GIS analysis which estimated patch-specific forest loss over a 12-year period. The 2001 patch areas (km^2) were compared with 1989 patch areas (km^2). The latter was estimated by digitising forest boundaries from 1991 topographical maps, originally derived from 1989 aerial photographs, in ArcMap (ArcInfo 8.3, ESRI Inc. 2002).

2.3.10 Statistics

To test the significance of forest protection status on the occurrence of recent disturbance activities within forests in the Kwale District a generalised linear model (GLM) with binomial error structure was used (Crawley, 1993) within the statistical software R, version 1.9.1 (www.r-project.org). Three independent models coded the presence or absence of either: (1) logging, (2) hunting or (3) charcoal production activities in all 124 forests as a binary response variable, with each forest regarded as a unit. The categorical explanatory variable in all three analyses was forest protection status, which comprised of three 'levels': Forest Reserve, Kaya or unprotected forest. If an overall significant effect of forest protection status was discovered within each of these three models further post-hoc analysis determined the independent significance of each forest protection status via a series of pair-wise 'level' comparisons. This latter analysis was achieved within a GLM model framework by simplifying factor levels (i.e. protection status types) in pairs, turning a three-level factor into two (Crawley, 2002). Each of the two-level models were compared to the original, three-level GLM model using F-tests for level of significance.

Forest loss (km^2) and tree damage (basal area m^2/ha) differences between Forest Reserves, Kayas and unprotected forests (*n* = 46) were tested using Kruskal-Wallis one-way analysis of variance tests (Siegel & Castellan, 1988). If an overall significant effect of forest protection status was discovered via this analysis, a post-hoc Kruskal-Wallis test, the multiple-comparison test (Siegel & Castellan, 1988) was used to test for independent significance of protection status type, via pair-wise comparisons.

It was hypothesised that unprotected forests would have higher levels of all disturbance activities (i.e. logging, hunting, charcoal, forest loss and tree damage). Kayas and Forest Reserves were expected to have significantly lower levels of disturbance due to the increased law enforcement and active local/governmental protection of these forests. The null hypothesis for both the GLM and Kruskal-Wallis analyses was no significant difference in the levels of forest disturbance between forests of differing protection status. All statistical tests were two-tailed.

2.4 Results

2.4.1 Forest Cover

A total of 124 forest patches were mapped and censused during this study (Fig. 2.1), covering an estimated total area of 25,514ha (255.1km^2) coastal forest cover for the Kwale District. The Shimba Hills National Reserve protects the largest area of forest for the District at 15,890ha. All other 123 forest patches ranged in size from 1 to 1,417ha: 54% of patches were less than 10ha in area, 29% were between 10-100ha, whilst 16% of patches were greater than 100ha. The descriptive statistics of forest cover by protection status are detailed in Table 2.1 and Figure 2.2.

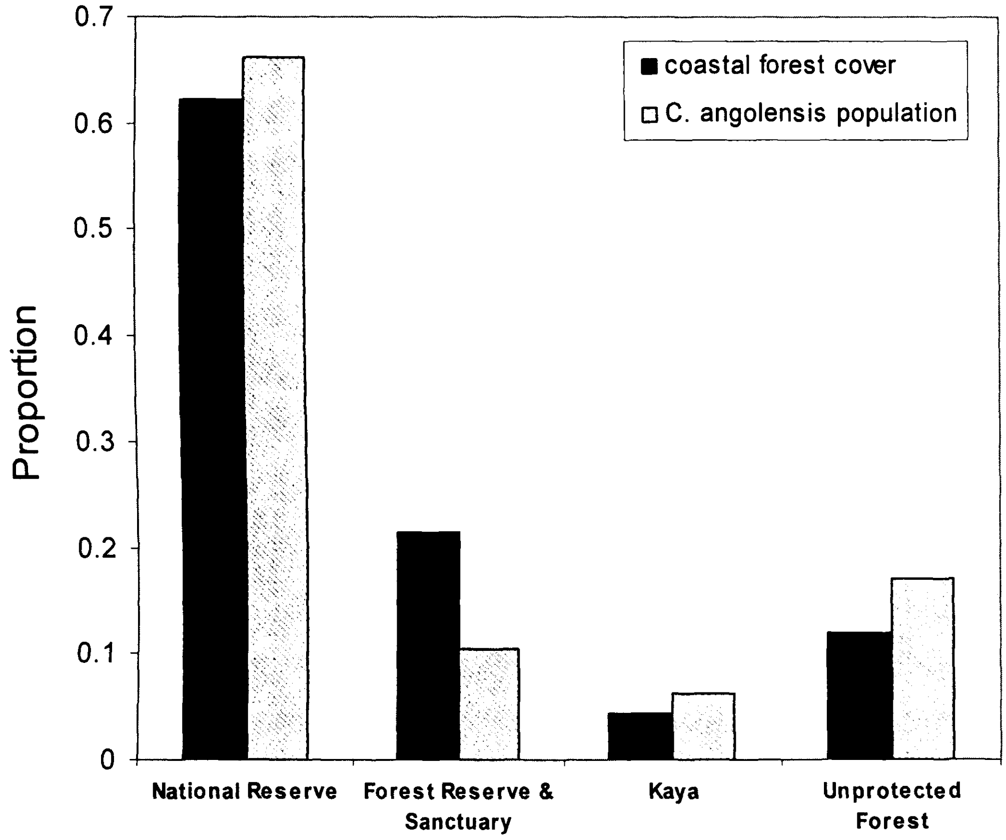


Fig. 2.2. Proportion of Kwale District's remaining coastal forest and *C. a. palliatus* population by protection status.

Table 2.1. Descriptive statistics of forest cover and colobus status in Kwale District, Kenya. [a] Total number of colobus groups either counted (in sweep surveys) or estimated (from the National Reserve line transects & DISTANCE 4.0); [b] Total number of solitary individuals counted in sweep surveys; [c] Total number of individuals in all patches; [d] National Reserve estimate is extrapolated from DISTANCE 4.0 using group density only. Final group total for Kenya may vary between 560 - 900 (95% CI); [e] National Reserve estimate is extrapolated from DISTANCE 4.0 using values of individual density. Final Kenya population total may therefore vary between 3,100 – 5,000 individuals (95% CI); [f] Riverbanks were included in this table for the overall Kenya *C. a. palliatus* population estimate only, as exact forest cover is unknown.

	Forest cover		Patch size (ha)		Colobus status & distribution			
Forest protection status	Total area (ha)	No. patches	median	range	Occupancy	# gps [a]	# sol [b]	# individuals [c]
Shimba Hills National Reserve	15,890	1	-	-	1(1.00)	458 [d]	-	2,436 [e]
Forest Reserve & Sanctuary	5,493	14	334	(15 - 1,417)	12 (0.86)	71	13	387
Kaya	1,090	30	12	(1 - 218)	20 (0.67)	41	13	229
Unprotected	3,041	79	5	(1 - 808)	22 (0.28)	100	4	630
Umba and Ramisi Rivers [f]	-	-	-	-	-	34	2	158
Total	25,514	124			55 (0.44)	704 [d]	32	3,840 [e]

2.4.2 Colobus status and distribution

Firstly, the Shimba Hills National Reserve. A total of 73 *C. a. palliatus* encounters (65 groups, 8 solitaries: within closed-canopy forest only) were recorded during the line transect survey of the Shimba Hills National Reserve. There were only four additional sightings of colobus outside closed canopy forest. These were within wooded shrubland (two groups and one solitary male) and shrub grassland (solitary male); however, transect sample effort was so small in these areas that a comparison of density could not be made with DISTANCE 4.0. Only during 9% of the colobus encounters in closed-canopy forest were groups observed in polyspecific association with Sykes monkeys (*Cercopithecus mitus albogularis).* The results of the DISTANCE 4.0 analysis are detailed in Table 2.2. The total population size for the Reserve was estimated at 2,436 individuals ± 458 S.E. (CI 95%: 1,689 - 3,515). A comparison of density estimates (Table 2.2) indicates that *C. a. palliatus* in the Shimba Hills National Reserve were found at higher group and individual densities than other subspecies in the Congo basin. However, similar encounter rates were recorded for the same subspecies within coastal forests in Tanzania. *C. angolensis* also tend to be found at lower densities than *C. guereza* (a black-and-white colobus species that is also found in the forests of western Kenya).

Table 2.2. Results of DISTANCE 4.0 analysis and comparison of *C. angolensis* and *C. guereza* encounter rates and density estimates for differing study sites. a DISTANCE 4.0 estimated from group sightings only; b DISTANCE 4.0 estimated from group and solitary sightings; c Within the West Kilombero Scarp Forest Reserve; d unlogged; e lightly logged

Species and locality	Encounter rate group/km	Density (± 1 SE) group/km^2	individual/km^2	Source
C. angolensis				
Shimba Hills, Kenya	0.20 ± 0.28 [a]	2.88 ± 0.52 [a]	15.33 ± 2.88 [b]	this study
Ituri, Zaire	-	1.16 ± 0.42	7.7 ± 4.0	Thomas, S. (1991)
Lomako, Zaire	-	1.16	5.8	McGraw, S. (1994)
Ndundulu [c], Tanzania	0.26 ± 0.07	-	-	Marshall, A. *et al* (2005)
C. guereza				
Kakamega, Kenya	1.20 ± 0.52	11.1 ± 0.37	-	Fashing, P. & Cords, M. (2000)
Kibale, Uganda	0.15[d], 0.31[e]	2.00[d], 4.83[e]	-	Chapman, C. *et al* (2000)

Secondly, of the 123 patches outside the National Reserve, only 54 (45.5%) were found to hold resident colobus populations (Table 2.1). Solitary individuals were discovered in two additional Kaya patches, but it was difficult to determine whether these individuals were representative of newly-established populations, i.e. in the process of 're-colonising' a previously empty patch (Hanski, 1994b, 1998), or were simply transient. Therefore, they were excluded from the population occupancy data. A total of 1,246 colobus individuals were discovered within the 'occupied' patches, comprising 30 solitaries and 212 social groups (range: 1-50 groups, 1-332 individuals per patch).

Thirdly, the river surveys covered a total length of 224.8km riverbank: Puma (46.7km), Mwena (9.5km), Umba (56.4km) and Ramisi (112.2km) rivers, respectively. Very little riverine vegetation now remains along these rivers (only 3.9% of all riverbank length surveyed), with agricultural encroachment dominating the riverbanks (Table 2.3). However, 158 colobus were found along the Umba and Ramisi rivers, and these sightings were not solely restricted to riverine vegetation. Colobus were also found within indigenous vegetation such as mangroves and wooded grassland, whilst 14 colobus groups were found within perennial plantations consisting of coconut palms, mango and cashewnut trees. In all areas of perennial plantations where colobus were found, the presence of remnant coastal forest trees were also noted. In ten observations the colobus were feeding from such trees.

Table 2.3. Riverbank vegetation profiles of the Puma, Mwena, Umba and Ramisi rivers (combined), summarising the total length of transects by vegetation cover and related colobus sightings. [a] Total number of groups and total number of individuals encountered over km's walked (included in Kenya population estimate, see Table 2.1); [b] Number of colobus groups encountered per km walked along the banks of all four rivers.

Vegetation cover	km walked	% transect cover	Total No. [a] gps (indiv)	Encounter rate [b] (groups/km)
Annual cropland	53.95	24.0	-	-
Perennial plantation	37.42	16.6	14 (70)	0.37
Wooded grassland	36.11	16.1	3 (11)	0.08
Shrubbed grassland	32.06	14.3	-	-
Grassland	27.87	12.4	-	-
Shrubland	18.30	8.1	-	-
Mangrove	10.08	4.5	1 (8)	0.10
Riverine vegetation	8.77	3.9	16 (69)	1.82
Human development	0.25	0.1	-	-

During the course of the study there were 13 additional, independent sightings of colobus groups and solitaries outside of coastal forest habitat. These were collected on an *ad hoc* basis when census teams were in non-forested areas, either travelling towards or leaving survey areas. The sightings included: four observations of colobus (3 groups and one solitary male) within shrubland, three observations of solitary males within wooded grassland and six sightings of colobus groups within perennial plantations (coconut, cashewnut and mango trees). However, these 61 individuals were excluded from the regional population estimate, as they were not part of a systematic survey of non-forest vegetation types.

From the quality 'three' ranking of colobus group counts from all groups encountered in the survey (n = 316), it was possible to determine *C. a. palliatus* group structure (n = 190), detailed in Table 2.4. Group size averaged six individuals, with a high prevalence for single-male groups: 88% single-male, 11% multi-male (two-males) and 1% multi-male (three-males) groups.

Table 2.4. *C. angolensis palliatus* group demographics. Adult males (>6yrs); adult females (>4yrs), sub-adult males (2-5yrs); sub-adult females (2-3yrs); juveniles (1-2yrs); infant (<1yr). [a] Two groups were discovered without any adult males, one was verified as being killed by local hunting dogs.

Group structure	mean	S.E.	range
Total group size	5.63	0.15	2 - 13
Adult males	1.12	0.03	0 - 3 [a]
Adult female	1.97	0.07	0 - 5
Sub-adult males	0.39	0.05	0 - 3
Sub-adult females	0.38	0.05	0 - 2
Juvenile males	0.26	0.04	0 - 2
Juvenile females	0.44	0.05	0 - 3
Infants	0.77	0.06	0 - 4

The distribution of colobus within protected and unprotected forest of Kwale District is detailed in Table 2.1 and Figure 2.2, whilst the locations of the ten largest colobus populations are listed in Table 2.5. The overall extent of occurrence in the District, estimated by drawing a minimum convex polygon (Beyer, 2004; IUCN, 2001) around all known sites containing colobus populations was 2,721km^2 (Fig. 2.1: *present subspecies range*). Total area of occupancy of the subspecies in Kenya, defined as the total area of occupied habitat within this extent of occurrence, was 248.85km^2.

Table 2.5. Locations of the ten largest *C. a. palliatus populations* in Kenya, detailing forest locations, legal protection status and present threats. [a] NR, National Reserve; U, unprotected; FR, Forest Reserve; K, Kaya. [b] L, illegal logging; Ch, charcoal production; F, firewood collection; H, hunting; E, encroachment. Comparison of activity level: -, minimal; +, light; ++, moderate; +++, heavy exploitation.

	Forest name	**Location**	**Protection [a] status**	**Forest area(ha)**	**Total No.colobus groups (individuals)**	**Present threats [b]**				
						L	**Ch**	**F**	**H**	**E**
1	Shimba Hills	4° 15' S, 39° 23' E	NR	15,890	458 (2,436)	+	-	-	+	-
2	Diani	4° 19' S, 39° 34' E	U	455	50 (332)	++	++	++	++	+++
3	Shimoni (west)	4° 37' S, 39° 22' E	U	1,222	20 (123)	+++	+++	+++	+++	+++
4	Marenji	4° 31' S, 39° 13' E	FR	1,417	21(110)	+++	+++	++	++	+
5	Mrima	4° 29' S, 39° 15' E	FR	382	13 (81)	+	-	+	+	-
6	Buda	4° 27' S, 39° 24' E	FR	677	8 (52)	++	+	+	+	-
7	Muhaka	4° 20' S, 39° 31' E	K	140	7 (35)	+	+	+	+	-
8	Gonja	4° 34' S, 39° 07' E	FR	422	7 (33)	+++	+	+	++	+
9	Gongoni	4° 24' S, 39° 27' E	FR	657	7 (31)	+	-	+	++	-
10	Dzombo	4° 26' S, 39° 12' E	FR	504	4 (23)	+	+	+	+++	+

2.4.3 Historical incidence

The general locations of historical interviews in the Kilifi and Mombasa Districts (by forest) are detailed in Fig. 2.3. Fourteen survey participants reported seeing colobus in Kilifi forests during their lifetime, whilst an additional thirteen stated that they had been told of their past occurrence in the area by older relatives. Six out of nine sites were reported as having once had colobus; Arabuko Sokoke Forest (sightings were reported to have occurred between the years 1928-1979), Takaungu village (<1950s, pre-forest clearance), and Kauma (1929-1939), Chonyi (1928-1937), Rabai (1924-1945) and Jibana (<1900s) Kayas. Participants also reported having seen colobus at five additional locations in north coast Kenya, outside the current survey area: e.g. Mangea Hill, reported by five independent survey participants as a site for colobus up until the mid 1950s. The locations of such reports are also illustrated in Fig. 2.3.

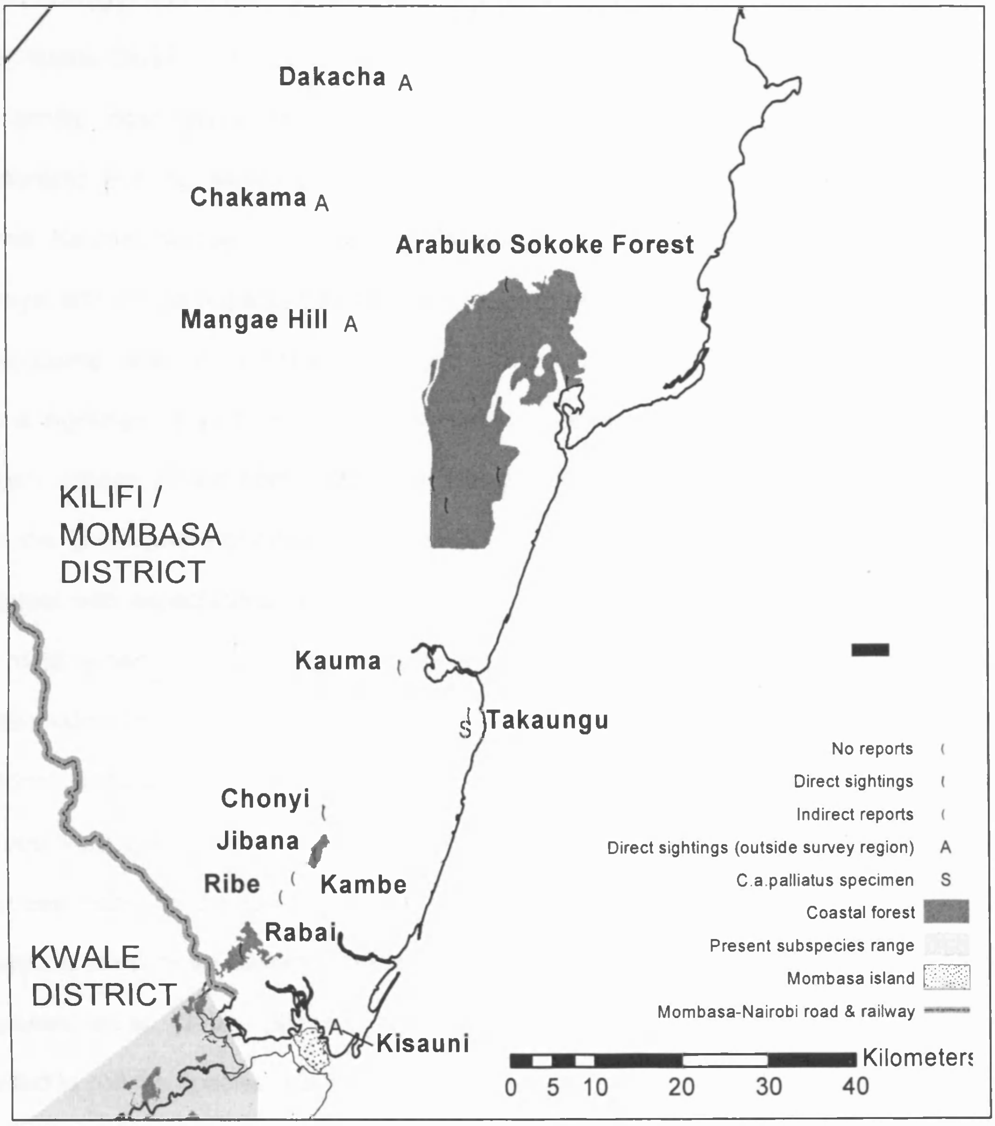


Fig. 2.3. Map of forest distribution and *C. a. palliatus* population occurrence within the Kwale District, Kenya

All participants were extremely knowledgeable concerning colobus behaviour and general ecology, and confirmed a present-day extent of *C. a. palliatus* range as the 'south coast', Kwale District only. When asked about the reasons for colobus disappearance in Kilifi, similar descriptions were given of forest clearance for settlement, followed by opportunistic hunting, skinning and eating of those colobus left in forest fragments. All Giriama, Kauma, Kambe, Jibana, Ribe, Rabai and Chonyi elders confirmed the eating of monkeys, with 28 participants having heard of, or witnessed colobus being eaten (the latter two accounts referred to Arabuko Sokoke Forest). The most comprehensive reports of colobus sightings came from ex-workers of the Danish Kajenson's sawmill, who logged in Arabuko Sokoke Forest from 1928-1958. Headmen gave details of: (1) specific locations within the forest where colobus were frequently found, (2) colobus feeding trees (that were consistent with expectations) and (3) subjective descriptions of declining colobus densities after 1940, when logging activity and general human disturbance increased in the forest. Colobus skins were used by local dancers (mainly purchased from Mombasa or south coast locations), whilst the meat was reported to be of little value. Songs about the colobus were recorded from the Giriama and Waata, whilst the latter tribe also provided an additional, north coast name for the species. The generic name for the Angola black-and-white colobus: "*mbega*", is used by all Mijikenda tribes at the coast and originates from the Digo language (Mwalonya *et al.*, 2004; Stigand, 1909). However, the north coast Waata tribe, were recorded to call the species "*k'amale wenyu*".

Archival research provided little documented evidence of colobus occurrence in the north coast Districts. However, five *C. a. palliatus* skin and skull specimens were found in the British Natural History Museum, London (Napier, 1995), collected from Takaungu forest, Kilifi (3°42' S, 39° 51' E) (Fig 2.3). these were collected in 1901 by A. B. Percival, the first Game Department ranger of Kenya (Percival, 1928).

2.4.4 Threats

At present, the greatest threat to *C. a. palliatus* populations in Kenya is habitat loss. The qualitative assessments around forest patches indicate that forest encroachment pressures include slash-and-burn clearance for agriculture, local settlements, coral-block mining and tourist development. The latter industry in particular, directly affects the Kayas and unprotected forests along the Indian Ocean coastline through forest clearance for hotels, associated businesses and settlements. Human extraction practices within forests included the debarking of trees for medicinal use (non-fatal) and rope making (fatal), and the illegal logging of trees for charcoal, fuel wood, building poles, fencing, furniture, construction timber and woodcarving. Illegal hardwood logging is widespread in all forests, particularly so in the Forest Reserves.

Forest management had an overall significant effect on four measures of human impact: the amount of forest loss (km^2) between 1989 and 2001 (Kruskal-Wallis: $x^2 = 15.0$, df = 2, p = 0.001), and the incidence of recent logging activity (binomial GLM: F = 8.4, df = 2, p = 0.004), hunting activity (F = 3.4, df = 2, p=0.04) and charcoal production (F = 12.5, df = 2, $p<0.001$). There was no significant effect of forest management on the absolute basal area (m^2/ha) of trees removed. Figure 2.4 illustrates the range (and significance levels) of disturbance differences by forest management type.

In concordance with the hypotheses under test, Kayas had significantly lower levels of forest loss (km^2) between 1989 and 2001 than unprotected forests (Fig. 2.4.a.). Occurrence of recent charcoal production (Fig. 2.4.e.) and logging activities (Fig. 2.4.c.) were also significantly lower in these forests. In addition, logging occurrence in Kayas was significantly lower than in the Forest Reserves (Fig. 2.4.c.)

In contrast, the Forest Reserves had significantly higher incidence of recent hunting activity compared to both unprotected and Kaya forests (Fig. 2.4.d.), whilst levels of tree damage (Fig. 2.4.b.), forest loss (Fig. 2.4.a.) and occurrence of recent logging activity (Fig. 2.4.c.) were not significantly different from unprotected forests. The only activity which was significantly lower within the Forest Reserves, when compared to unprotected forest, was the incidence of charcoal production.

The *ad lib* anectodotal reports of crop raiding indicate that human-wildlife conflict does not seem to be a direct threat to *C. a. palliatus* populations, compared with other crop-raiding primates in the District: the yellow baboon (*P. h. cynocephalus*) Syke's monkey (*C. m. albogularis*) and vervet monkey (*C. aethiops*). However, reports of colobus periodically eating the skins of unripe mangoes (*Mangifera indica*), oranges (*Citrus aurantuim* and *C.*

sinensis) and leaves of cassava (*Manihot esculenta*), sweet potato (*Ipomoea batatas*) and cow pea (*Vigna unguiculata*) crops were reported within the southernmost region of the Kwale District (an administrative sub-location called Vanga) which was near the border of Tanzania.

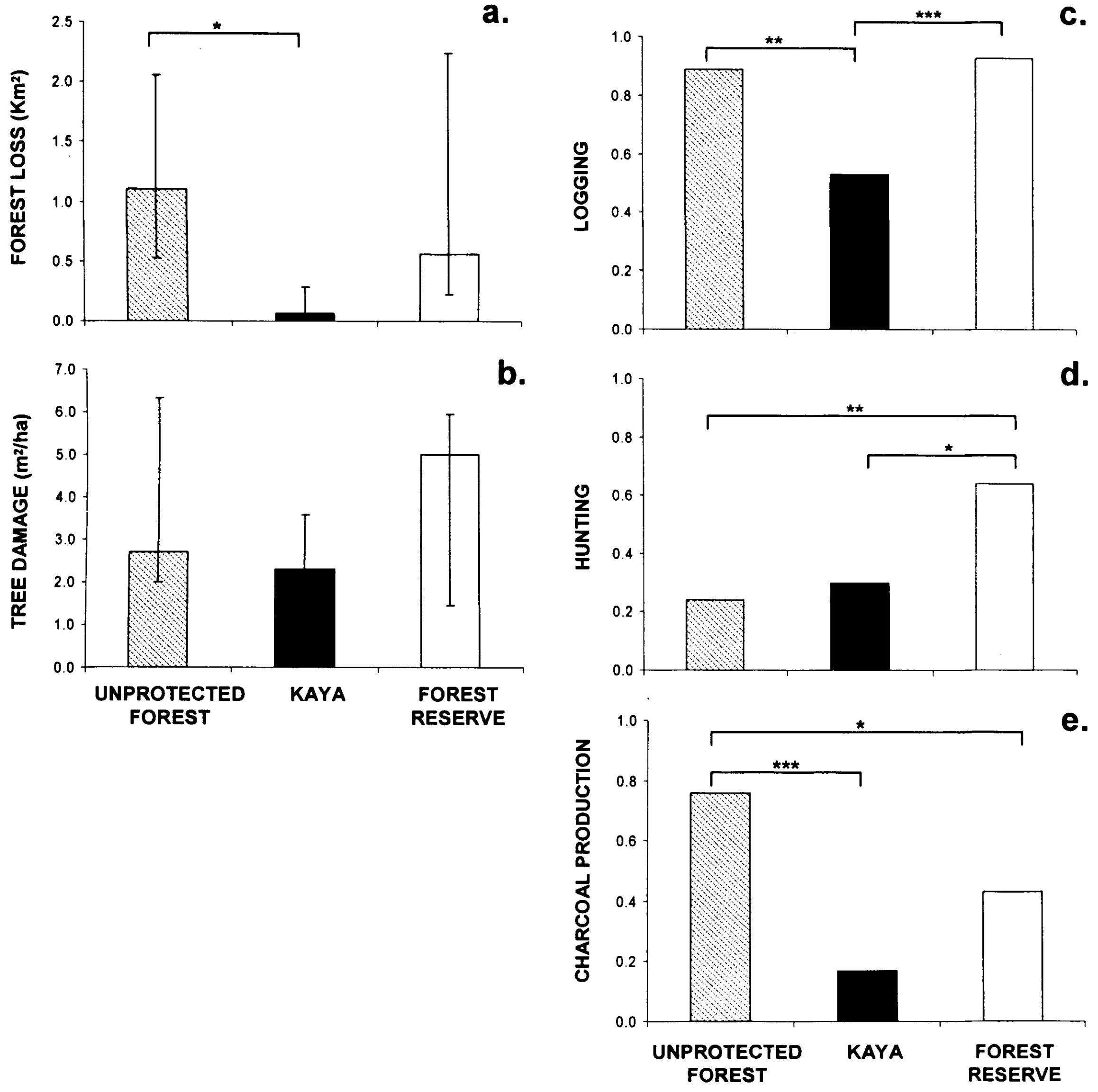


Fig. 2.4. Summary of forest disturbance by forest management type. Graph **a**. shows the median amount of forest loss (km^2) from unprotected, Kaya and Forest Reserves between 1989 and 2001 (error bars = 25% and 75% C.I.), **$p<0.05$* (significance from Kruskal-Wallis multiple comparisons test, two-tailed). Graph **b.** indicates the median basal area (m^2/ha) of human-caused tree damage within each of the three forest categories (error bars = 25% and 75% C.I.). Graphs **c.**, **d.** and **e.** indicate the proportion of forests within each management category: recent logging (evidence of recent logging activity, pitsaws, presence of loggers during survey), hunting (presence of ground snares, traps and/or hunters with bows, arrows & dogs) and charcoal-production activities (evidence of recently used charcoal pits) respectively, **$p<0.05$*, ***$p<0.01$* and ****$p<0.001$* (significance from Binomial GLM pair-wise comparisons).

2.5. Discussion

2.5.1 Colobus status within the forests of Kwale District

The Shimba Hills National Reserve jointly protects the largest proportion of remnant coastal forest and the largest Kenyan population of *C. a. palliatus* within the Kwale District. Results for the National Reserve indicate that colobus densities are very similar to those of a neighbouring *C. a. palliatus* Tanzanian population when encounter rates are compared. However, *C. a. palliatus* group and individual densities are higher than all *C. angolensis* populations studied to date within the Congo basin (Zaire). The species overall, tends to be found at lower densities than *C. guereza*, although it should be noted that a unique population of *C. a. ruwenzorii* have been found to form super-troops of over 300 individuals within the Nyungwe Forest in south-western Rwanda (although colobus density estimates from this site are unknown) (Fashing *et al.*, 2004; Fimbel *et al.*, 2001; Vedder & Fashing, 2002).

The Forest Reserves provide the largest area of forest cover (both in total coverage and per patch) for colobus populations outside the National Reserve, comprising almost 21% of the District's forest cover under Forest Department protection. Individual reserves are generally larger in area and higher in occupancy than the Kayas and unprotected forests. Indeed, six of the ten largest *C. a. palliatus* populations within the District can be found within Forest Reserves, highlighting the importance of these sites for species protection.

Over 3,000ha of coastal forest (12%) still remain unprotected within the District however. Despite the highly fragmented nature of these forests, they continue to provide habitat for a significant proportion of the Kenyan *C. a. palliatus* population (17%), greater than the colobus population estimates for the Forest Reserves and Kayas combined. Two forests are particularly vulnerable, Diani and Shimoni, as they contain two of the largest colobus populations in the District, yet receive no formal protection.

The extent of Riverine forest within Kwale has been greatly reduced by the intensity of localised farming along the banks of the four major rivers. Surprisingly, colobus were found to persist in thin remnant strips of this indigenous vegetation along the Umba and Ramisi rivers. It is likely, however, that the pattern of utilisation of these areas was dependent upon the nature of the surrounding vegetation, namely the distribution of perennial plantations (i.e. coconut, cashewnut and mango tree crops) which provide an arboreal canopy that facilitates colobus movement between riverine patches. Encounter rates of colobus within perennial plantations also suggest this. Similarly, incidental sighting of colobus in wooded shrubland, wooded grassland, shrub grassland and mangrove provides preliminary evidence for the limited movement, and possible dispersal, of colobus between forest patches. The diversity and structural complexity of non-forest vegetation within the District, often referred to as 'matrix' (Gascon et al., 1999; Pardini, 2004; Ricketts, 2001), may have implications for the dynamics of the population as a whole and will be explored in later chapters (Chapters 4 and 6).

It is extremely difficult to assess the viability of individual colobus populations within Kwale District based solely upon population sizes. In fact, reference to a standard minimum viable population (MVP) has been fraught with controversy (Burgman, Ferson & Akcakaya, 1993; Harcourt, 2002; Soule, 1987) as MVPs are known to be both species and site-specific. Variation in forest quality, patch connectivity and local threat processes may independently influence the distribution and viability of colobus populations within all 124 forest patches. Given the existence of small populations within the fragmented Kaya and unprotected forests, and the probable occurrence of limited movement of colobus within the matrix, a more expansive outlook of forest conservation that incorporates the unprotected forests, may be more applicable. In this approach, conservation management would focus on the preservation of the Kenyan *C. a. palliatus* population in a metapopulation framework (Baguette & Schtickzelle, 2003; Hanski, 1998; Hanski & Gilpin, 1991; Hanski et al., 1996a) rather than on a forest-by-forest basis.

2.5.2 Historical incidence

The present-day Kenyan distribution of *C. a. palliatus* is solely restricted to the southern coastal forests of the Kwale District. The absence of this species from the northern coastal forests of Kilifi District is intriguing, given the similarity of vegetation types, species composition and relative proximity of Kilifi forests to the northern-most occupied forests of Kwale (Fig. 2.3). The only geographical barrier between south and north coast forests is the highly concentrated settlement/development of the Mariakani - Mombasa region, incorporating the Mombasa - Nairobi railroad and highway. Although this may prevent present-day re-colonisation of Kilifi forests by dispersing colobus (construction of the railroad began in the early 1900s), the historical influence of these barriers would be negligible. Pre-1900s, Kwale and Kilifi forests would have once been part of a continuous vegetation mosaic of unique forest, thicket and woodland (Hawthorne, 1993). The only northern geographical barrier to the ancestral radiation of colobus from Tanzania and south coast Kenya, after the last ice age, would have been the lower floodplains of the Tana Delta, situated far north of the Kilifi forests (Rodgers *et al.*, 1982).

The discovery of *C. a. palliatus* specimens collected in 1901 from Takaungu forest, Kilifi, 50km north of present-day colobus extent, confirms a minimum contraction of this same distance of *C. a. palliatus* range within the past 100 years. This finding also supports the reports collected in this study of the subspecies occurrence in Takaungu, prior to complete deforestation of the region in 1950. With the exception of the Aruboko Sokoke Forest Reserve, there are very few patches of coastal forest left in the Kilifi and Mombasa Districts (particularly near the Indian Ocean coastline) (Burgess *et al.*, 2000). This is in contrast to the network of coastal forests, still in existence in Kwale District. It was difficult to ascertain from archival research whether intensive tourism development, local settlement or pre-1900s land conversion for the sisal, mining and dairy industries in the region precipitated the extensive loss of existing 'north coast' coastal forest, and/or whether the original coastal plains (up until the mid 1800s) were historically covered by woodland rather than the coastal forest found in Kwale District (A. Githitho, pers. comm). However, it does seem that *C. a. palliatus* individuals were observed within remnant Kilifi Kaya forests along the inland hills and ridges up until the 1940s (based on oral history). Anecdotal reports of colobus sightings in the Arabuko Sokoke Forest Reserve until 1979 suggest a potentially recent extinction timescale. Considering the large area of this forest (37,000ha), it seems the most probable refuge in Kilifi for any remnant colobus population. The rare nature of colobus sighting events expressed by the north coast survey participants (leading as far back as the 1920s) made these sightings particularly memorable to participants. Colobus numbers must therefore have been extremely low in the Kilifi District during this time, with major population declines occurring before the 1900s.

The most striking difference between north and south coast that could explain the loss of *C. a. palliatus* from Kilifi forests involves the cultural differences between coastal Mijikenda that inhabit these regions. Namely, the 'north coast' Mijikenda; the Rabai, Chonyi, Kambe, Jibana, Giriama, Kauma and Ribe all hunt and eat monkeys, whilst the Digo and Duruma of south coast do not. The north coast Mijikenda trap monkeys, and also hunt them with dogs. Subsistence hunting of primates within the Arabuko Sokoke Forest for example, has been found to occur at unsustainable levels (Fitzgibbon, Mogaka & Fanshawe, 1995). Large bodied, slow moving and less visually alert (Oates, 1996b), colobus may have been more vulnerable to similar historical levels of hunting pressure, than other coastal primate species. In addition, past interest and the value of black-and-white colobus skin for local dancers (Kahumbu, 1997), medicine men (Adamson, 1967), international export and the tourist market (Mittermeier, 1973; Oates, 1977b) may have increased the benefits of north coast hunters to target colobus specifically. Rodgers (1981) also noted in his distribution survey of *C. a. palliatus* range in Tanzania that the 1981 southern limit of the subspecies range, i.e. the north bank of the Rufiji River, once extended further south (for specific localities, see Rodgers, 1981). Historical reports suggested that colobus were commonly seen in areas south of the Rufiji River before the advent of European rule, but that vegetation clearance and hunting for skins destroyed most populations.

2.5.3 Current threats and conservation initiatives

Unprotected forests in the Kwale District are under the heaviest exploitation. Illegal logging and charcoal production are the most prominent activities occurring in these forests. However, two additional patterns emerge when comparing forests by protection status. Firstly, forest loss and tree damage within Forest Reserves is not significantly different from unprotected patches. Moreover, the incidence of recent logging and hunting activity is high in Forest Reserves, thus increasing the vulnerability of colobus populations within these forests to further habitat loss, fragmentation and degradation. Forest Reserve status in Kenya has been criticised in the past for allowing considerable resource exploitation with little investment in protection (Lovett & Wasser, 1993). Most timber extraction observed within the Forest Reserves was illegal, with forestry guards lacking the resources, such as transport, capacity or training, to police areas effectively. It is clear that increasing law enforcement and management of the reserves would greatly improve their future preservation (Struhsaker, Struhsaker & Siex, 2005). To be effective, however, additional conservation strategies are required, incorporating local education and the development of both (1) Kenyan forest policy, i.e. forest protection, international timber trade, and (2) alternative wood resources, especially for the hardwood and woodcarving industries. For an extensive overview of the Kenyan timber trade (commercial and domestic), conservation problems and practical recommendations, see Marshall and Jenkins (1994).

Illegal hunting and snaring of wildlife was most evident within the Forest Reserves. It is also interesting to note the rising trend of hunting activity with increasing forest protection status (Fig. 2.4.d.). This may reflect covariation in the occurrence of other mammal species with forest protection status, but additional data on forest mammal densities are required to establish whether this is the case. Snaring is thought to be of minimal impact to the colobus (snares and traps are designed for terrestrial duiker and pig species), although there have been occasional reports of opportunistic hunting for colobus skins within the District (pers. obs). Nevertheless, the threat is thought to be minimal. Due to widespread local knowledge of Kenya Wildlife Service legislation, it was extremely difficult to obtain quantitative information about possible colobus poaching activities across the survey area.

The second emerging pattern from this study concerns the Kayas, which have lost relatively little forest cover (since 1989) compared to the unprotected forests. These forests are also exposed to relatively lower impacts of logging, hunting and charcoal activity. A partnership between local communities and the National Museums of Kenya may have been critical to successful Kaya forest protection (Githitho, 1998) because this partnership has (1) strengthened traditional Mijikenda forest values/protection (previously weakened by social, cultural and demographic changes in the District), and (2) provided additional conservation support to local communities fighting the commercial development of forested sites. The role of local community involvement within Kwale District forest management is presently undervalued (pers. obs.), and should be transferable to future conservation initiatives involving unprotected forests in the District.

The Diani and Shimoni forests provide essential habitat for two of the largest *C. a. palliatus* populations in the Kwale District. However, to date they remain unprotected and are heavily impacted by all local threat processes, particularly forest clearance for development and agriculture (Kahumbu, 1997; Struhsaker, 1981b). Logging, charcoal, firewood and hunting pressures were moderate in Diani when compared directly with Shimoni, but these differences are attributable to the ongoing conservation efforts of Wakuluzu, Friends of the Colobus Trust, based at this site (Cunneyworth & Rhys-Hurn, 2004). In both unprotected forests, involvement of local stakeholders is likely to be critical to the successful preservation of remaining forest habitat, focusing primarily on the economic potential of the colobus and coastal forest in these significant tourism centres (Hackel, 1999; Navrud & Mungatana, 1994).

It is also worth mentioning two future threats that may become more prevalent for the conservation of *C. a. palliatus* in Kwale District. Fristly, given the possible historical influence of Mijikenda hunting preference on colobus distribution in north coast, we should not rule out the potential increase in hunting of colobus for subsistence, with influxes of north coast or other Kenyan ethnic groups to the south coast as Kwale coastal development increases (Hoorweg, 2000). Secondly, present levels of *C. a. palliatus* crop-raiding are rare, and solely reported within the southernmost (Vanga) region of the Kwale District. However, *C. guereza* in western Kenya have been killed by locals in the belief that they cause major damage to crops (Oates, 1977b, pers. obs.). More research is required in the southern region of Kwale, to (1) quantify and monitor levels of human-wildlife conflict, and (2) determine whether regional differences in habitat loss are driving the localised occurrence of this behaviour.

Lastly, equivalent colobus surveys are required in Tanzania to determine the present status of *C. a. palliatus* within its entire East African range (IUCN, 2004). At present the most recent, published data concerning the national status of *C. a. palliatus* in Tanzania concerns a distribution study from 20 years ago (Rodgers, 1981). It is hoped that the results of this study will initiate future interest to replicate Kenyan *C. a. palliatus* population survey efforts within the coastal forests and Eastern Arc Mountains of Tanzania, or amalgamate presently unpublished subpopulation estimates for particular regions. The results of this study will also provide a baseline for strategic management and action plans specifically targeting *C. a. palliatus* and coastal forest conservation in Kenya.

3. Effects of forest fragmentation and habitat quality on the abundance of *Colobus angolensis palliatus* in Kenya's coastal forests.

3.1 Abstract

The Angola black-and-white colobus (*Colobus angolensis palliatus*) exists in forest patches across the southern coastal Kwale District of Kenya. These forest patches can be quite heterogeneous, and many suffer from anthropogenic impacts, but there is currently no information available to indicate how such factors affect the occurrence and abundance of colobus monkeys. In order to answer this question, 46 coastal forest fragments ranging from 1ha to >1,400ha were surveyed in 2001. In each patch, the occurrence and abundance of colobus monkeys were recorded, together with information on the spatial, structural, resource and disturbance characteristics of the forest. Thirteen hypotheses were tested to explain variation in patch occupancy and abundance patterns of *C. a. palliatus* in relation to these habitat attributes. Minimal adequate models indicated that the occurrence of colobus monkeys in forest fragments was positively associated with fragment area and canopy cover, whereas the density of colobus monkeys in occupied fragments was attributable to forest area, the proportion of forest change over the previous 12 years, and the basal area of 14 major food trees. Large-scale illegal extraction of major colobus food trees in the District for human resource use (in both protected and unprotected forests), together with ongoing forest clearance and modification, are highlighted as the major threats to *C. a. palliatus* in Kenya.

3.2 Introduction

Habitat loss, fragmentation and modification have long been cited as leading threats to the persistence of primate communities in East African tropical forests (Oates, 1996b; Rodgers & Homewood, 1982; Struhsaker, 1981b; Struhsaker & Siex, 1998). Massive human population growth in the region has led to high demand for forest resources (including fuelwood, charcoal, poles, and timber) and widespread agricultural expansion (primarily in the form of food crops and exotic tree plantations). This, in turn, has had a dramatic impact on East African forests, such that only a small fraction of the original forest cover now remains (Sayer, Harcourt & Collins, 1992). The impacts of forest loss alone, independent of the effects of fragmentation and modification in the remaining forest habitat, are estimated to threaten between 2-5 endemic primate species (17-39% of all species) with extinction in this region (Cowlishaw, 1999).

Colobine monkeys may be particularly vulnerable to these threats. Colobines are highly arboreal species that depend on leaves, seeds and unripe fruit (Davies, 1994), and may therefore be at high risk of extinction from deforestation (Davies, 1994; Marsh, Johns & Ayres, 1987). In West Africa, Colobine monkeys can also be highly vulnerable to the bushmeat trade (Oates, 1996b) as they are particularly sought after by hunters for their large-body size and higher financial returns (Davies, 1987; Lahm, 1993; Martin & Asibey, 1979). However, the impact of the bushmeat trade is less problematic in the present study, since the people of East Africa consume much less primate meat (Oates, 1996b).

Previous studies have found positive relationships between colobus abundance and forest habitat characteristics such as the basal area of food trees (Mbora, 2004), protein-to-fibre ratio of mature leaves (Oates *et al.*, 1990; Wasserman & Chapman, 2003), and canopy height and tree cover (Medley, 1993). Colobus occupancy in forest patches has also been found to be related to the amount of forest edge and canopy tree species composition (Mbora, 2004). However it would be incorrect to infer general trends for this subfamily of primates, since at species, or even subspecies level, populations can respond differently to habitat alteration (Cowlishaw & Dunbar, 2000b). For example, Asian colobine biomass has been positively correlated with the abundance of leguminous trees (Davies, 1994) whilst similar research has failed to find this relationship within the African colobines (Chapman *et al.*, 2002; Davies, Oates & Dasilva, 1999). Similarly, sympatric studies at Kibale Forest, Uganda, have found that *Colobus guereza* densities increased in light and heavily logged forest, but in contrast, *Procolobus badius* densities declined under the same habitat modification (Chapman & Chapman, 2002; Plumptre & Reynolds, 1994; Skorupa, 1986). The difficulty of making generalisations across taxa emphasises the need for detailed studies of individual species.

The Angola black-and-white colobus (*Colobus angolensis* Sclater 1860) is found within the forests of north-east Angola, Democratic Republic of Congo, Rwanda, Tanzania and Kenya (Kingdon, 1997). Relatively little is known about the species abundance in these regions (Mate, Colell & Escobar, 1995), nor its response to habitat fragmentation. However, from the limited data available, it is known that the species can achieve a diverse range of mean group sizes within differing forest habitats, from six individuals in the Diani Forest, Kenya (Kanga, 2001) to super-troops comprising 300 or more individuals in the Nyungwe Forest of south-western Rwanda (Fashing *et al.*, 2004; Fimbel *et al.*, 2001; Vedder & Fashing, 2002). Although the species is not currently listed as threatened, the subspecies *C. angolensis palliatus* Peters 1868, confined to islands of fragmented forest in coastal Kenya, Tanzania and the Eastern Arc Mountains (Kingdon, 1997; Rodgers, 1981; Tarara, 1986), has been highlighted as vulnerable to extinction due to deforestation caused by tourist development schemes (Kahumbu, 1997; Struhsaker, 1981b). Rapid rates of human population growth in the region have also led to heightened requirements for local timber resources (Marshall & Jenkins, 1994; Robertson & Luke, 1993), together with an intensification of forest clearance for animal husbandry and agricultural practices (UNEP, 1982), adding further pressure on the remaining *C. angolensis* populations. The IUCN African Primate Action Plan also recommended that the status of this subspecies needed to be assessed in Kenya, in conjunction with stringent management plans to conserve remaining coastal forest fragments within the region (IUCN, 1996).

Given the lack of knowledge concerning this subspecies and the conservation priorities linked to its future existence in Kenya, the aims of this research were to 1) identify the key habitat attributes that determine *C. angolensis palliatus* occupancy within coastal forest patches in Kenya and 2) identify those attributes that determine the abundance of *C. angolensis palliatus* populations in those occupied patches. In this analysis, we test thirteen hypotheses that relate colobus patch occupancy and abundance to the quality of the patch, which we define according to its spatial attributes, food resources, structural attributes, and human disturbance. These hypotheses are based on the findings of previous research on colobine abundance, and are summarised in Table 3.1.

Table 3.1. Independent habitat variables examined in the GLM statistical analysis and the hypothesized relationships with colobus abundance and occupancy.

Habitat Attributes	Proposed relationship	Hypothesised relationships with colobus abundance
Spatial		
Forest size	+	A greater coverage of food resources will encourage population occurrence and support greater numbers of colobus (Connor, Courtney & Yoder, 2000; Estrada & Coates-Estrada, 1996). Density responses are unknown (see Discussion).
Habitat edge	+	Patches with a greater degree of forest edge will support a greater density/occupancy of colobus due to the species exploitation of successional food resources i.e. young leaves, lianes and vines that arise from edge-effects (Coley & Barone, 1996; Johns & Skorupa, 1987)
Forest isolation distance	-	As a forest becomes increasingly isolated, chance immigrations from neighbouring colobus populations lessen. Small populations of colobus may risk future declines or extinction due to a breakdown of 'rescue effects'. (Brown & Kodric-Brown, 1977; Dunbar, 1987).
Resource		
Tree diversity	+	A greater variety of food resources, including infrequently used items, may enhance the resource quality and thus carrying capacity of forest patches (Chapman & Chapman, 1999; Medley, 1993). Lesser known tree species may also provide important fallback foods at times of food scarcity, thus encouraging colobus occupancy/abundance in patches (Cowlishaw & Dunbar, 2000b).
Tree, food tree & major food tree density	+	Increased density of trees will provide greater food resources (Chapman & Chapman, 1999; Mbora, 2004) and canopy coverage (Medley, 1993) for colobus. The degree of dietary flexibility within *C. a. palliatus* may be revealed through the relative influence of food trees and major food trees on colobus density/occupancy.
Structural		
Forest canopy height	+	Higher mean canopy heights greatly improve the canopy structure for an arboreal primate that rarely descends below 10m in the canopy (McGraw, 1998a; Medley, 1993), facilitating habitat occupancy and higher colobus densities.
Forest canopy cover	+	Greater degree of canopy coverage facilitates arboreal access to food resources (McGraw, 1998a; Medley, 1993), also providing greater shelter from avian predators (Struhsaker, 2000; Struhsaker & Leakey, 1990). Increased density/occupancy predicted.
Disturbance		
History of forest loss	+	Patches with a lower proportion of 1989 forest cover (<1), will have lower densities (or extinctions) of colobus due to reduction of food resources and lowered carrying capacity of forest. Conversely, patches which gain forest cover since 1991 (>1) will increase both carrying capacity and colobus density/occupancy (Bender, Contreras & Fahrig, 1998; Marsh, 1986).
Tree damage	-	The removal of trees from forest patches ultimately depletes food resources (Medley, 1993) and disrupts the structural characteristics of the forest (Chapman & Chapman, 1999), limiting the locomotion of an arboreal primate. Decreased abundance/occupancy predicted.
Human utilization (4 variables)	-	1) Villages near forests, 2) hunting, 3) logging and charcoal activities may have negative effects on colobus densities. Each activity can cause noise and structural disturbance to the forest (Cowlishaw & Dunbar, 2000b; Marsh *et al.*, 1987), 4) Paths and roads will also further fragment existing patches, encouraging higher levels of human traffic and additional noise disturbance. Decreased abundance/occupancy predicted.

3.3 Methods

3.3.1 Study Site

Kwale District, in the Coastal Province of Kenya, lies between Mombasa and the border of North Eastern Tanzania (3°30', 4°45'S; 38°31' and 39°31'E). Roughly 8,322km^2 in area, the District is largely an agro-ecological zone (Muchoki, 1990) resulting in a heterogeneous mix of land cover types that includes grasslands, woodlands, swamps, shrublands, forestry plantations, and annual and perennial cropland. Average temperature is about 26°C for the District, with highest mean temperatures of 33°C reached between November and April. The rainfall pattern is bimodal (long rains between March and July, short rains occur in October to December). Precipitation diminishes from the coastline to the hinterland, with the initial 36km from the sea: the 'coastal forest belt' (Clarke, 2000) receives 900-1500mm of rainfall annually (Jaetzold & Schmidt, 1983). Altitude varies from sea level along the Indian Ocean shore, to slightly over 1000m in the hinterland (HSEDCO, 1998). Due to the altitudinal and climatic conditions of the coastal belt, the area is also interspersed with fragmented and largely threatened coastal forest. These forests are remnants of what was once an extensive coverage of lowland rain forest, swamp forest, scrub forest and undifferentiated forest types (Clarke, 2000). Part of the 'Zanzibar-Inhambane floristic region' (White, 1976), and recently re-classified as the 'Swahilian Regional Centre of Endemism' (Clarke, 1998), these unique forests largely grow on coastal sedimentary rocks (Hawthorne, 1993) and provide habitat for the present-day Kenyan distribution of the Angola black-and-white colobus monkey (*Colobus angolensis palliatus*) (Fig. 3.I). There are 124 coastal forest fragments remaining in Kwale District, ranging in size from 1ha to 160km^2. Some forest patches are occupied by *C. a. palliatus* populations, while others are not. Both 'occupied' and 'empty' forest patches were the focus of this study.

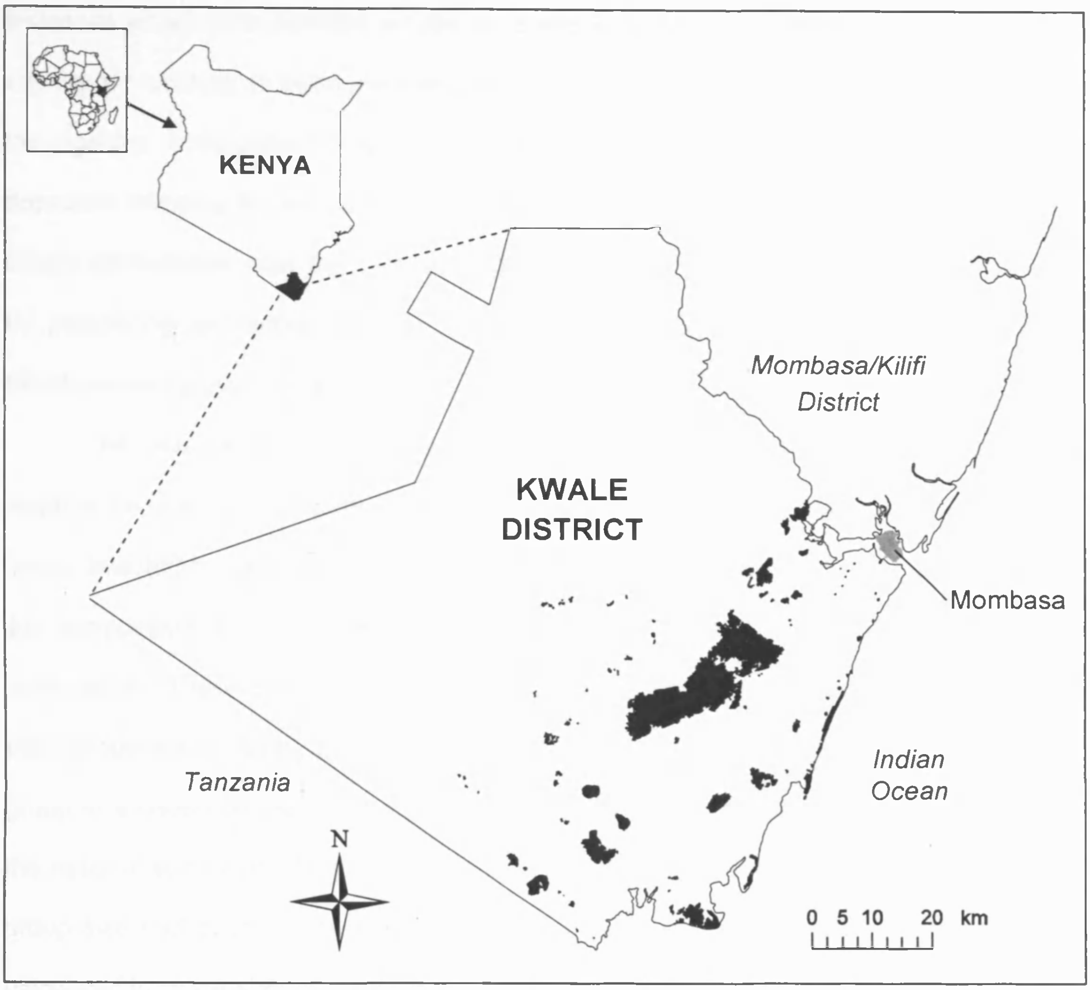


Fig. 3.1. The distribution of coastal forest fragments in Kwale District, Kenya.

3.3.2 Colobus incidence and abundance

Forty-six forest patches were randomly chosen for detailed ecological study from a larger national survey involving all 127 forest patches (see Chapter 1). Between July - November 2001, each of the 46 patches were systematically surveyed using a one-day "sweep sample" technique (Whitesides *et al.*, 1988) to obtain an estimate of colobus density for each forest patch. Four or more survey teams, each comprised of two trained observers plus one experienced colobus field researcher (from Wakuluzu, Friends of the Colobus Trust, Diani Beach, Kenya), began surveys between 06.30-07.00am each day. Teams walked parallel transects 100m apart, along pre-determined routes (Struhsaker, 1981a) until an entire forest patch had been covered. Total survey time was thus a function of patch area and the number of census teams. All primate encounters were recorded in relation to species, group size and age-sex composition, time, and location along the transect. In all instances where *C. a. palliatus* groups were encountered, up to ten minutes was spent with each group utilising all three members of each survey team to count and accurately identify the age-sex composition of group members. The time and direction of primate group departure following the encounter were also recorded. All teams discussed and enumerated results immediately after the completion of each survey and 'double-counts' were removed by comparing similarities in team observations, i.e. primate sighting times, departure directions and group compositions.

All primate encounters were ranked on a four-point scale in accordance with observation quality: 0, primate vocalisation detected but no individuals observed; 1, primate group detected but group count incomplete; 2, primate group detected and counted but age-sex composition incomplete; and 3, primate group detected with complete count and age-sex composition. These codes were used to guide the subsequent allocation of group size to each group encountered, as follows: 0, data discarded (no confirmed group encounter), 1, group size based on the mean group size obtained from all group counts of quality three in the national survey (n=196 groups), 2 and 3, group size taken from the actual count. Once group size had been established for all groups, the number of colobus in each patch was calculated from the sum of individuals in each group plus all solitary animals recorded.

3.3.3 Habitat attributes

During the same survey period all forest patch boundaries were mapped on foot by traversing the patch perimeter and recording positional data at 10 second intervals using a Garmin 12XL global positioning systems (GPS). These GPS data were then downloaded into MapSource software (MapSource 5.3, Garmin Corporation 1999), before being imported into an ArcView geographic information system (ArcView GIS 3.2, ESRI Inc. 1999) where subsequent GIS analysis using Xtools (Version 6.1, 2001) and Nearest Features (Version 3.6e, 2001) extensions allowed for the detailed estimation of forest spatial attributes, including forest area (ha), perimeter (m), habitat edge (area-to-perimeter ratio), and patch isolation distance (m).

Four botanical survey teams, each comprising two researchers, used transects to collect data on forest resource and disturbance for each of the 46 patches. Between 3-26 transects were carried out in each patch, depending on the patch area. Transect length also varied between patches (longer transects were used in larger patches), so that total transect length varied between 100m-3,000m per patch. The systematic placement of transects throughout each forest also ensured an accurate representation of each patch. Transect data can be divided into three headings: forest resources, forest structure, and forest disturbance. In the first case, forest resources, all trees $\geq$10cm in diameter at breast height (DBH) were enumerated within 4m of the transect (Grieg-Smith, 1983). Tree species, height (m) and DBH (cm) were also recorded, the latter providing a relative index of canopy cover (and possible resource availability) for the colobus (Decker, 1994). These data were used to calculate tree diversity (number tree species/ha), absolute tree density (basal area m^2/ha), absolute food tree density (basal area m^2/ha) and absolute major food tree density (basal area m^2/ha). Food trees were identified from ongoing research involving whole-day follows of colobus groups within the Diani Forest, Kwale, conducted by the Colobus Trust (unpubl. data). The Diani Forest is one of the 124 patches studied in our national survey of Kenya's coastal forest system, but it was not one of the 46 patches chosen for more detailed study here. Feeding behaviour and plant food species were recorded through instantaneous scan sampling of all group members at ten-minute intervals. This provided us with a basic list of food trees that was supplemented by feeding observations during the course of our 2001 survey and by local field-assistant knowledge of colobus inhabiting other forests within the District. Major food trees were established by calculating the proportion of colobus feeding bouts (*n*=14,445 individual feeding scans) for each tree species recorded by the field researchers during the periods of Aug-Oct 1999 and Feb-June 2003.

In the second case, forest structure, the canopy height (m) and canopy cover (%) were recorded every 50m along the transect. Mean values were then calculated for each patch. In the third case, forest disturbance, four types of data were collected: (1) all tree damage within 4m of the transect, including stump/stem diameters, tree species, type of damage (natural death, animal damage, logging, debarking), and age of damage (recent, old, very old); (2) the perpendicular distances of all visible snares, pitsaws and charcoal pits from the transect; and (3) all encounters with loggers, hunters, firewood collectors, access paths and roads along the transect. In addition, at 100m intervals along the patch perimeter, we estimated the minimum distance of human settlement to the forest. Patch disturbance was thus summarised as the absolute density of tree damage (basal area m^2/ha), minimum distance (m) to human settlement, density of snares (snares/km), relative density of human paths and roads (number of paths and roads/km), and the incidence of pitsaws and charcoal pits (presence vs. absence).

3.3.4 Historical forest loss

To determine the effect of recent deforestation we digitised eight topographical maps covering the Kwale District. These 1:50,000 maps were based on 1989 aerial photographs and field survey work by the Japan International Cooperation Agency and Survey of Kenya (Edition 4 – JICA, 1991). Scanned TIFF files of the maps were imported into ArcMap (ArcInfo 8.3, ESRI Inc. 2002) and geo-referenced. The forest boundaries were then digitised. We measured forest change for each of the patches as the proportional change in forest cover between 1989 and 2001 (i.e. values <1 indicated loss in forest cover, 1=no change, and >1 indicated gain in forest cover).

3.3.5 Statistics

A generalised linear model (GLM) framework (Crawley, 1993) was used for the analysis of both colobus patch occupancy and density, using the statistical software R, version 1.9.1 (www.r-project.org). The first model, a stepwise GLM analysis with binomial error structure, identified the habitat attributes that influenced colobus occupancy within 46 forest patches. Each forest patch was regarded as a unit, with presence or absence of populations coded as a binary response variable. All explanatory variables detailed in Table 3.1 were entered into a full model and log (base e) transformed to normalise the distribution of these variables. The only exceptions were canopy cover, canopy height and proportion of forest change, since their distributions were already normal. All non-significant variables were sequentially removed, least significant first, until a minimal adequate model was reached. Statistical significance was tested using deletion F-tests corrected for over-dispersion.

The second model analysed colobus density in occupied patches using a stepwise GLM with Poisson error structure. The total number of colobus individuals within each of the

33 occupied patches was the response variable, with patch area as an offset parameter. The influence of the habitat variables in Table 3.1 was tested by finding the minimal adequate model, using the same approach as for presence-absence data.

During the exploratory phases of both occupancy- and density-model fitting, three variations in the estimation of resource availability were tested, namely the basal area of all trees, food trees and major food trees. These variables were closely correlated and not expected to have independent effects, so were not tested jointly in any given model. Rather these alternatives were tested in order to determine which, if any, had the strongest effect on density and occupancy.

3.4 Results

3.4.1 Colobus occurrence & density

Thirteen empty and thirty-three (71.7%) occupied forest patches were surveyed, which ranged in size from 1ha to 1,417ha. A total of 769 Angola black-and-white colobus monkeys were recorded within 136 social groups. Mean colobus group size was 6 (median = 6), ranging between 2-13 individuals per group. In two of the 33 occupied patches we found only solitary individuals. Patterns of abundance varied dramatically between forest patches. Colobus numbers varied between 0-110 individuals per patch, whilst densities ranged from 0.04-1.3 individuals/ha (4.3-129.0 individuals/km^2). Resident colobus groups were found within small forest fragments (the smallest being 3.1ha) which gave rise to unusually high densities of colobus within those fragments.

3.4.2 Habitat attributes

From the 875,217m^2 of vegetation transects we enumerated 325 tree species in 53 families. From this tree list it was possible to establish 116 species as *C. a. palliatus* food trees (Colobus Trust unpub.) and thus calculate food tree abundance (basal area of food trees) in each patch. Fourteen tree species make up over 75% of *C. a. palliatus* diet in the Diani Forest, Kenya (Table 3.2).

Table 3.2. Major *C. a. palliatus* food trees responsible for >75% feeding records in the Diani Forest, Kenya. Local human use is also recorded since this may reflect possible human resource conflicts.

Family	Species	Part eaten [a]	Common, Swahili name	Local human use
Anacardiaceae	*Lannae welwitschii*	YL, ML, P, Fl, Fr, B	Muyumbu-Maji	Charcoal, furniture, fruit-edible, bark-rope and medicinal
Araliaceae	*Cussonia zimmermannii*	YL, ML, P, Fl, Fr, S	Cabbage Tree, Mbomba Maji	Furniture
Bombacaceae	*Adansonia digitata*	YL, ML, P, Fl, Fr, B	Baobab, Mbuyu	Fruit-edible, bark-ropes,weaving and medicinal, roots-dye and medicinal
Combretaceae	*Combretum schumannii*	YL, ML, P, Fl, F, S	Mgurure, Mpera-Mwitu	Hardwood timber, building timber and poles, charcoal, fuelwood, woodcarving
Euphorbiaceae	*Drypetes reticulata*	YL, ML, P, Fr	unknown	Charcoal, building timber and poles
Meliaceae	*Trichilia emetica*	YL, ML, Fr, S	Mnwamaji	Fuelwood, building timber, furniture, roots-medicinal and seeds-oil used for soap
Moraceae	*Milicia excelsa*	YL, ML, Fl, Fr, S	Iroko, Mvuli	Building timber, boat building, furniture, joinery and bark-medicinal
Papilionaceae	*Millettia usaramensis*	YL,ML	Mwino, Mtupa	Hardwood timber used in building
Rutaceae	*Zanthoxylum chalybeum*	YL, ML, P, Fr	Knobwood, Mjafari	Building timber, bark and leaves-medicinal
Sapindaceae	*Lecaniodiscus fraxinifolius*	YL, ML, P, Fl, Fr, S	Mkunguma	Hardwood timber used in building
	Lepisanthes senegalensis	YL, ML, S	unknown	Building timber and furniture
Sapotaceae	*Sideroxylon inerme*	YL, ML, P, Fl, Fr, S	Mkokobara, Mtunda	Fruit-edible
Tiliaceae	*Grewia vaughanii*	YL, ML	unknown	Building poles, fuelwood, bows and fruit-edible
	Grewia plagiophylla	YL, ML, P	Mkone, Mfukufuku	Building timber, fuelwood, bows, arrows, rungus, fruit-edible, roots-medicinal

[a] Plant parts eaten by *C. angolensis* are: YL = young leaves, ML = mature leaves, P = petioles, Fl= flowers, Fr = fruit, S = seeds, B = bark

Overall resource abundance, as measured by basal area m^2/ha for all trees, was found to be highly variable between patches, and unrelated to forest area (Pearson correlation; $n=46$, $r=-0.08$, $p=0.6$). Not only did we find considerable variation in overall tree density, but the availability of colobus food and major-food resources also differed between forests (Fig 3.2). The severity of forest disturbance also ranged widely from 3-44% basal area tree removal between patches (median 10%). Extraction practices included the local collection of firewood, building poles and medicinal bark (small-scale disturbance), as well as illegal hardwood timber logging and charcoal production (large-scale clearance).

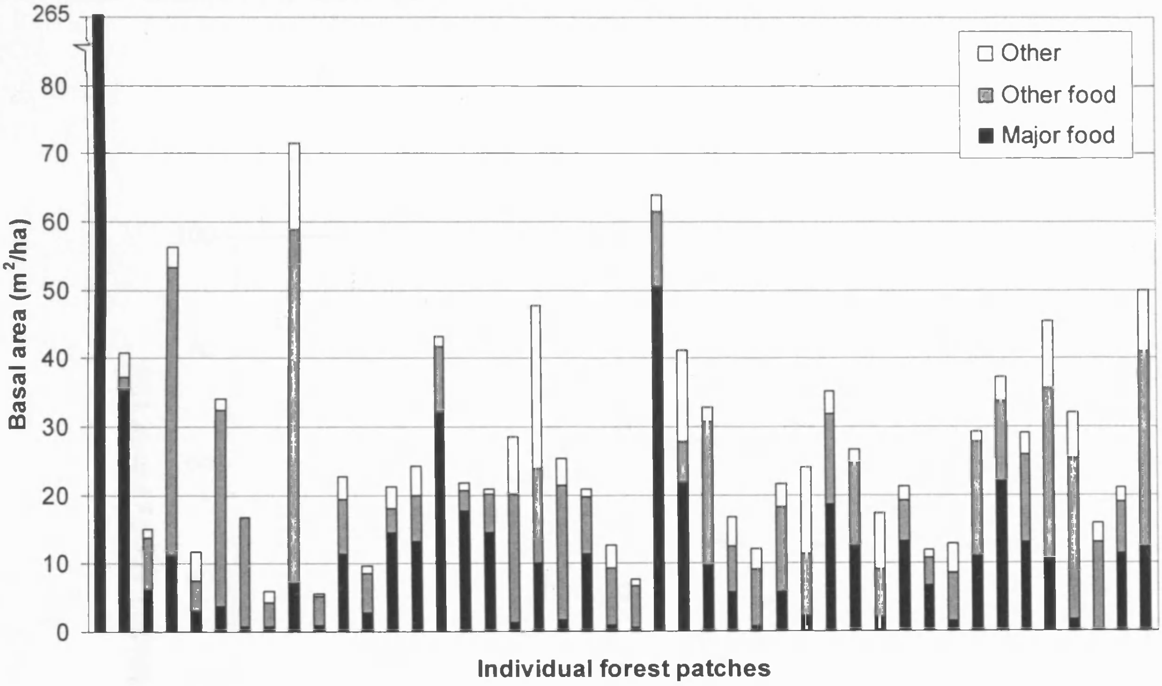


Fig 3.2 Basal area coverage of major food trees, other food trees and other trees, highlighting the resource variability between forest fragments. Patches plotted in order of increasing forest area (ha). The smallest forest patch has an unusually high major food tree density due to the prevalence of baobab *Adansonia digitata* within that patch (tree species known for < 1000 cm dbh).

Occupancy of forest patches by colobus monkeys was positively related to forest area and to degree of canopy cover (Table 3.3). The presence of colobus thus became increasingly rare as patch area diminished and canopy cover declined (Fig 3.3). The combination of these two factors explained 31.7% of the variance in occupancy of colobus populations observed in this study. None of the remaining eleven habitat attributes (Table 3.1) predicted occupancy in the model.

Table 3.3. GLM analysis of habitat variables determining *C. a. palliatus* occupancy and density.

Response variable	Predictor variable	Parameter co-efficient	SE	F	p
Occupancy [1]	Area	0.84	0.297	14.38	0.0004
	Canopy cover	0.05	0.024	5.96	0.02
Individual colobus density [2]	Area	-0.55	0.027	52.43	<0.0001
	Proportion of forest change	1.11	0.152	9.33	0.005
	Major food tree density (m2/ha)	0.17	0.033	4.95	0.03

[1] GLM Binomial presence/absence model (null deviance = 54.78, residual deviance = 37.42, df = 43,1)
[2] GLM Poisson density model (null deviance = 473.99, residual deviance = 156.66, df = 29,1).

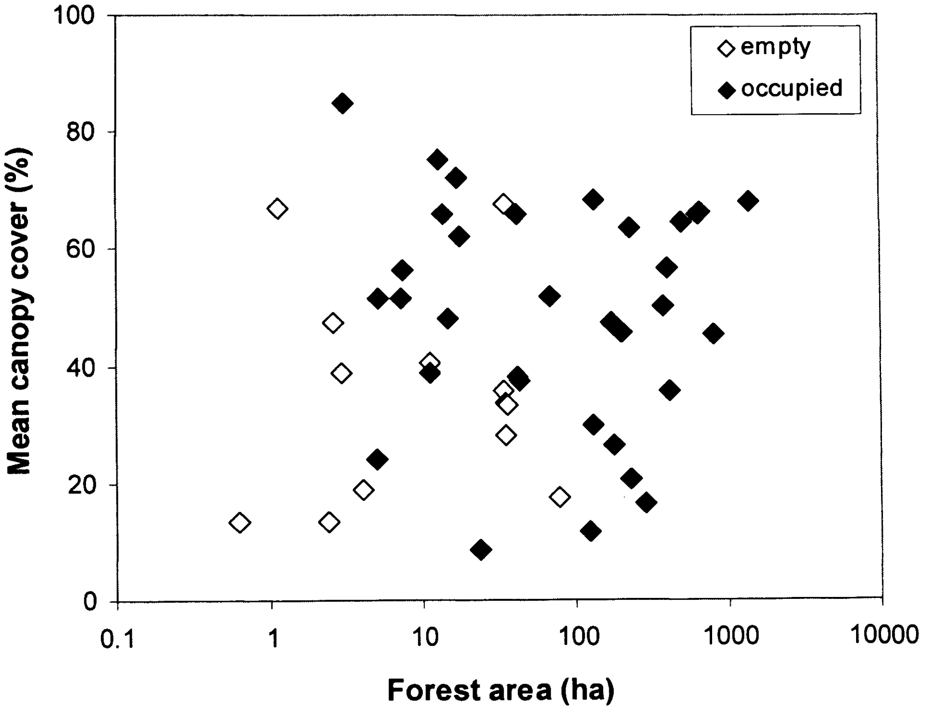


Fig. 3.3 Occupancy patterns of *C. a. palliatus* populations within forest fragments.

In the occupied patches, colobus density was positively associated with both the proportion of forest change and the density of major food trees $\geq$10cm DBH, and negatively associated with patch area (Table 3.3). Although colobus density increased in smaller patches (Fig 3.4) the effect was evidently a relatively small one, since the absolute number of colobus still showed a significant positive relationship with forest area (regression; B = 0.49, t = 6.32, df =31, $p<0.0001$, $R^2_{adjusted}=0.55$) (Fig 3.5). Overall this model, encompassing these three explanatory variables, accounted for 67.1% of the variance in colobus density. None of the other ten habitat attributes (Table 3.1) explained any further variance.

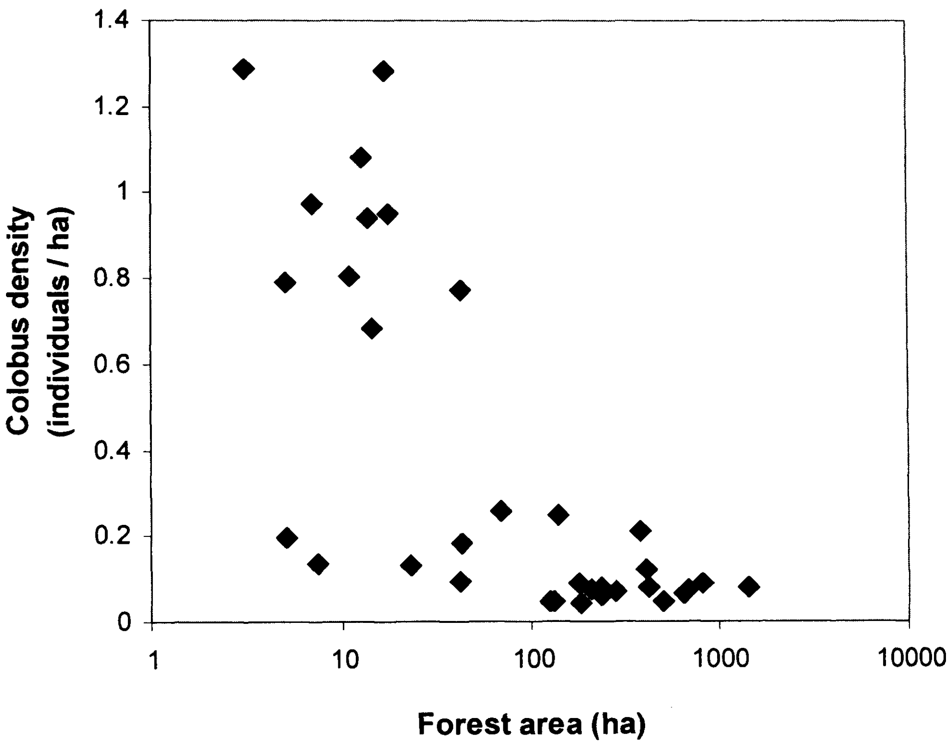


Fig. 3.4 Population density of *C. a. palliatus* in forest fragments, Kenya

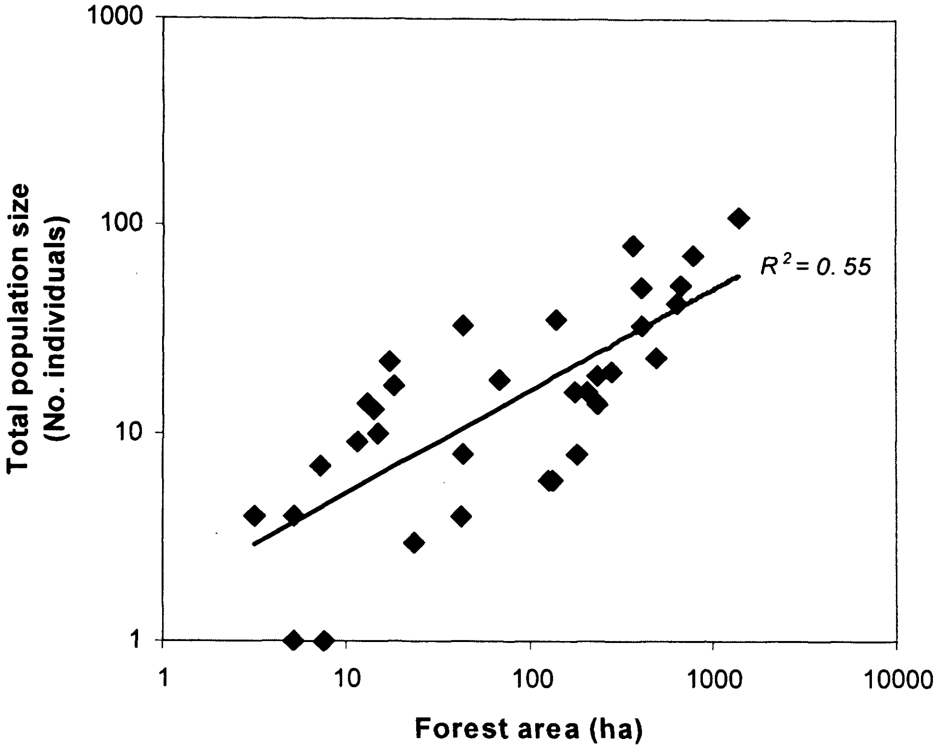


Fig. 3.5 Population size of *C. a. palliatus* in forest fragments, Kenya

3.5 Discussion

This study highlights the wide range of population responses that a colobine species can exhibit to ongoing habitat modification, fragmentation, and loss. Importantly, the occurrence and abundance of *C. angolensis palliatus* populations in Kenyan coastal forest fragments was found to be significantly influenced by a number of habitat attributes, encompassing multiple aspects of forest spatial, resource, structural and disturbance characteristics. Here I will review these effects in more detail and consider their implications for the conservation management of the Angola black-and-white colobus monkey in the coastal forests of Kenya.

3.5.1 Forest spatial attributes

Forest area is the most influential of all habitat variables, strongly affecting patterns of both patch occupancy and density in *C. a. palliatus* populations. The former effect might be expected given the initial hypothesis (Table 3.1) and the widespread positive species-area relationships that have been addressed explicitly by island biogeography theory (MacArthur & Wilson, 1967) and more recently in metapopulation theory (Hanski & Gilpin, 1991). In contrast, recent colobine studies of *Procolobus rufomitratus* in Tana River, Kenya (Mbora, 2004), and *Procolobus badius* and *C. guereza* in Kibale, Uganda (Onderdonk & Chapman, 2000), found no evidence of a relationship between species occupancy and patch area. Mbora (2004) suggested possible metapopulation dynamics could be influencing the observation of 'suitable' unoccupied patches within the Tana River system, whilst Onderdonk & Chapman (2000) highlighted a high degree of dietary flexibility within the Kibale Forest colobines allowing species to exist as remnant populations in small patches. However, rather than infer any underlying differences between these species and *C. a. palliatus*, this disparity may simply be the result of a greater number and size-range of forest patches within this analysis that has permitted the detection of this effect. Studies of another folivorous primate, *Aloutta palliata*, may highlight this point: species incidence was found to increase in larger patches across 64 forest fragments in Southern Veracruz, Mexico (Rodriguez-Toledo, Mandujano & Garcia-Orduna, 2003).

The relationship between forest area and primate density is rather more complex. Although colobus population size increased with increasing patch area (Fig 5), the increase was not proportional, resulting in lower colobus densities in larger forest patches (Fig 4). A similar pattern has been described for *Allouata palliata* abundance by Rodriguez-Toledo *et al* (2003). There are two possible reasons for this increase in density in smaller patches. Firstly, it may be the outcome of random processes, and not a real effect. This may arise because small absolute deviations from the expected number of groups counted in the smallest patches can lead to very high densities, purely at random. Due to the density analysis excluding unoccupied patches, these high densities are not then offset by zero counts, and a negative relationship between patch area and density might therefore arise without any underlying functional pattern. Secondly, small patches with high colobus densities may be those that have recently undergone a substantial contraction of area, in which densities of colobus have not yet adjusted to a new equilibrium (Cowlishaw & Dunbar, 2000b). However, the analysis of the effects of proportional forest change, below, do not support this possibility. Nevertheless, this process cannot be ruled out entirely, since this analysis only measured change over a 12-year period and this time-frame may be inadequate for demographic readjustment to take place where habitat loss has occurred more recently (e.g. in the last 2-3 years).

No evidence was found for the expected positive relationship between colobus abundance/occupancy and the extent of edge habitat, i.e. the forest area-to-perimeter ratio (Johns, 1987; Johns & Skorupa, 1987; Mbora, 2004). *Colobus guereza* differ from *C. a. palliatus* (at least in southern Kenya) in that they principally exploit the understory of forests rather than the high canopy (Oates, 1977a). They also thrive in moderately disturbed habitat (Chapman *et al.*, 2004; Johns, 1985; Skorupa, 1986), feeding on the proliferation of young leaf growth and vines which accompany the increased light conditions within forest gaps and edges (Coley & Barone, 1996; Ganzhorn, 1995). The absence of habitat edge effects on *C. a. palliatus* populations may therefore highlight different responses to habitat fragmentation between these species as a result of differences in feeding ecology. In fact, the relationship between proportional forest change and *C. a. palliatus* density (see below) suggests that this species may be negatively affected by the amount of habitat edge, because as forest is progressively lost a reduction in forest area will increase the amount of edge habitat within each patch (Bender *et al.*, 1998). Further differences in the feeding ecology and habitat use of black-and-white colobus species can be found in a detailed comparison of niche separation in sympatric *C. guereza* and *C. angolensis* populations within the Ituri Forest of north-eastern Zaire (Bocian, 1997).

Abundance and occupancy patterns did not reveal any effects of patch isolation, even though patch isolation distances varied between 0.008-6.6km. This would suggest that dispersal by *C. a. palliatus* between patches is not strongly limited by distance in this system. This implies that the intervening matrix between fragments (Berggren, Carlson & Kindvall, 2001; Gascon *et al.*, 1999; Ricketts, 2001) may be sufficiently permeable to make both recolonisation and "rescue effects" (Brown & Kodric-Brown, 1977) equally likely at both short and long isolation distances. In fact, colobus were sighted within various matrix vegetation types (e.g. mangrove, perennial cropland, coastal shrubland) in the course of the field research (J. Anderson, unpubl.), and further analyses will expore the extent and relative importance of this additional habitat variable in primate occupancy patterns in the coastal forests of Kenya (see Chapters 4 and 6).

3.5.2 Forest resource attributes

The abundance of major food resources positively influences colobus density. The influence of one of the 14 tree species, the baobab *Adansonia digitata* with its unusually large trunk diameter ≤ 1000cm (Beentje, 1994), could have biased these analyses through an overestimation of major food availability, since basal area is used as a relative index of canopy cover, and thus food availability (Decker, 1994). However, when basal areas of *A. digitata* were substituted with mean basal areas of food trees (that excluded *A. digitata* in the calculation, and were patch specific), the significance of this variable remained constant.

It is particularly interesting that neither the density nor diversity of all trees, food trees or major food trees predicted occupancy, whilst only the latter predicted density. It may be that *C. a. palliatus* exhibits a high degree of dietary flexibility, eating low-quality, less preferred foods when required, allowing populations to occupy patches when resource quality is relatively low. The large number of indigenous tree species (*n*=116) exploited by the colobus in south coast Kenya, may already highlight this phenomenon. However, the relationship between major food tree density and colobus abundance indicates that, once a patch is occupied, the key local food resources can play an important role in supporting high colobus population densities. The importance of food trees in predicting colobine abundance has also been found in a number of African study sites (Chapman & Chapman, 1999; Decker, 1989; Mbora, 2004; Skorupa, 1986). In addition, Chapman & Chapman (1999) discovered that dietary composition varied dramatically between colobus populations in Kibale forest fragments, Uganda. A similar situation could be inferred from the coastal forest fragments of Kenya, given the differences in food resource distribution illustrated in Fig 3.2. A clearer validation of this result would come from further studies of the feeding ecology of *C. a. palliatus* within differing forest fragments, as well as research into the nutrient quality (Moreno-Black & Bent, 1982), especially the protein and fibre content (Chapman *et al.*, 2004; Oates *et al.*, 1990; Wasserman & Chapman, 2003), of colobus food plants in the region.

3.5.3 Forest structural attributes

In light of current theories that focus on the geometry of forest fragments to explain patterns of occupancy (Hanski & Gilpin, 1991), it is interesting to note a characteristic of habitat quality, i.e. canopy cover, was found to be a significant predictor of population incidence. Umapathy & Kumar (2000) found a similar effect of forest structure in south India: two arboreal primate species, *Trachypithecus johnii* and *Macaca silenus*, were more likely to occur in fragments with high tree density, canopy height and canopy cover. Our result is likely to reflect the fact that canopy cover will be extremely important to an arboreal primate that relies heavily on continuous canopy to gain access to food resources (Arosen, 2004; McGraw, 1998b) and also to avoid predators. Avian predation on colobines has been well documented in East and West Africa (Struhsaker, 2000; Struhsaker & Leakey, 1990) and high rates of terrestrial predation on *Presbytis entellus* in India have been linked to low canopy cover (Ross & Srivastava, 1994). The same may apply to *C. a. palliatus* in the Kwale District, where sea eagle predation on primates has been observed (pers. obs.) and broken forest canopies are known to increase the proportion of time colobus spend on the ground, thus increasing the frequency of incidental encounters with both feral dogs and hunters' dogs. These effects were observed in one colobus group that contained no adults as a result of repeated dog attacks (confirmed through local interviews).

3.5.4 Forest disturbance attributes

Colobus density was significantly affected by the proportion of forest change between 1989 and 2001: colobus density was higher in patches with increasing forest area but, conversely, was lower in patches with declining forest area. Although some forest patches were observed to grow in size over this period, probably through the abandonment of agricultural plots on the boundaries of forests (Ganade, 2001) and the implementation of Kenyan Forestry Department plantation schemes over the past 12 years (Marshall & Jenkins, 1994), these forest patch gains were in a clear minority. Thirty-eight of the patches suffered 3–96% declines in forest coverage with corresponding reductions in colobus numbers. The combined effects of reduced patch size, increased resource competition, and decreased connectivity of the landscape (Bender *et al.*, 1998), may be jointly responsible for these changes in colobus abundance beyond those associated with habitat area alone.

More direct measures of disturbance, as measured by the density of tree removal, paths, roads, snares, the presence of charcoal activities and proximity to human settlement, were not found to significantly affect colobus abundance as independent variables. This need not mean that they lack influence in particular cases, but that there was no consistent effect overall that we could detect in this sample. There can be little doubt that *C. a. palliatus* is vulnerable to human disturbances, given that a study in the Ituri Forest, Zaire, found that the abundance of colobus was more than halved between mixed and logged forests (Thomas, 1991). In fact, our analyses may indicate longer term effects of disturbance on colobus populations, since two of our four significant habitat measures (canopy cover and food tree density), may reflect historical disturbance that is now only detectable through these structural/compositional forest attributes.

What is certain from the analysis is that there is a major degree of resource overlap between colobus food trees and human extraction practices. From our analyses of absolute density of tree damage we identified 216 tree species which were logged for hardwood timber, woodcarving, domestic timber, fuelwood and charcoal within the forests of the Kwale District. Over 45% of this extraction targeted just 10 species of indigenous tree. Nine of these species are food trees of the colobus whilst four are major food trees, namely; *Millettia usaramensis*, *Combretum schumannii*, *Grewia sp.*, and *Lecaniodiscus fraxinifolius*. Given the relative importance of these food trees for colobus abundance, and their continued extraction by humans, it may only be a matter of time before *C. a. palliatus* populations decline and/or become extinct in response to the permanent removal of these major food resources (Decker, 1989; Skorupa, 1986).

3.5.5 Concluding remarks

This study highlights the negative impact of coastal forest habitat destruction on *C. a. palliatus* populations in the Kwale District, Kenya. Identification of the precise mechanisms responsible for the variety of occupancy and abundance patterns observed in primate studies is extremely complex, particularly with regard to independent measures of forest disturbance. However, our GLMs were successful in attributing >65% of the variance in colobus density, and 32% of the variance in occupancy, to habitat attributes. The latter response still has a considerable amount of variance left unexplained: a more comprehensive analysis, encompassing all 124 forest patches, of forest spatial attributes and intervening matrix structure, may provide a better understanding of patch dynamics and subsequent colobus occupancy patterns in a regional metapopulation context (Gustafson & Gardner, 1996; Hanski, 1999a; Vandermeer & Carvajal, 2001).

Forest loss and ongoing tree extraction in the Kwale District is a dynamic and ongoing process, even within protected Forest Reserves and Kayas (sacred local forests, gazetted as National Monuments) (Robertson & Luke, 1993). The high degree of human and colobus resource overlap, with local human populations showing a propensity for extracting the major food trees of the colobus, has serious implications. As a result of ongoing forest loss, and the extraction of food trees in the remaining forests (affecting both the availability of food resources and the structure of the forest canopy), it is very likely that we shall witness future declines of *C. a. palliatus* densities, and increased population extinctions, over the coming years. The outcomes of this study therefore highlight the importance of maintaining large closed-canopy forests within the District, and the restoration of degraded habitat, wherever possible. This will require improved law enforcement of illegal logging, better forest management, and the promotion of alternative human resources.

4. Does the matrix matter? : Heterogeneous 'non-habitat' between forest fragments and its relevance to an arboreal primate.

4.1 Abstract

Rarely in the study of tropical forest fragmentation and its effects on primates is the matrix habitat surrounding fragments considered. The ability of primates to utilise such heterogeneous regions between forest fragments may greatly influence their vulnerability in fragmented landscapes. Using semi-structured interviews, matrix vegetation sampling and remote sensing techniques, this study focused on an arboreal forest-dependent primate: the Angola black-and-white colobus (*Colobus angolensis palliatus*) and its use of the matrix within the fragmented coastal forest landscape of southern Kenya. Both colobus individuals and groups were observed (by the local community) within the matrix up to 4km from nearby forest fragments. Colobus frequently travelled through indigenous matrix vegetation such as mangrove, wooded shrubland and shrubland areas, additionally using these matrix types as supplementary foraging habitats. Anthropogenic matrix such as perennial plantation (of coconut, mango and cashew nut) was also used for colobus travel. Individuals utilised the dense, 'arboreal-friendly' tree canopy of this matrix type to gain access to additional food resources, i.e. sparsely distributed indigenous tree species that were remnant within this habitat. The probability of sighting colobus individuals within the matrix was positively related to the proportion of tall (>6m) vegetation cover and the proportion of colobus food tree cover. Sighting probability was also negatively associated with distance from core forest habitat. By utilising remote sensing and land-cover GIS mapping techniques as an additional, spatially-explicit tool for understanding the complexities of matrix heterogeneity in fragmented tropical forest regions, wildlife managers can effectively: (1) visualise the extent of important matrix habitats, (2) highlight the differing levels of connectivity between forest fragments, and thus (3) prioritise 'landscape-level' habitat management which includes the matrix, that could bolster primate conservation initiatives in fragmented landscapes.

4.2 Introduction

Research into tropical deforestation and its effects on primate populations has largely focused on three major components of habitat fragmentation, namely the degradation of original forest habitat, the reduction in habitat patch size, and the increasing isolation of habitat patches (Andren, 1994; Marsh, 2003b). The quality and spatial characteristics of forest fragments is significant in understanding any remnant population's behaviour, density, viability, and ultimately species conservation and management (Chapman & Lambert, 2000; Fahrig, 2003; Marsh, 2003a). Most studies tend to measure habitat quality in terms of forest size, structural characteristics, food resource abundance and levels of disturbance. Most, if not all, quantifiable research takes place within the boundaries of the forest fragments (e.g. Medley, 1993; Onderdonk & Chapman, 2000). The complex mosaic of vegetation types that buffer forest boundaries therefore receives little attention in these analyses. Often referred to as "matrix" (Gascon *et al.*, 1999; Ricketts, 2001; Vandermeer & Carvajal, 2001), these 'non-forest' vegetation types are believed to be of limited use to forest-dwelling primates.

Theories of island biogeography (MacArthur & Wilson, 1967) and more recently, metapopulation dynamics (Hanski, 1998; Hanski & Gilpin, 1991; Levins, 1969a) also assume that suitable habitat patches are isolated from one another by homogeneous, inhospitable matrix (Addicott *et al.*, 1987; Vandermeer & Carvajal, 2001). Limited dispersal of individuals between patches (a crucial assumption of metapopulation theory) is assumed to be influenced by distance only (Hanski, Alho & Moilanen, 2000), ignoring the possibility that matrix vegetation could facilitate or impede an animal's dispersal, depending on the structural characteristics of the matrix and the dispersal ability of the study species (With & Crist, 1995). The arboreal colobines for example, are thought to rarely leave forest patches due to their dependence on continuous, closed forest canopy (Chapman *et al.*, 2004; Marsh *et al.*, 1987), questioning the applicability of the metapopulation concept as a framework in which to describe, assess and manage fragmented colobine populations.

Whilst extensive examples of individual primate dispersal between groups, also known as 'social dispersal' or 'transfer', can be found throughout the primate literature (Field & Guatelli-Steinberg, 2003; Isbell & VanVuren, 1996; Pusey & Packer, 1986) and, more specifically, the colobine literature (Korstjens & Schippers, 2003; Oates, 1977c; Rajpurohit, Sommer & Mohnot, 1995; Sterck, 1995), these studies solely focus on individual movements between social groups within the same habitat patch. In these cases, the research focus is primarily driven by hypotheses concerning the evolutionary reasons for primate dispersal, i.e. intragroup competition for resources, intrasexual competition for mates and inbreeding avoidance. In contrast, 'locational' primate dispersal, i.e. the movement of individuals away from familiar areas (Isbell & VanVuren, 1996), with particular reference to long-distance dispersal movements between habitat patches, has yet to be systematically studied.

It is now recognised that primates can exhibit great ecological and behavioural flexibility in response to their changing environment. For example, anthropogenic land transformation has allowed some species to exploit agricultural matrix on the boundaries of their natural habitats (Cowlishaw & Dunbar, 2000b). Local subsistence crops can offer an alternative food resource to most of the frugivorous cercopithecine and pongid species (Cowlishaw & Dunbar, 2000b; Naughton-Treves, 1998; Reynolds, Wallis & Kyamanywa, 2003; Wolfheim, 1983), whilst colobines are also documented as occasional crop raiders (Naughton-Treves, 1998). Indigenous matrix vegetation can also provide additional food resources for colobus in the form of mangrove foliage (Siex, 2003, pers. obs.) or secondary vegetation found within abandoned agricultural plots and coastal shrubland areas (Moreno-Black & Maples, 1977). The structure of the matrix, i.e. the number of canopy layers, canopy height, density of large supports and canopy cover, may influence an arboreal primate's access to such food resources (Aronsen, 2004a; McGraw, 1998a; Umapathy & Kumar, 2000), as well as hinder or facilitate dispersal between habitat patches. A number of anecdotal reports have been found of arboreal primates dispersing through plantations (Laidlaw, 2000; Li, 2004; Olupot & Waser, 2001; Umapathy & Kumar, 2000) and wooded shrubland (Marsh, 1979; Wieczkowski, 2004), which suggests that continuous, closed-canopy matrix may be important to facilitate these movements.

The recent integration of landscape ecology, the study of landscape structure and its effects on ecological processes (Turner, 1989), with studies of forest fragmentation, have highlighted the importance of studying fragments within a larger, dynamic landscape mosaic (Fahrig & Merriam, 1994). For example, matrix composition and connectivity have been found to influence the dispersal, diversity, abundance and population persistence of insects (Bonte *et al.*, 2003; Goodwin & Fahrig, 2002), birds (Aberg *et al.*, 1995; Jokimaki & Huhta, 1996; Wethered & Lawes, 2003) and mammals (Cook, Anderson & Schweiger, 2004; Gascon *et al.*, 1999; Goheen *et al.*, 2003; Laurance & Laurance, 1999; Pardini, 2004; Reunanen, Monkkonen & Nikula, 2000; Schippers *et al.*, 1996). In the latter, both terrestrial and arboreal mammal species were studied; however, this approach has yet to be considered for primates. If indeed 'the matrix matters' (Ricketts, 2001), further investigation into its potential effects may be vitally important for the future conservation management of fragmented primate populations.

The Kwale District of southern Kenya provides an ideal landscape for the study of matrix quality and its significance to arboreal primates. Firstly, Angola black-and-white colobus (*Colobus angolensis palliatus*) populations inhabit 55 out of the 124 coastal forest fragments in this region (Chapter 2). The species is largely folivorous and forest-dependent (Davies, 1994; Moreno-Black & Maples, 1977), with a greater commitment to arboreality than the sympatric cercopithecines found within the District: the Syke's monkey (*Cercopethicus mitus albogularis*), yellow baboon (*Papio hamadryas cynocephalus*) and vervet monkey (*Chlorocebus aethiops*) (Aronsen, 2004a, b; Bocian, 1997; Moreno-Black & Maples, 1977; Strasser, 1992). Recent research has also discovered a significant influence of canopy structure on the incidence of *C. a. palliatus* populations within these 124 habitat patches (Chapter 3), which further confirms a dependency on closed-canopy vegetation structure for colobus movement. Secondly, the existing 124 forest fragments in the District are threatened by further anthropogenic landscape change and are listed as one of 11 'priority regions' for international conservation investment (Brooks *et al.*, 2002) due to the ongoing forest destruction in the area (CEPF, 2003; Oates, 1996a). The forest fragments are also surrounded by a heterogeneous mix of agriculture, development and indigenous (non-forest) vegetation. Thirdly, the regional dynamics of *C. a. palliatus* populations may also function at a metapopulation level (Hanski, 1994b, 1998), therefore any information regarding limited colobus dispersal between forest patches would help to elucidate this possibility. Consequently, the three main aims of this study were: (1) to investigate the occurrence and behaviour of *C. a. palliatus* in 'non-forest' matrix, (2) identify the key habitat attributes that determine *C. a. palliatus* usage of the matrix, and (3) establish the extent of important matrix habitat within the range of the subspecies, for the development of future *C. a. palliatus* conservation management plans within Kenya.

4.3 Methods

4.3.1 Study site

The Kwale District, in the Coastal Province of Kenya, lies between Mombasa and the border of north-eastern Tanzania (3°30', 4°45'S; 38°31' and 39°31'E). The District comprises approximately 8,322km^2 and is largely an agro-ecological zone (Muchoki, 1990) with only 3% of the District's land cover encompassing true, closed-canopy, indigenous coastal forest (i.e. 255km^2, within 124 forest fragments) (Chapter 2). Human development and agricultural land transformation in the District has given rise to a heterogeneous mix of 'matrix' land cover types. Indigenous matrix within the District comprises mangrove, coastal shrubland, and shrub or wooded grassland areas, which can also contain small clusters of indigenous (forest) tree species (these clusters are too small in area to warrant a 'forest habitat' classification). Historical human land use in the region has transformed coastal forest (and other regions of indigenous matrix) into pastoral grasslands, perennial plantations (i.e. coconut, cashew nut, mango), timber plantations, annual croplands (e.g. maize, rice, sugar cane and root vegetable crops) and areas of human development and settlement (CEPF, 2003; Muchoki, 1990; Nzoika, Ojiambo & Gang, 2003). Most agriculture in the District is locally managed. Large-scale commercial production of sugar cane, bixa and cashew nut collapsed in the pre-1990s, with the closure of the District's main agro-factories (Nzoika *et al.*, 2003). For the purpose of this study, the author classified 'matrix' into the 17 categories listed in Table 4.1. These categories were based on gross structural characteristics of the matrix: i.e. primary vegetation type (if any), canopy cover and height (Grunblatt, Ottichilo & Sinange, 1989) and were divided into 'indigenous' and 'human land use' types.

Table 4.1. Matrix types within the Kwale District, Kenya. [a] Matrix structure details the % coverage and height (m) of dominant vegetation types (Grunblatt *et al.*, 1989). [b] For more detailed descriptions and lists of tree species see (Burgess *et al.*, 2000; Robertson & Luke, 1993; White, 1983). [c] For descriptions of species see (Richmond, 1997). [d] For descriptions of commonly used cultivated food species see (Maundu, Ngugi & Kabuye, 1999).

	Matrix type	**Matrix structure [a] (height)**	**Examples of matrix composition**
	Indigenous		
1	Indigenous coastal forest vegetation	80-100% closed-canopy tree coverage (>10m), remnants of the coastal forests [b]	*Adansonia digitata, Combretum schumannii, Lecaniodiscus fraxinifolius, Ficus spp.*
2	Mangrove	80-100% closed-canopy mangrove (>10m), encompassing eight tree species [c]	*Rhizophora mucronata, Ceriops tagal, Bruguiera gymnorrhiza, Avicennia marina.*
3	Wooded shrubland	50-79% dense shrubs (1-6m), 20-49% indigenous coastal trees (>10m)	*Grewia spp., Brachystigia spiciformis, Cynometra webberi, Paramacrolobium spp.*
4	Wooded grassland	50-79% dense grass (<1m), 20-49% indigenous coastal trees (>10m)	*Acacia spp., Commiphora edulis, Hyphaene compressa, Terminalia spp.*
5	Shrubland	80-100% closed shrub (1-6m), 2-19% indigenous coastal trees (>10m)	*Manilkara sulcata, Diospyros conmii, Croton spp., Dobera glabra, Adenia spp.*
6	Shrub grassland	50-79% dense grass (<1m), 20-49% shrubs	*Acacia spp., Thespia danis, Lantana spp., Annona senegalensis, Phoenix reticulate.*
7	Bare ground	0% canopy coverage (0m), no secondary vegetation (0m)	Sandy or rocky, bare ground only.
8	Sand	0% canopy coverage (0m), no secondary vegetation (0m)	Deposits of coral and sands ≤ 30m from the Indian Ocean shoreline.
9	Swamp	2-19% sparse trees (>10m), 50-79% water (0m)	*Phoenix reclinata, Hyphaene spp., Elaeis guineensis, Raphia spp.*
10	Water	100% water = no vegetation (0m)	Indian Ocean, rivers, lakes.
	Human land use		
11	Perennial plantation	50-79% dense trees (>10m), 20-49% grass, shrubs or annual crops (<3m)	*Anacardium occidentale, Cocus nucifera, Mangifera indica.*
12	Timber plantation	50-79% dense trees (>10m), 20-49% grass or shrubs (<3m)	*Casuarina equisetifolia, Eucalyptus spp., Pinus spp., Cupressus spp.*
13	Annual cropland <1m	80-100% closed crops (<1m) [d]	*Solanum tuberosum, Vigna ungiculata, Oryza sativa, Zea mays, Manihot esculenta.*
14	Annual cropland 1-3m	80-100% closed crops (1-3m) [d]	*Saccharum officinarum, Musa spp., Carica papaya, Zea mays, Manihot esculenta.*
15	Grassland	80-100% closed grass (<1m)	*Hyparrhenia spp., Digitaria mombasana, Andropogon spp., Setaria spp.*
16	Human development	0% vegetation cover (0m)	Buildings, tarmac roads and settlements.
17	Quarry	0% vegetation cover (0m)	Open quarries for coral, lime and minerals.

4.3.2 Sampling colobus in the matrix

Since observations of *C. a. palliatus* in any given matrix type were expected to be relatively rare events, standard primate survey techniques such as line-transects or quadrats (Plumptre, 2000; Struhsaker, 1981a) were considered to be inappropriate sampling methods for the purposes of this study. Therefore, alternative methods of gathering information about colobus incidence in the non-forest matrix had to be found. Rather than use extensive teams of surveyors to traverse the landscape, a more productive (and cost-effective) method was designed which focused on the local community inhabiting the matrix. Two researchers (the author and a field researcher from Wakuluzu, Friends of the Colobus Trust, Kenya) used semi-structured interview techniques (Bernard, 2002) to gather information from the local community concerning colobus sightings outside of the forest. Using this method the author was utilising the historical knowledge of the local interviewees' experience, treating the local community as the 'surveyors' of their own landscape.

To achieve representative sampling within the matrix, a median of seven sites (mode = 9, range = 3 – 9) were selected for each of 10 selected matrix types, i.e. mangrove, shrubland, wooded shrubland, grassland, shrub grassland, wooded grassland, annual cropland 1-3m, perennial plantation, timber plantation and swamp. Matrix types were chosen that would provide a wide spectrum of matrix structural differences to compare and contrast. Sites were chosen within the District that represented homogeneous expanses of each matrix type (>10ha). The number of sample sites was estimated as proportional to the heterogeneous land cover within the District. During the period of February until June 2003 a minimum of six interviews were obtained from each sample site. A day was spent within each site, scanning the area for interview candidates who were either: (1) actively working in the matrix at the time of the survey, or (2) were living in settlements surrounded by the matrix type of interest. Participants were selected on the basis of their knowledge of *C. a. palliatus* and length of 'exposure' to the sample site they inhabited. Thus, key informants were locals who spent a significant proportion of their working day outside, e.g. farmers and herdsmen living within the agricultural and grassland matrix, and fishermen working within mangrove areas. For swamp, timber plantations and mangrove matrix, participants lived and worked on the edges of these matrix types. When participant sourcing methods proved difficult over large distances, snowball sampling was used to locate key informants (Bernard, 2002), i.e. after the completion of each interview, participants were asked to name and direct the interviewer towards appropriate, additional locals within each sample site for interview.

All interviews were geo-referenced using a Garmin 12XL global positioning system (GPS) and distances to nearest forest boundaries were calculated using ArcView geographic information system (ArcView GIS 3.2, ESRI Inc. 1999) and Nearest Features extension (Version 3.6e, 2001). A standardised framework of questions was put to each participant in a semi-structured interview (see *Appendix II*). However, interviews were flexible in terms of the scope, extent, order and emphasis with which different questions were explored. Participant credibility was assessed by quantifying their exposure to the sample site (i.e. total number of hours) in terms of working hours per day, days per week, number of seasons and years. Participants were also asked if they were born at the site, with historical exposure quantified wherever possible. Colobus knowledge was then tested using a three-stage process; participants had to list all the monkey species within the District (and mention colobus), describe two things about the colobus (e.g. appearance, uniqueness of white infants, habitat preference, arboreal nature or movement, ecology or behaviour), and lastly, correctly identify the subspecies from five primate photo ID cards (see *Appendix III*). Participants were also ranked in accordance to the level of prompting required, i.e. 0 (none) to 3 (excessive). The interview responses used in this analysis were restricted to those participants who expressed a good level of knowledge about the colobus (with little or no prompting) and spent $\geq$ 3,000 hours (i.e. the equivalent of 1 year, 5 days/wk, 4 hrs/day) within the matrix. All other interviewees were excluded from the analysis. Participants who were classed as 'incidental' in the matrix (i.e. those who lived within the matrix, but worked daily elsewhere), were also excluded.

The interviews established if participants had observed colobus within their lifetime at the sample site and recorded details of the frequency of sightings both within the past year (i.e. weekly, monthly, rarely, never), and historically. In all cases, the participant's exact response was documented in detail and classified by the interviewer post-hoc. Rare sightings were summarised by the number of sightings/year, or number of sightings/hour of participant exposure time. If colobus sightings were reported, details regarding: (1) the number of animals observed, (2) colobus locomotion (arboreal, terrestrial), (3) height above ground, support use, and speed of travel (feeding/resting, slow and fast), and (4) reasons for movement, were discussed. Responses to the latter question were later summarised by the interviewer as either 'travelling', 'feeding' (including details of food types) or 'chased' (e.g. dogs, people throwing stones). In some instances, participants could take the interviewers to the exact location of the colobus sighting, e.g. the feeding tree, and these points (n = 53) were also geo-referenced using a GPS. Using the GIS mentioned above, the minimum distance (km) of each geo-referenced colobus sighting to the nearest forest boundary could be calculated. Only sightings within two years of the interview survey period were used in the GIS (n = 48) as these were directly comparable with the 2001 GPS forest boundary maps.

Interviews ended with a discussion on primates as local agricultural pests, to determine the severity of conflict between people and colobus within the District. Sometimes participants had no direct experience of observing colobus in the sample matrix. However they had observed colobus outside the forest, within matrix elsewhere in the Kwale District. In these instances, the same interview format was adhered to, gathering as much information as possible about these additional sightings.

A total of 386 interviews were completed during the 2003 field season, however only 347 reports were used in the analysis based on the 'credibility' filter regarding the participant's knowledge and exposure. The majority of participants were male (76%), between the ages of 40 to 60 years (53%). Occupations of most participants were either farmers (67%), fishermen (12%), herdsmen (10%), or miscellaneous outdoor workers, e.g. kiosk owners, medicine men, loggers, carpenters and maintenance workers (12%), with a history of working an average of 85,000 hours ± 4,000 S.E. (range = 3,000 – 481,000 hrs) within, or on the edge of, their respective matrix sites.

4.3.3 Matrix vegetation surveys

Within each of the local interview sample sites four intercept vegetation transects (Bullock, 1996; Grieg-Smith, 1983), each measuring 150m in length, were randomly placed within the study matrix type. Using this method the beginning and endings of noticeable gaps in the upper vegetation canopy (if any) were noted along each transect. Every 5m along the transect, the presence of colobus food trees, bare ground, dwarf <1m (short grass, crops, shrubs), low 1-3m (overgrown grass, crops, shrubs) and tall >6m (shrubs, trees) vegetation were recorded, as well as the height (m) of the uppermost canopy level. Crop and canopy tree species (i.e. indigenous or perennial trees >6m) were recorded if the canopy was directly above the 5m (transect) sampling point. Human paths, roads and rivers that intersected transects were also recorded as possible barriers. Exceptions to the sampling frequency were swamps (no sites sampled), mangrove and coastal shrubland (two sites sampled respectively), as these matrix types were logistically too difficult to measure due to water or thick vegetation barriers. Any primate groups observed during vegetation sampling were recorded by species, group size, sighting height, time, compass bearing and estimated distance (m) from the vegetation transect, to first animal seen. The start and end points of each transect were logged by GPS.

4.3.4 Statistics

Using the statistical software R, version 1.9.1 (www.r-project.org), a stepwise generalised linear model (GLM) analysis with binomial error structure (Crawley, 1993) identified the key attributes that influence the frequency of *C. a. palliatus* sightings within the matrix. Each matrix site was regarded as a unit, with the proportion of colobus sightings weighted as a 'two-vector' response variable (i.e. total number of 'positive' responses were bound together with the total number of 'negative' responses into a single object, and weighted by sample size). Using data gathered from the intercept vegetation transects it was possible to calculate the average canopy height (m), number of canopy gaps, gap length (m), proportion of bare ground cover, dwarf (<1m), low (1-3m), and tall (>6m) vegetation cover, and proportion of colobus food tree cover for 47 matrix sites, across nine matrix types. The distances (km) of the 47 matrix sites to nearby forest were also estimated from the average distances of site interviews (n = 47 sites, n = 165 interviews). The habitat structure and distance variables for each site were subsequently entered into a full model, then sequentially removed, least significant first, until a minimal adequate model was reached. Statistical significance was tested using deletion F-tests.

4.3.5 Matrix vegetation classification

In order to determine the extent of matrix cover within the range of existing forest habitat in the Kwale District, a comprehensive land cover map of the District was derived using remotely sensed satellite data. A 2003 Landsat-TM image of the study site (166/063, 30-01-03, resolution: 25m x 25m) was the only suitable data source for the coastal area showing less than 10% cloud coverage (see *Appendix IV.(A).*). Using ENVI software (ENVI 3.5, Research Systems Inc. 2001) an image-to-map rectification was first performed using GPS-gathered road references from the District as ground control points (GCPs). Remaining clouds and shadows present in the Landsat TM data were removed using simple cloud masks before performing a supervised maximum-likelihood classification using all eight spectral bands of the image (ERDAS, 1999). The classification used a training dataset of 44,000 GCPs (Lillesand & Kiefer, 2000) gathered from vegetation transects, field reconnaissance and aerial surveys between the period of February and June 2003. The GCPs were defined according to the 17 land cover classes originally classified at the beginning of the study (Table 4.1). The accuracy of the ENVI land cover classification was tested using an additional testing GCP dataset (of equal size, but differing locations) in an ENVI post-classification. Finally, image noise was smoothed by the application of a median filter (Pratt, 1991).

The resulting land cover map in raster grid format (1 pixel = 25m x 25 m) was imported into ArcGIS (ArcInfo 9.0, ESRI Inc. 2002) (see *Appendix IV.(B)*) together with an overlay of the 124 coastal forest patches within the District. The latter dataset was obtained from a previous 2001 forest mapping study of the District (Chapter 2). To estimate the extent of matrix cover within realistic range of existing colobus forest habitat (i.e. that colobus individuals could possibly utilise) a sub-region of the Kwale District was created which encompassed all 124 forests. To achieve this: (1) 5km buffer zones were formed around all 124 forest patches using ArcGIS, (2) a minimum polygon was then digitised that encompassed all the buffer zones of the western-most forests, the northern and southern limits of the Kwale District, and the eastern land border with the Indian Ocean (see *Appendix IV.B*). The extent of matrix cover within the resulting sub-region was calculated using zonal statistics in ArcGIS Spatial Analyst, with each matrix type summarised by percentage cover and total area (km^2).

Each identifiable matrix type (Table 4.1) was then allocated a 'quality' rank based on the hypothesis that colobus movement through the matrix would be more likely when the vegetation structure was similar to that of habitat fragments (Pearson, 1993; Stouffer & Bierregaard, 1995). If beneficial matrix structure also had a high proportional coverage of colobus food trees, then general colobus locomotion and foraging efficiency were assumed to improve further during inter-patch dispersal (Aronsen, 2004b; McGraw, 1998a). The matrix 'quality' ranks were as follows; 0, matrix type offers no benefit to arboreal locomotion and may even hinder primate dispersal; 1, matrix type offers limited access to arboreal locomotion with limited occurrence of colobus food trees; 2, matrix type offers dense tall canopy and unhindered arboreal locomotion with limited occurrence of colobus food trees; 3, matrix type offers closed tall canopy, unhindered arboreal locomotion and high occurrence of colobus food trees. In all cases, the proportion of tall vegetation cover was viewed as the most important factor influencing dispersal, whilst colobus food trees were viewed as an additional benefit only. The original land cover map was then reclassified into a 'matrix quality' map using ArcGIS Spatial Analyst.

4.4 Results

4.4.1 Colobus in the matrix

A total of 98 out of 347 reports documented colobus within the matrix (Table 4.2). These positive sightings were divided into two explicit report types. Firstly, 54 reports (15% of all reports) were specific to 23 matrix sites visited (i.e. 34% of all matrix sites). It was difficult to rule out the possibility of pseudo-replication *within* sites (participants within the same site observing the same colobus individuals), therefore results are explicitly summarised by the number of positive 'site' results as well as the number of positive 'interview' results. Secondly, 44 participants gave additional information regarding colobus sightings in the matrix within other regions of the Kwale District. All 98 reports of colobus sightings were used to document the qualitative information concerning the nature of colobus behaviour within the matrix. However, only the 54 colobus sightings associated to sample sites were used to estimate colobus sighting frequencies in the matrix, as these reports were more accurately related to the participants' exposure time within each matrix site. The patterns of colobus incidence across matrix types showed a strong pattern of variation, which was consistent whether the data were summarised by site or by interview (Table 4.2).

Table 4.2. Results of semi-structured interviews, summarising the total number of matrix sites visited (n_s) and the total number of interviews completed (n_i) for each matrix type. n_{ps} (propn) = total number (and proportion) of *positive sites* where colobus were observed in the matrix; n_{piSITE} (propn) = total number (and proportion) of *positive interviews* reporting colobus in the matrix, where interview reports relate specifically to the sample site; $n_{piEXTRA}$ = additional reports of colobus in the matrix elsewhere in the Kwale District. Total ^{a} = $n_{piSITE} + n_{piEXTRA}$.

	SITES		INDIVIDUAL INTERVIEWS			
MATRIX TYPE	n_s	n_{ps} **(propn)**	n_i	n_{piSITE} **(propn)**	$n_{piEXTRA}$	Total ^{a}
Wooded shrubland	3	3 (1.00)	11	8 (0.73)	10	18
Perennial plantation	9	7 (0.78)	50	20 (0.40)	24	44
Mangrove	9	6 (0.67)	46	16 (0.35)	5	21
Shrubland	4	2 (0.50)	17	2 (0.12)	2	4
Wooded grassland	8	3 (0.37)	46	6 (0.13)	3	9
Timber plantation	6	1 (0.17)	32	1 (0.03)	0	1
Annual cropland 1-3m	7	1 (0.14)	37	1 (0.03)	0	1
Grassland	7	0 (0)	33	0 (0)	0	0
Shrub grassland	6	0 (0)	35	0 (0)	0	0
Swamp	9	0 (0)	40	0 (0)	0	0
Total	68	23 (0.34)	347	54 (0.15)	44	98

Both wooded shrubland and shrubland were sampled less intensively (Table 4.2) due to the difficulty of finding large homogeneous areas of these remnant matrix types within the Kwale District. An overall trend is apparent, however, whether one looks at the proportion of matrix sites reporting colobus, the proportion of positive sightings of colobus within the matrix, or the distribution of extra reports. Namely, *C. a. palliatus* is observed within three main matrix types; wooded shrubland, perennial plantation (mixed coconut, cashew nut and mango), and mangrove. In contrast, colobus were never reported within grassland, shrub grassland or swamp vegetation. Despite the low sample effort within shrubland areas, colobus sightings were reported within half of these sites. The significance of this fourth matrix type is highlighted more clearly when sightings frequencies are summarised for each matrix site (Fig. 4.1).

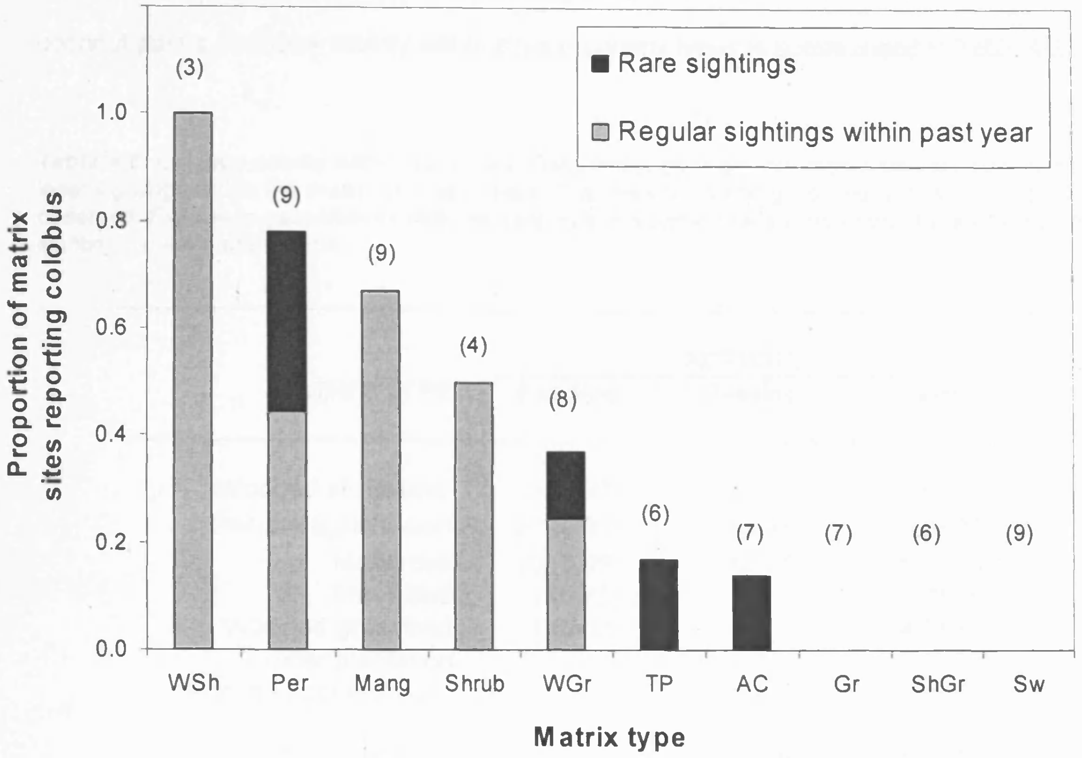


Fig. 4.1. Proportion of matrix sites reporting colobus. Matrix types = *WSh*, wooded shrubland; *Per*, perennial plantation; *Mang*, mangrove; *Shrub*, shrubland; *WGr*, wooded grassland; *TP*, timber plantion; *AC*, annual crops 1-3m; *Gr*, grassland; *ShGr*, shrub grassland; *Sw*, swamp. *Regular sightings* = the proportion of sites where the modal interview response to colobus sighting frequency (within the past year) was 'weekly' or 'monthly'; *Rare sightings* = the proportion of sites where sightings occurred only once or twice within the historic experience of the participant.

Within all wooded shrubland, mangrove and shrubland sites (where colobus were reported), all participants gave accounts of regular colobus sightings (i.e. weekly or monthly, within the past year). Interviewees in only four out of seven perennial plantation sites reported regular colobus sightings, the remaining sites only reported rare encounters. Details of all rare encounters of colobus were as follows; three perennial sites (only once within 16, 23 and 38 years respectively), and one wooded grassland (once in 48 years), timber plantation (once in 8 years) and annual cropland site (twice in 54 years).

Both solitaries (10%) and colobus groups (90%) were observed within the matrix (*n* = 98). Locomotion was primarily arboreal climbing, quadrupedalism and leaping (90%), however quadrupedal ground movement was also observed (10%) (*n* = 98). During arboreal locomotion, the supporting branches of mangroves, coastal shrubs, timber tree spp., indigenous tree spp., cashew nut and mango trees were utilised, as well as the fronds of coconut palms. Colobus activity within differing matrix types is summarised in Table 4.3.

Table 4.3. Colobus activity within the matrix. Data under each column represents the total number of local sightings within the matrix (*n* = 98) where *C. a. palliatus* feeding, resting or travelling activity was observed. Figures in parentheses indicate each colobus activity as a proportion of the total number of sightings in each matrix type.

	ACTIVITY		
MATRIX TYPE	**Feeding**	**Resting**	**Travel**
Wooded shrubland	15 (0.83)	-	3 (0.17)
Perennial plantation	27 (0.61)	2 (0.05)	15 (0.34)
Mangrove	10 (0.48)	3 (0.14)	8 (0.38)
Shrubland	3 (0.75)	-	1 (0.25)
Wooded grassland	3 (0.33)	-	4 (0.66)
Timber plantation	-	-	1 (1.00)
Annual cropland 1-3m	-	-	1 (1.00)
Total sightings	58 (0.59)	5 (0.05)	35 (0.36)

Feeding activity was the most frequently observed colobus behaviour within the matrix, occurring largely within wooded shrubland, perennial plantations, shrubland and mangrove. Colobus were reported to eat the leaf buds and young leaves of *Rhizophora mucronata, Heritiera littoralis* and *Ceriops tagal* mangrove. Within perennial plantations, colobus were reported to feed primarily on the leaves of indigenous trees: *Adansonia digitata, Albizia gummifera, Afzelia quanzensis, Cussonia zimmermannii, Ficus spp., Grewia plagiophylla, Harrisonia abyssinica, Lannea welwischii, Sideroxylon inerme, Sorindeia madagascariensis, Tamarindicus indica, Terminalia catappa,* and *Zanthoxylum chalybeum.* The tree species listed above are retained within perennial plantations either as sacred trees, shade trees, meeting places, or sources of fruit and/or medicinal products. Colobus were also reported to feed on the exotic timber tree species of *Ceiba pentador* and *Azadirachta indica*, and ornamental species of *Delonix regia* and *Bougainvillea spectabilis*, within the same matrix type.

It was generally difficult to determine the nature of colobus travelling activity as direct evidence of *C. a. palliatus* dispersal between habitat patches. This was due to the general subjective nature of reports and the possibility that the interviewees themselves caused the movement of colobus due to disturbance. Of the 35 local reports of colobus travelling in the matrix, 60% of the interviewees clarified that 'travel' was the initial colobus behaviour observed, however after some time watching the colobus, interviewees noticed that the colobus individual (or group) stopped travelling, arrived at an indigenous tree and proceeded to feed. Also, within 23% of these reports the interviewee did not continue observations over an extended period to determine the reason for colobus occurence in the matrix. On one occasion an interviewee observed a colobus individual within perennial plantation being chased and killed by people with dogs. Therefore, all instances of 'travelling' activity should only be viewed as additional evidence for the potential of colobus dispersal between habitat patches, and not as direct evidence of dispersal events.

All interviewees stated that *C. a. palliatus* was not a significant agricultural pest compared with the District's more frugivorous primates, i.e. the yellow baboon (*Papio hamadryas cynocephalus*), Syke's monkey (*Cercopethicus mitus albogularis*), and vervet monkey (*Chlorocebus aethiops*). However, within the southern-most region of Kwale, close to the border of Tanzania (i.e. Vanga: a sub-location of Kwale District), colobus were reported to periodically eat the skins of unripe mangos (*Mangifera indica*) and oranges (*Citrus sinensis*), and the leaves of cassava (*Manihot esculenta*), sweet potato (*Ipomoea batatas*) and cow pea (*Vigna unguiculata*) crops. These reports were unique to this area only.

Analysis of GPS sighting locations data indicated that colobus were found to travel within the matrix up to 4.2km from the nearest forest boundaries with a median travel distance of 0.6km (range = 0.07 - 4.2km, *n* = 48). There was no significant difference between travel distances of solitaries (median = 1.6km, range 0.2 – 4.2km, *n* = 6) and colobus groups (median = 0.6km, range 0.07 – 4.1km, *n* = 42) (Mann-Whitney test, U = 72, Z = -1.68, p = 0.096). Since travel distances were calculated as the shortest (Euclidean) distances from nearby forest, it is possible that this method is underestimating the potential range of true travelling distances for *C. a. palliatus*, as individuals would seldom disperse in straight-lines and would be influenced by species-specific matrix preference (Bennett, 1998; Opdam, 1990).

4.4.2 Matrix attributes

Primates were not observed in the matrix during the intercept vegetation transect sampling. However, from the GLM analysis of local interviews and matrix structure data it was found that the probability of sighting *C. a. palliatus* individuals within the matrix was negatively associated with distance from core forest habitat, i.e. colobus sightings became increasingly rare with increasing distance from the forest edge (Table 4.4). When controlling for distance, two matrix-quality variables also proved to be important: colobus sightings were positively related to the proportion of tall (>6m) vegetation cover and the proportion of colobus food tree cover (Table 4.4 and Fig. 4.2). The combination of these three factors explained 34.5% of the variance in colobus sighting reports. Neither matrix canopy height (m), number of canopy gaps, gap length (m), proportion of bare ground cover, or proportion of dwarf (<1m) or low (1-3m) vegetation cover explained any further variance.

Table 4.4. GLM analysis of the variables influencing local sightings of *C. a. palliatus* within the matrix. GLM binomial proportional model (null deviance = 104.05, residual deviance = 68.19, df = 43,1).

Predictor variable	parameter co-efficient	SE	F	p
Distance from forest	-0.67	0.211	6.77	0.01
Coverage of colobus foodplants	5.37	1.724	5.99	0.02
Coverage of tall (>6m) vegetation	3.11	1.168	4.39	0.04

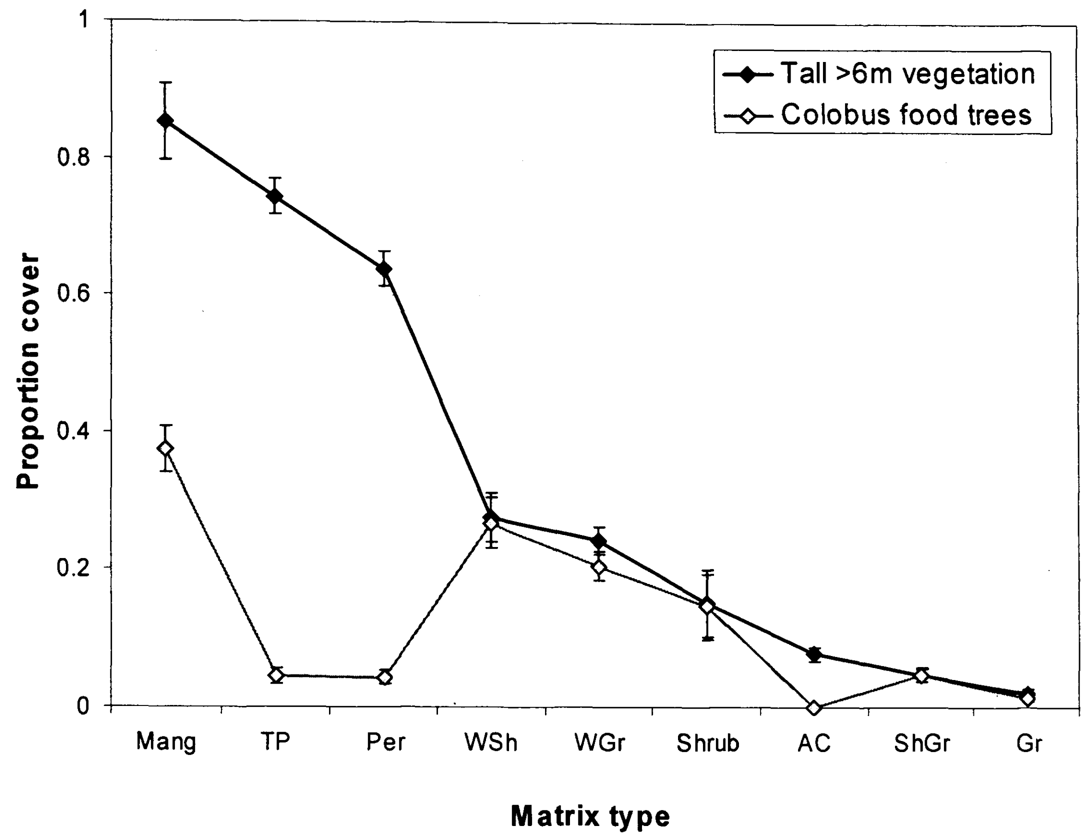


Fig. 4.2. Differences in the proportion of tall (>6m) vegetation cover and colobus food tree cover by matrix type. Ordered on x-axis in declining value of tall vegetation cover. Values on y-axis represent the mean proportional cover ± 1 S.E., derived from all intercept vegetation transects within each matrix type. *Mang*, mangrove; *TP*, timber plantation; *Per*, perennial plantation; *WSh*, wooded shrubland; *WGr*, wooded grassland; *Shrub*, shrubland; *AC*, annual cropland 1-3m; *ShGr*, shrub grassland; *Gr*, grassland.

4.4.3 Extent of matrix land cover

Post-classification of the Landsat TM image established 86.1% overall accuracy of the Landsat TM land cover classification (Kappa coefficient = 0.67) (ERDAS, 1999). The resulting post-classification, contingency matrix (Congalton, 1991) detailed in Table 4.5 shows that timber plantations, annual cropland 1-3m, swamp, bare ground and water land cover types had a lower classification accuracy. Timber plantation GCPs were confused with indigenous coastal forest, but this will have little effect on the subsequent 'matrix quality' mapping as the canopy structure of these two land cover types are of similar height and cover for colobus arboreal locomotion. The latter four land cover types (all of low structural quality) were confused with coastal forest, wooded shrubland and shrubland, accumulating to 1077/1693 (64%) of the classification errors within these GCPs. This should be kept in mind when viewing the land cover maps of the Kwale District, as coverage of these matrix types may be underestimated. Conversely, forest, wooded shrubland and shrubland cover may equally be overestimated.

Table 4.5. Results of remote sensing post-classification of Landsat TM data. The table details the percentage of ground control points (GCPs) which were correctly and incorrectly classified into different types of land cover by ENVI. Overall accuracy of post-classification: 37,938/44,047, (86.1%), Kappa Coefficient = 0.67; *n* = total number of GCPs used in ENVI post-classification. Ground-truthed land cover types that are correctly classified are highlighted in black, whilst ground-truthed land cover types with lower percentages of accurate classification are marked within borders.

		ENVI post-classification																	
Ground-truthed class	*n*	Unclassified	Indigenous coastal forest	Mangrove	Shrubland	Wooded shrubland	Grassland	Shrubbed grassland	Wooded grassland	Annual cropland <1m	Annual cropland 1-3m	Perrenial plantation	Timber plantation	Swamp	Bare ground	Sand	Water	Human development	Quarry
Indigenous coastal forest	34,754	0	**90**	0	1	2	1	0	0	1	1	1	1	1	1	0	1	0	0
Mangrove	615	11	0	**77**	0	1	0	7	1	0	0	0	0	0	0	1	0	0	0
Shrubland	209	0	2	0	**38**	20	3	0	0	8	7	4	2	1	4	5	3	1	0
Wooded shrubland	187	1	9	0	22	**29**	10	0	1	7	8	1	1	2	4	3	4	1	0
Grassland	124	0	11	2	1	27	**31**	0	0	3	10	5	2	1	3	0	2	1	1
Shrubbed grassland	95	8	0	25	0	0	0	**54**	0	1	0	0	1	8	0	1	0	0	1
Wooded grassland	5,666	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0
Annual cropland <1m	21	0	10	0	19	10	14	0	0	**29**	5	10	0	0	0	5	0	0	0
Annual cropland 1-3m	141	0	7	0	14	23	9	0	0	11	15	4	2	0	8	4	2	1	0
Perennial plantation	159	0	11	1	8	15	8	1	0	6	4	**22**	1	3	8	6	4	1	1
Timber plantation	266	0	29	0	1	7	8	2	0	0	2	1	15	4	4	2	5	1	20
Swamp	86	0	16	1	7	8	7	7	0	13	1	8	7	9	0	7	6	0	2
Bare ground	1,415	0	13	1	19	16	10	1	0	7	9	6	2	1	6	4	4	2	1
Sand	144	0	8	0	8	17	5	1	0	6	9	8	3	1	2	**25**	8	1	0
Water	51	0	16	2	16	10	8	2	0	10	2	4	4	0	4	2	14	2	6
Human development	84	7	1	2	2	2	4	10	0	1	0	1	2	0	2	0	4	**60**	1
Quarry	30	0	0	0	0	0	0	3	0	0	0	0	20	0	0	0	3	0	**73**
Total GCPs	44,047																		

The relative area of each matrix type was derived from the sub-region of the Kwale District which encompassed a total area 3,878km^2 (Fig. 4.3.a.). This sub-region can be further separated into: (1) 255 km^2 of indigenous coastal forest in 124 forest fragments, and (2) a heterogeneous mix of matrix types between these forest fragments which totalled an area of 3,623 km^2. The total coverage and 'quality' ranking of each matrix type within this 3,623 km^2 are detailed in Table 4.6.

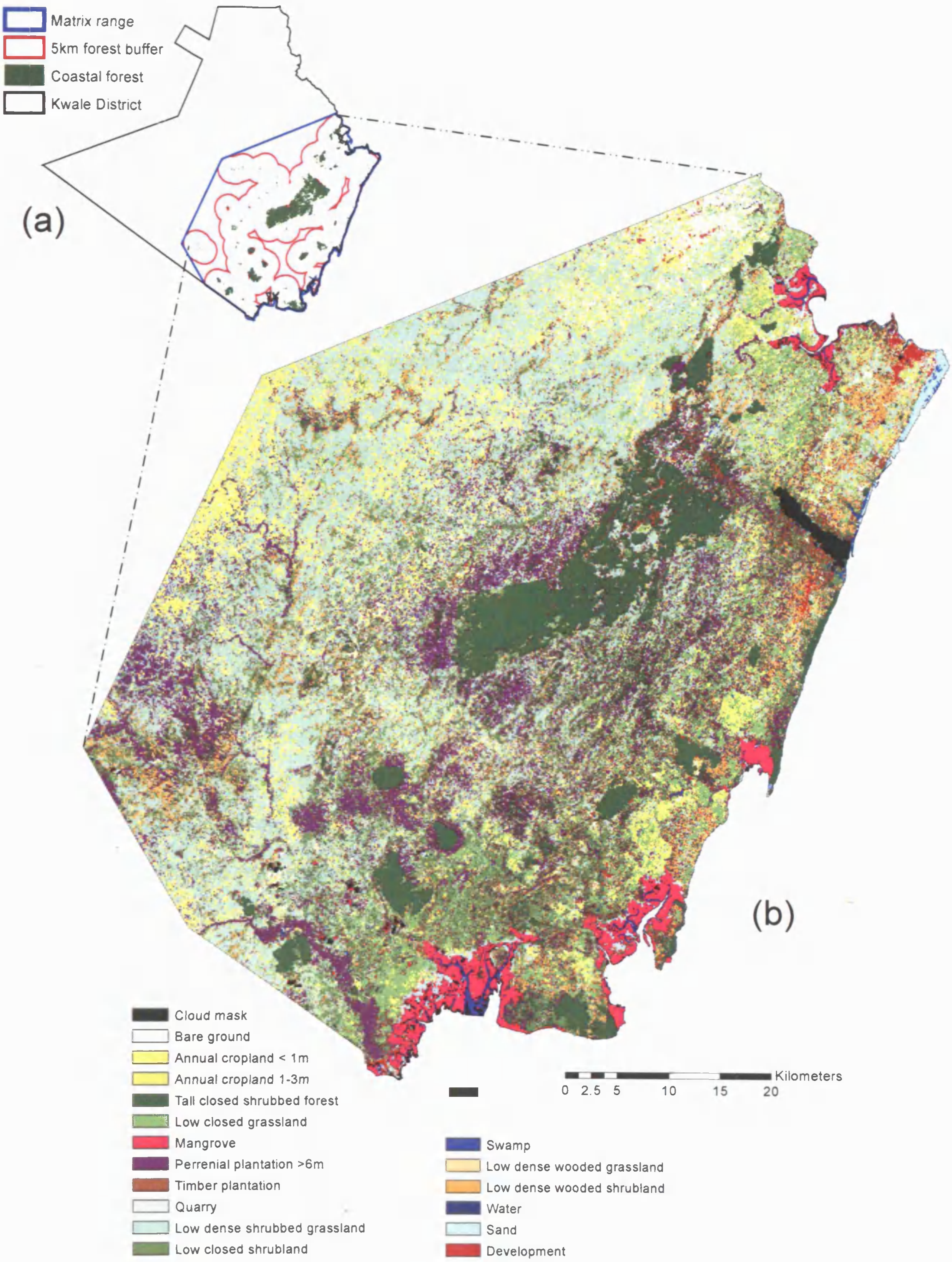


Fig. 4.3. Landsat TM classification of matrix cover within the Kwale District, Kenya. (a) = illustrates the methodology to derive a suitable sub-region for analysis. (b) = resultant land cover classification (ENVI) of the Kwale sub-region.

Shrub grassland (35%) and shrubland (16%) were the most extensive of the indigenous matrix types. In addition, it was found that almost 90km^2 of mangrove (3%) still remains within the Kwale District. The surprisingly high coverage of shrubland may in fact be more representative of agricultural crops mixed within shrubland, hence the low incidence of obvious (homogeneous) sites to sample during the interview period. Perennial plantation (13%) was the greatest of all agricultural matrix. Two percent of the matrix range was classified as indigenous coastal forest vegetation. Figure 4.3 shows that the main distribution of this vegetation (outside coastal forest patches) can be found within the perennial plantations around the Shimba Hills National Reserve and towards the Indian Ocean coastline. It is difficult to decipher whether the remote sensing of the perennial plantations reflects higher coverage of colobus food trees than were found during the vegetation surveys of this matrix type (Fig. 4.2), or if perennial trees are being wrongly classified as indigenous vegetation (Table 4.5). Whichever is the case, the presence of such indigenous tall vegetation cover within perennial matrix can only augment an already dense (arboreal) matrix canopy within the Kwale District.

Following the re-classification of the original matrix land cover map (Fig. 4.3) in ArcGIS to the new 'matrix quality' ranks listed in Table 4.6, the matrix of the Kwale District could now be viewed from a hypothetical *C. a. palliatus* perspective (Fig. 4.4). As Figures 4.4.(a) and (b) illustrate, there are some forest patches in the Kwale District that are less isolated than others in the fragmented network due to the high-quality matrix that provides potential corridors for colobus dispersal between them. If only the spatial distribution of forest habitat was considered important for this subspecies, then the two patches (*ά* and *β*) illustrated in Figure 4.4.(c) would also be viewed as significantly isolated from one another. However, if the matrix is considered, these two patches are effectively connected by continuous closed-canopy mangrove and may in fact warrant re-classification as one composite habitat patch.

Table 4.6. Coverage and characteristics of matrix types and their suitability for *C. a. palliatus* dispersal within Kwale District, Kenya. [a] Data from remote-sensing landcover classification; [b] Data from vegetation transects = *closed* (80-100%), *dense* (50-79%), *open* (20-49%), *sparse* (2-19%), *none* (0%) (Grunblatt *et al.*, 1989); [c] Predicted locomotion of colobus individuals within the matrix given the variation in tall canopy cover; [d] Reflects the quality of each matrix type in facilitating arboreal dispersal between forest patches; [e] Unclassified land cover was allocated a median rank.

	Matrix cover [a]		**Matrix characteristics [b]**		**Predicted [c]**	**Quality [d]**
Matrix type	**km^2**	**%**	**> 6m trees**	**food trees**	**locomotion**	**rank**
Indigenous						
Indigenous coastal forest vegetation	81.34	2.2	closed	dense	unhindered arboreal	3
Mangrove	89.81	2.5	closed	open	unhindered arboreal	3
Wooded shrubland	170.06	4.7	open	open	intermediate arboreal	1
Wooded grassland	69.29	1.9	open	sparse	intermediate arboreal	1
Shrubland	566.49	15.6	sparse	sparse	intermediate arboreal	1
Shrub grassland	1,282.74	35.4	sparse	sparse	terrestrial	0
Bare ground	91.68	2.5	none	none	terrestrial	0
Sand	39.45	1.1	none	none	terrestrial	0
Swamp	49.55	1.4	none	none	none	0
Water	0.58	0.0	none	none	none	0
Human land use / other						
Perennial plantation	458.86	12.7	dense	sparse	unhindered arboreal	2
Timber plantation	81.88	2.3	dense	sparse	unhindered arboreal	2
Annual cropland <1m	155.45	4.3	sparse	none	terrestrial	0
Annual cropland 1-3m	196.98	5.4	sparse	none	terrestrial	0
Grassland	258.92	7.1	sparse	none	terrestrial	0
Human development	13.33	0.4	none	none	terrestrial	0
Quarry	0.14	0.0	none	none	terrestrial	0
Unclassified (cloud mask)	15.94	0.4	-	-	-	0 [e]

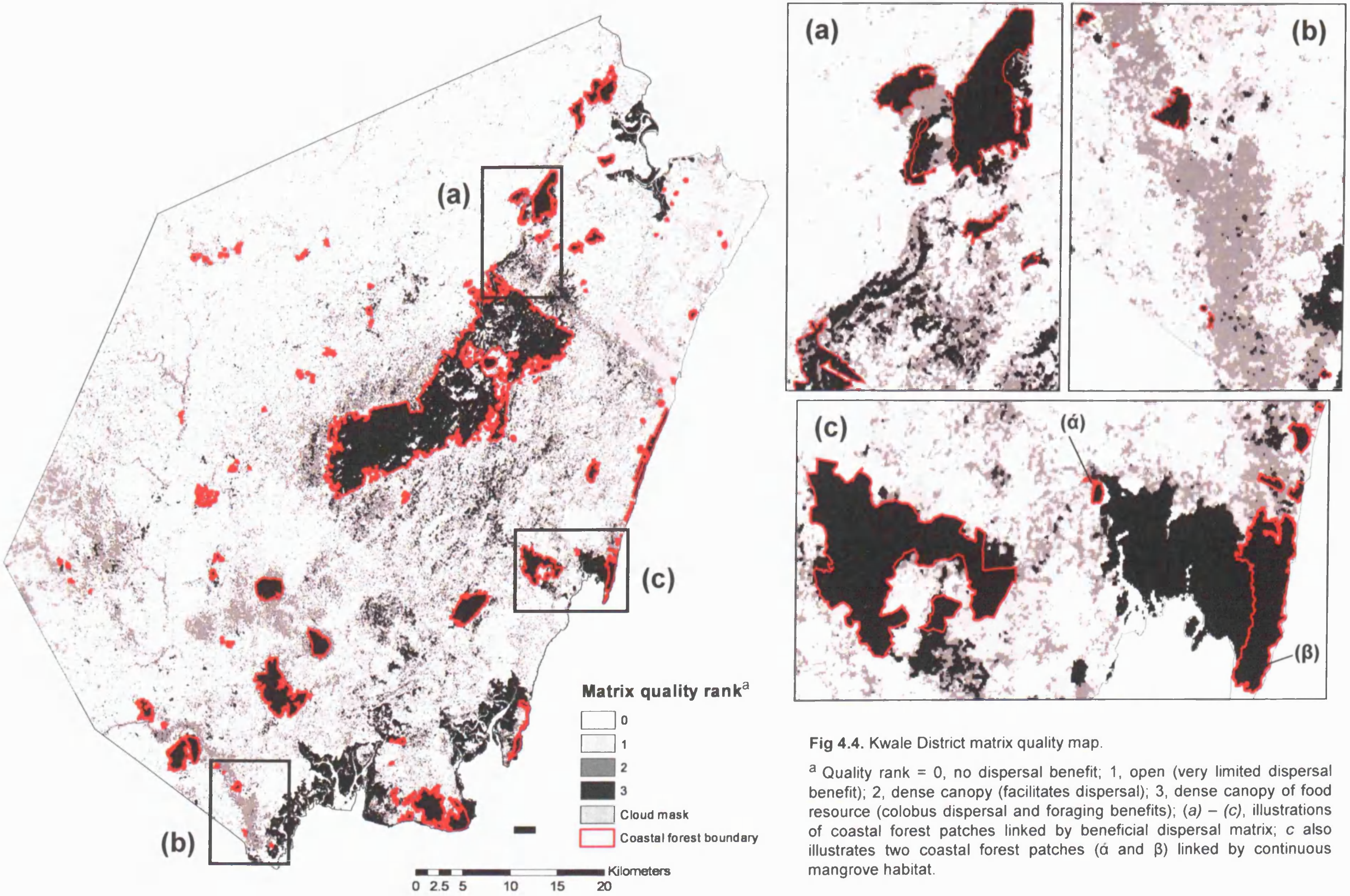


Fig 4.4. Kwale District matrix quality map.

[a] Quality rank = 0, no dispersal benefit; 1, open (very limited dispersal benefit); 2, dense canopy (facilitates dispersal); 3, dense canopy of food resource (colobus dispersal and foraging benefits); *(a) – (c)*, illustrations of coastal forest patches linked by beneficial dispersal matrix; *c* also illustrates two coastal forest patches (ά and β) linked by continuous mangrove habitat.

4.5 Discussion

Information concerning species dispersal movements can be difficult and time-consuming to collect. This is largely due to the rarity of dispersal events between habitat patches and the difficulty of tracking animal movements through a complex landscape (Bennett, 1998; Bowne & Bowers, 2004; Sutherland *et al.*, 2000). However, this study illustrates that valuable qualitative and quantitative data can be gathered within a short time period by drawing on local knowledge to determine an arboreal primate's use of, and movement within, non-forested matrix. The results suggest that, in the case of *C. a. palliatus*, the matrix does indeed matter, and colobus individuals show considerable locomotory and behavioural flexibility within the heterogeneous 'non-forest' matrix of Kwale District, Kenya. Both colobus groups and individuals use the matrix to move out of forest patches, thereby having the potential to disperse between forests or forage on the additional food resources the matrix provides. The relative use of each matrix type appears to depend on its structural similarity to closed-canopy coastal forest (i.e. the proportional coverage of tall >6m vegetation), the availability of colobus food trees, and the distance from coastal forest boundaries. The frequency of local colobus sightings varied between matrix types and within matrix sites, and may underline fundamental differences between *C. a. palliatus* dispersal events and the use of the matrix for purposes other than movement between patches. The two potential influences of the matrix on this taxon are therefore discussed independently, since the conservation implications for each may also differ.

4.5.1 The matrix as a facilitator of inter-patch dispersal

The potential for *C. a. palliatus* to move out of coastal forest habitat and hence disperse to other patches in the Kwale forest network was higher than expected for an arboreal, forest-dependent colobine moving within non-forest matrix. Colobus individuals and groups were found up to 4.2km from nearby coastal forest, and it is likely that higher dispersal distances might occur given that only straight-line, shortest-distance calculations could be explored with the data available. These distances are perhaps not so surprising, however, when you account for the structural nature of the Kwale District matrix and the 8kg body size of *C. a. palliatus*, which could provide sufficient energetic reserves for the extended exploration of an individual's environment (Peters, 1983; Sutherland *et al.*, 2000). Comparable dispersal distances have also been recorded in two arboreal primate species of similar body mass. A female Tana river red colobus (*Procolobus rufomitratus*) was observed to travel 2km from her original group's range (Marsh, 1979), whilst the longest documented dispersal distance of female mantled howler monkeys (*Alouatta palliata*) in Costa Rica was 3km (Glander, 1992).

The range of matrix types that *C. a. palliatus* could move through were quite diverse, with seven matrix types recorded in total. Mangrove provides the greatest coverage of tall (>6m) vegetation (closed, 80-100%), and has a comparably high incidence of colobus movement. Perennial and timber plantations also provide colobus with dense coverage (50-79%) of tall vegetation. Surprisingly, very few locals on the edges of timber plantations reported colobus sightings. Eucalyptus and teak plantations have been known to facilitate Nilgiri langur (*Trachypithecus johnii*) movements between forest patches in India (Umapathy & Kumar, 2000), whilst dusky leaf monkeys (*Trachypithecus obscurus*) and banded langurs (*Presbytis melalophos*) have been found within rubber plantations that neighbour forest boundaries in Peninsular Malaysia (Laidlaw, 2000). However in the Kwale District, the spatial location of timber plantation sites and the amount of time locals spent within timber (compared to perennial) plantations may have influenced reporting frequencies. In contrast to the perennial plantations, locals live on the edges of private or government-controlled timber plantations and rarely enter these areas to farm or extract resources. In some instances it is forbidden. This would subsequently reduce the daily probability of interviewees noticing colobus within such an area.

In mangrove, timber and perennial plantations, the surrounding vegetation provides an abundance of large structural supports required for efficient arboreal (quadrupedal) colobine locomotion (Gebo & Chapman, 1995; McGraw, 1998a). This vegetation also minimises energetically-expensive movements such as leaping, bridging, climbing, or terrestrial locomotion (Aronsen, 2004b). These three matrix types may therefore offer the most optimal 'structural' connectivity between habitat patches (Tischendorf & Fahrig, 2000), facilitating dispersal of colobus individuals between otherwise-isolated patches of habitat.

C. a. palliatus movement does not seem to be strictly dependent upon closed, arboreal canopy *per se*. Colobus were reported to move through areas of wooded shrubland, wooded grassland and shrubland. One report of colobus moving within annual cropland 1-3m, and the additional local observations of colobus' terrestrial locomotion within open matrix, illustrates that *C. a. palliatus* can exhibit great adaptability in movement when individuals are forced to move through such open habitats. Howler monkeys (*Alouatta* spp.) in Mexico also display this flexibility, as they are commonly seen travelling on the ground, over 15-656m across corn crops and grassland, whilst dispersing between forest fragments (Mandujano, Escobedo-Morales & Palacios-Silva, 2004; Pozo-Montuy & Serio-Silva, 2003). Tutin (1999; 1997) similarly documented rare movements of black colobus (*Colobus satanus*) from continuous forest, through 200m of savanna grassland, to visit forest fragments in the Lope Reserve, Gabon. At all of these sites, including Kwale District, long-distance terrestrial movement of arboreal primates through sub-optimal matrix will be less frequent, and more costly, for individuals. Here 'costs' would entail greater energy expenditure and increased exposure to predation (Bélichon, Clobert & Massot, 1996; Olupot & Waser, 2001; Waser, Creel & Lucas, 1994). Resources such as food, shelter and refuge from predators are also scarce in these matrix types, and may be critical for dispersal movements over long distances, where individuals may persist in an area for hours or days, to forage or rest before continuing with their journey (Baum *et al.*, 2004; Bennett, 1998; Estrada *et al.*, 1993). In the Kwale District, domestic dog predation and road traffic accidents are just two of the documented risks to *C. a. palliatus* in the open matrix (Cunneyworth & Rhys-Hurn, 2004; Kanga, 2000).

4.5.2 The matrix as an additional foraging habitat

It is evident from the results of this study that *C. a. palliatus* groups and individuals exploit certain matrix types for their availability of food resources. Mangrove comes out as one of the most beneficial matrix for this subspecies, containing the greatest proportion of colobus food trees. The Zanzibar red colobus (*Procolobus kirkii*) also eat mangrove species, particularly during the dry season when food availability is low within farmland and forested areas (Siex, 2003). Temminck's red colobus (*Procolobus badius temminicki*) have recently been documented to use mangrove areas as additional foraging sites and refuges from ongoing human disturbance.(Galat-Luong & Galat, 2005). *C. a. palliatus* populations inhabiting coastal forests directly along the Indian Ocean coastline may similarly be utilising neighbouring mangrove areas as important foraging habitats. More study is required to determine the extent of *C. a. palliatus* utilisation of these mangrove areas as alternative habitats.

Wooded shrubland, wooded grassland and shrubland were additional indigenous matrix types where feeding, or travelling towards food trees, was observed. All of these matrix types exhibit a 20-49% coverage of colobus food trees. Intercept vegetation transects also uncovered differences between the forest clearance methods for cultivation in Kwale District. Annual crop cultivation (e.g. maize, cassava, sugarcane) tends to rely on the 'clear-cutting' (slash and burn) method of coastal forest clearance, resulting in little to no indigenous coastal forest remnants within this present-day matrix type. In contrast, sparse distribution of remnant forest tree species can still be found in mixed perennial plantations (i.e. coconut, mango, cashew nut) as they provide shade, aesthetic and medicinal values for settlements within this land cover type. If forest canopy is replaced by a perennial canopy during human modification of the landscape, *C. a. palliatus* can still access the indigenous food tree remnants, even when they are sparsely distributed. These coastal forest remnants may also provide an additional source of food for colobus when resources are scarce in either small or poor-quality forest fragments (Cowlishaw & Dunbar, 2000b). In this respect, it is of interest to note that one of the reports of 'weekly' colobus sightings at a perennial plantation occurred in a matrix site where the nearest forest was only 3ha in area. *C. a. palliatus*' ability to exploit perennial plantations may have allowed such persistence to occur. *P. kirkii* also exploits perennial plantations for indigenous foods, and regularly eat mango leaves and immature coconuts (Siex & Struhsaker, 1999). *C. a. palliatus* do not show such preferences for plantation produce, although a few reports of colobus consumption of unripe produce, coupled with an adult colobus being chased and killed by locals within this matrix type, may highlight future human-wildlife conflict in specific areas of the Kwale District.

As an added note, indigenous matrix or perennial plantations may also limit any detrimental edge effects in Kwale forest fragments (Gascon *et al.*, 1999), providing a less pronounced physical and biotic gradient to forest boundaries, which in turn protects the resource quality of the forest fragments themselves (Didham & Lawton, 1999; Laurance & Yensen, 1991; Mesquita, Delamonica & Laurance, 1999; Ries *et al.*, 2004; Schtickzelle & Baguette, 2003).

4.5.3 The value of a landscape approach

Remote sensing and matrix-quality maps are useful methods to illustrate the heterogeneous nature of the matrix and highlight differing levels of connectivity between forest fragments in the Kwale District. Seasonal changes in the landscape are of minimal significance in this region, as the only annual rotational land use documented within the District involved grassland, annual cropland (<1m) and annual cropland (1-3m) turnover, none of which were reported to be used by *C. a. palliatus*. By quantifying the coverage of matrix types that may be useful to *C. a. palliatus,* and understanding the distribution of such habitats, wildlife managers have a spatially-explicit, species-specific framework to instigate landscape-level habitat management that could benefit colobus populations within coastal forest fragments.

High-quality (structural) matrix can be found between a number of coastal forest fragments in the Kwale District (e.g. Fig. 4.4). Conservation objectives should therefore emphasise the preservation or improvement of existing matrix structure within these areas either as (1) viable 'corridors': linear strips of suitable habitat that structurally link habitat patches (Beier & Noss, 1998; Bennett, 1998; Hess & Fischer, 2001); or (2) 'stepping stones': a series of small patches connecting otherwise isolated patches (Baum *et al.*, 2004). In metapopulation theory (Hanski, 1998; Hanski & Gilpin, 1991; Levins, 1969a), enhanced movement between populations is thought to lower the expected time to re-colonisation of a patch that has suffered extinction. The genetic and demographic contributions of emigrants from well-populated patches may also 'rescue' patches with small populations (Brown & Kodric-Brown, 1977). In combination these phenomenon are believed to reduce the probability of species extinction.

The results of this study indicate that it will be useful for wildlife managers to gain a greater understanding of matrix habitat within the Kwale District - to promote *C. a. palliatus* movement, population continuity and the management of specific habitats within the landscape, with the ultimate goal of ensuring the future persistence of Angola black-and-white colobus populations in southern Kenya. These findings, however, should not detract from the overall importance of coastal forest preservation within the District. *C. a. palliatus* has been found to use the matrix both to travel and forage, but these activities would not be possible without adequate forest refuges for resident populations (Cowlishaw & Dunbar, 2000b). Instead, a more integrated land management approach could be adopted that involves:

1. Preservation and enrichment of remaining coastal forest fragments within the Kwale District, with an additional conservation focus on the preservation of remnant mangrove areas as valuable natural corridors and additional habitat for *C. a. palliatus*.

2. Preservation of indigenous matrix habitats such as shrubland and wooded shrubland (e.g. existing within 1km of coastal forest habitat). These matrix habitats can offer a barrier to edge effects within coastal forests, increasing the effective interior of such fragments (Didham & Lawton, 1999; Mesquita *et al.*, 1999) whilst providing additional foraging habitat for *C. a. palliatus* populations in small forest fragments.

3. Enrichment of existing perennial and timber plantations: either structurally by maintaining or improving connectivity between forest patches (Taylor *et al.*, 1993); or functionally by providing additional colobus food trees within these matrix types (Medellin & Equihua, 1998). The latter activity may include the planting of indigenous or non-indigenous species which benefit both colobus and the local community, e.g. *Delonix regia* and *Azadrachta indica* (Bicca-Marques & Calegaro-Marques, 1994; Ganzhorn, 1985; Grimes & Paterson, 2000; Ratsimbazafy, 2002). Such tree species could provide foliage for *C. a. palliatus* without direct food resource conflict with the local community. More study is required to assess the impacts of enriching such areas both for the colobus and the local community.

This study has established that *C. a. palliatus* can move across non-forest matrix and forage within these habitat mosaics. Given the frequency of sightings within certain areas of the Kwale District, e.g. Vanga, a more intensive study is both feasible and necessary. This could combine research on group range use, habitat preference, individual animal movements, and the characteristics of remnant forest patches within this forest-mangrove-perennial plantation mosaic. These studies could thus establish the nature of the colobus forest-matrix interchange, the significance of human-wildlife conflict, and the true range of dispersal distances the subspecies can achieve within the region.

There is significant value in adopting a landscape approach to tropical deforestation and its effects on nominally primary-forest dependent species. Results of this study will add to a growing body of research that is now discovering that: (1) forest species are capable of using such matrix habitats, and (2) the quality of the surrounding matrix acts as a selective filter for wildlife movement between tropical forest fragments (Antongiovanni & Metzger, 2005a; Gascon *et al.*, 1999; Viveiros de Castro & Fernandez, 2004), a result that accords well with the findings of Gascon *et al.* (1999) for Amazonian tropical forest birds, amphibians and mammals, and Laurance *et al.* (1994; 1999; 1991) for Australian tropical rainforest mammals. By integrating the heterogeneous matrix into forest fragmentation studies we can enhance our understanding of wildlife population dynamics and assess the vulnerability of species in fragments based on their ability to use or tolerate the matrix.

5. Potential metapopulation dynamics of the Angola black-and-white colobus (*Colobus angolensis palliatus*) in fragmented coastal forest, southern Kenya.

5.1 Abstract

The fragmented coastal forests of southern Kenya are critical habitat for the Angola black-and-white colobus (*Colobus angolensis palliatus*). Only 55 of the remaining 124 forest patches in this region have resident colobus populations. Using generalised linear model and incidence function (metapopulation) model approaches, *C. a. palliatus* occupancy patterns were investigated in relation to the spatial distribution of forest habitat. Both forest area and isolation distances to neighbouring colobus populations were found to be significant indicators of population occurrence in the forest network. The spatially explicit metapopulation model provided a framework in which to explore the future metapopulation dynamics of this subspecies. Simulations of future habitat loss found that the largest patches in the forest network were critical for future metapopulation persistence. Removal of only 4% of the largest forest patches in the network was enough to render the entire network unstable with the metapopulation failing to re-establish an equilibrium state of patch occupancy. In contrast, removal of small patches, had little influence on the metapopulation. The Shimba Hills National Reserve, Forest Reserves and a presently unprotected forest (Shimoni west) had a large effect on future metapopulation persistence. Unprotected forests in general were also found to be of critical importance: a reduction in the area of these forests (10-50% loss) had a greater impact on the metapopulation than similar percentage losses in Forest Reserves or Sacred Forests (Kayas). Incidence function models may provide a good conceptual framework to explore the qualitative metapopulation dynamics of the Angola black-and-white colobus. However, the model results should be interpreted with a clear understanding of their inherent limits and assumptions. Metapopulation models can be most valuable when used in conjunction with more quantitative conservation assessments, contributing information about spatial scale, connectivity and species metapopulation processes.

5.2 Introduction

Habitat loss and fragmentation has been widely recognised as the greatest present-day threat to biodiversity (Mace & Balmford, 2000; Pimm & Raven, 2001; Sala *et al.*, 2000; WCMC, 1992). For tropical forests in particular, anthropogenic land transformation has been ranked as the major driver influencing deforestation rates in these regions for the next 100 years (Sala et al., 2000). The most pervasive and conspicuous outcome of deforestation is the reduction of area and subdivision of once continuous blocks of forest habitat. The wildlife populations which also depend on these habitats also reduce and subdivide, resulting in heterogeneous distributions of populations at different spatial scales across fragmented landscapes (Fahrig & Merriam, 1994; Laurance & Vasceoncelos, 2004; Wiens, 1989). The main challenge for contemporary ecologists and conservationists working in these regions is to understand the impacts of population dynamics and persistence of species within such patchy and disjunct habitats (Davies et al., 2001; Fahrig, 2003; Hoopes & Harrison, 1998). One way to meet this challenge has been for researchers to shift focus from 'local-population' to 'metapopulation' preservation, expanding the current ecological understanding of the spatial scale of population dynamics in patchy landscapes from the 'within-fragment' paradigm to 'between-fragment' processes. Theoretical frameworks in which to explore these effects have consequently widened, with the equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967) now largely surpassed by concepts such as metapopulation, source-sink and disturbance dynamics (Hoopes & Harrison, 1998; Peltonen & Hanski, 1991).

The metapopulation concept in particular has received much attention in the conservation literature over the past two decades (Baguette, 2004; Nobis & Wohlgemuth, 2004). In this concept, fragmented populations are viewed as networks of local populations in discrete habitat patches, interacting via inter-patch dispersal of individuals. Such species networks are buffered against extinction by the exchange of individuals between populations, which can lead to rescue effects or re-colonisation after local extinction (Hanski, 1994b; Hanski & Gilpin, 1991; Levins, 1969b, 1970). In essence, a metapopulation can be thought of as a 'population of populations' (Hanski, 1994b; Levins, 1969b), persisting over time in an equilibrium state of recurring local population extinctions and colonisations. Such stochastic patch occupancy models are particularly appealing in conservation because they can yield inferences about the status of populations based only on the presence or absence of individuals in suitable habitats. These are data that can be relatively easily collected (Lopez & Pfister, 2001). The models are also spatially explicit, allowing for the inclusion of biologically realistic functions as descriptors of colonisation and extinction events. For example, in the incidence function model (Hanski, 1994a, b; Hanski & Gilpin, 1991), habitat colonisation can depend on the distance and size of nearby patches, and local population extinction can be a modelled as a declining function of patch size (Wahlberg et al., 1996). Such modelling approaches have assisted with our understanding of species distribution patterns and population turnover dynamics (Hanski, 1998), landscape ecology (Akcakaya *et al.*, 2004; Hanski & Ovaskainen, 2003; Moilanen & Hanski, 1998), population viability and time to extinction (Hanski & Ovaskainen, 2002; Keymer *et al.*, 2000; Ovaskainen & Hanski, 2003a) and the ecological consequences of migration (Heino & Hanski, 2001; Paradis, Baillie & Sutherland, 2002; Paradis *et al.*, 1999).

The number of species in which 'metapopulations' have been identified have multiplied in the literature, with examples of both theoretical and empirical metapopulation studies focusing on plant (Freckleton & Watkinson, 2002; Quintana-Ascencio & Menges, 1996; Verheyen *et al.*, 2004), invertebrate (Bonte *et al.*, 2003; Hanski *et al.*, 1996b), amphibian (Sjogren-Gulve, 1994; Smith & Green, 2005), bird (Akcakaya *et al.*, 2003; 2004; Lahaye, Gutierrez & Akcakaya, 1994), small mammal (Lindenmayer, McCarthy & Pope, 1999; McCarthy & Lindenmayer, 2000; Moilanen, Smith & Hanski, 1998; Peltonen & Hanski, 1991; Telfer *et al.*, 2001) and large mammal (Arnold *et al.*, 1993; Rodriguez & Delibes, 2003; Sweanor, Logan & Hornocker, 2000; Walters, 2001) species. Primates are a relatively new addition to this list. Regardless of the many studies focusing on primates in forest fragments (Marsh, 2003b), research has traditionally concentrated on the dynamics of individual populations (Chapman & Peres, 2001; Dobson & Lyles, 1989; Harcourt, 1995), independent from neighbouring populations and the spatial complexity of the surrounding forest fragments. Only four studies to date have considered the importance of metapopulation dynamics on the population biology of primates: samango monkeys *Cercopithecus mitis* in South Africa (Lawes, Mealin & Piper, 2000; Swart & Lawes, 1996), black-and-white colobus *Colobus guereza* in Uganda (Chapman et al., 2003), Tana river red colobus *Procolobus* *badius*, crested mangabey *Cercocebus galeritus* and Sykes monkeys *Cercopithecus albogularis* in Kenya (Cowlishaw & Dunbar, 2000c), and howler monkeys *Allouatta palliata* in Mexico (Mandujano et al., in press). All have shown that a metapopulation approach can be a useful tool to provide additional information for the management of primates in fragmented landscapes.

The Angola black-and-white colobus (*Colobus angolensis palliatus*) is an arboreal primate found within the coastal forests of north-eastern Tanzania and southern Kenya (Kingdon, 1997). Relatively little is known concerning the subspecies habitat requirements and response to habitat fragmentation. Within the northern extent of the taxon's range, i.e. the Kwale District, southern Kenya, a recent (national) primate census found 55 *C. a. palliatus* populations within a network of 124 coastal forest fragments (Chapter 2). This region is an important focus for further study as the need for future conservation management plans based on Kenyan *C. a. palliatus* preservation has been highlighted (Oates, 1996a; Struhsaker, 1981b) and the preservation of remaining coastal forests in this region is of both national and international priority (Brooks *et al.*, 2002; Myers *et al.*, 2000; Robertson & Luke, 1993). In addition, human population growth and agricultural land use in southern Kenya have been highlighted as major threats to the future existence of coastal forests and *C. a. palliatus* populations within this region (Oates, 1996a; Schipper & Burgess, 2004).

Given the lack of knowledge concerning the future viability of *C. a. palliatus* in this fragmented forest network it may be useful to explore the applicability of a metapopulation approach to gain further insight into the population dynamics of this subspecies. In addition, this approach may also provide a suitable framework in which to compare alternative scenarios of future landscape change, e.g. forest decline or destruction (Hill & Caswell, 2001; Kallimanis *et al.*, 2005; Ovaskainen & Hanski, 2002; Wiegand, Revilla & Moloney, 2005), and to identify those forest patches that are likely to be critical for colobus persistence in the region. It is particularly in this latter instance that metapopulation models have been highlighted as helpful tools for the conservation management of fragmented populations (Burgman *et al.*, 1993; Hanski, 1998; Hanski & Simberloff, 1997; McCullough, 1996).

A metapopulation approach is appropriate for *C. a palliatus* as the taxon fulfils the four necessary conditions for metapopulation-level persistence, detailed by Hanski and

Gilpin (1997): (1) *C. a. palliatus* is largely dependent upon coastal forest which occurs as spatially discrete habitat patches in the Kwale District; (2) even the largest local populations within the forest network have a risk of extinction; (3) habitat patches are not too isolated to prevent re-colonisation and there is potential for limited colobus dispersal between forest patches across non-forested 'matrix' (Ricketts, 2001) (see Chapter 4); and (4) asynchronous patch dynamics are likely due to the wide range of *C. a. palliatus* subpopulation sizes and patch qualities occurring in the network (Chapters 2 and 3). A crude comparison of average adult female-to-immature (i.e. juvenile and infant) ratios between habitat patches also shows significant variation (see *Appendix V*) indicating possible differences in sub-population growth rates.

Hanski's incidence function model (Hanski, 1994b, 1999b; Hanski *et al.*, 1996b) was chosen as the most appropriate metapopulation model for this study. It has the benefit of being simple yet spatially explicit, modelling the finite number, size and location of all habitat patches in the fragmented network. Although there is one unusually large patch in the network, the Shimba Hills National Reserve (>150km^2), the colobus metapopulation in the Kwale forest network is not treated here as a 'mainland-island' system (Hanski, 1997; Hanski & Gyllenberg, 1993). This is because the mainland-island incidence function model makes restrictive assumptions about patch connectivity and persistance (e.g. 'islands' only receive immigrants from the mainland not from each other, and the entire metapopulation collapses if the 'mainland' becomes extinct) that are unlikely to apply in this case.

The rise in popularity of metapopulation theory and a broadening of model usage within the conservation community has correspondingly been met with tales of caution. Incidence function models have been criticised for being over-simplistic, omitting the influence of factors such as patch quality and matrix heterogeneity on population dynamics (Baguette & Mennechez, 2004; Elmhagen & Angerbjorn, 2001; Hanski, 1999b; Hanski *et al.*, 1996b; Ricketts, 2001; Shreeve, Dennis & Van Dyck, 2004). In addition, the reality of a quasi-equilibrium state of patch occupancy in the natural world, an important assumption of the incidence function model at the onset of modelling and parameter estimation, has also been questioned (Baguette, 2004; Harrison, 1997).

Given the need for more rigorous, empirical applications of metapopulation models in conservation biology, and the need to understand how spatial geometry influences primate population persistence in fragmented landscapes, this study aims to use Hanski's (1994b) incidence function model to: (1) explore the theoretical persistence of *C. a. palliatus* populations in a spatially realistic, fragmented forest landscape in southern Kenya, (2) explore the influence of future habitat destruction on *C. a. palliatus* metapopulation persistence, including an assessment of the key habitat patches involved in this process, and (3) provide a critique of the general applicability of the metapopulation concept to understanding colobus population dynamics in a fragmented landscape.

5.3 Methods

5.3.1 Incidence function model

The incidence function model is based on a first-order, linear Markov chain model for the occupancy of a single habitat patch (Hanski, 1994b). In this model a habitat patch has two possible states; occupied or empty. Forecasts of patch occupancy are based on two key processes: the extinction of populations in occupied patches and colonisation of empty patches. The model has six parameters, b, α , A_o, x, e and y, described below (Table 5.1, also see *5.3.2*), and uses patch area (A_i) and patch connectivity (S_i) as variables. For each forest patch (i), the probability of extinction (E_i) is defined as a function of area:

$$E_i = \min\left[\frac{e}{A_i^x}, 1\right] \tag{1}$$

where e and x are parameters to be estimated. The model assumes that expected population size is positively correlated with patch area, and that small populations are more likely to go extinct than large ones (Caughley & Gunn, 1996; Simberloff, 1998). For simplicity, Hanski assumes that extinction risk, in the absence of colonisation, is not affected by connectivity (however see the 'rescue effect' below). Colonisation probability (C_i) per patch is defined as a sigmoid function of connectivity (S_i):

$$C_i = \frac{1}{1+\left(\frac{y}{S_i}\right)^2} \tag{2}$$

where y is a parameter to be estimated, and connectivity of patch i is defined as:

$$S_i = \sum_{j \neq i} p_i \exp(-\alpha d_{ij}) A_j^b \tag{3}$$

where p_i is the observed incidence of the patch (simply a 'snapshot' of data, resulting in the input of species presence = 1, or absence = 0), and d_{ij} is the distance between patches i and j. Since the size of neighbouring populations could affect the number of migrants reaching the focal patch i, A_j is included in Equation (3). In this equation b is a parameter determining how population size scales with patch area, whilst parameter α determines the rate of decline in survival with increasing distance moved. Bringing together these two assumptions, the probability of occupancy for patch i (J_i), is given by:

$$J_i = \frac{C_i}{C_i + E_i} \tag{4}$$

The incidence function model variant adopted for this study includes the 'rescue effect', i.e. a lowered extinction risk of local populations due to the influx of immigrants increasing local population size (Brown & Kodric-Brown, 1977). The simplest way to include a rescue effect in the incidence function model is to replace E_i with (1-C_i) E_i (Hanski, 1994b), which associates lowered extinction rates with the probability of patch colonisation. This effect is especially important for small patches (with large E_i) which are located close to large populations (giving a large C_i). The modified equation for J_i is therefore:

$$J_i = \frac{C_i}{C_i + E_i - C_i E_i} \tag{5}$$

Substituting Equations (1) and (2) into Equation (5) therefore, gives:

$$J_i = \frac{1}{1 + \frac{e'}{S_i^2 A_i^x}} \tag{6}$$

where e' is a composite of the two parameters = ey^2.

5.3.2 Parameter estimation and model fitting

The incidence function model has six parameters. The descriptions of each parameter and the methods of estimation are detailed in Table 5.1. Colobus population presence/absence data from a 2001 primate census (*Section 5.3.3*) was fitted to the incidence function model. The best fit between the observed incidence data (p_i) and the model's predicted incidence (J_i) was found by minimising the likelihood estimator:

$$-\sum p_i \ln J_i + (1-p_i)\ln(1-J_i) \qquad (7)$$

A second null model was also used when fitting the colobus incidence data to the incidence function model in Equation (7). In the null model, predicted incidence (J_i) was replaced with observed average occupancy.

For reference to all the equation symbols used in this chapter (and also Chapter 6) please refer to *Appendix VI*

Table 5.1. Incidence function model parameters and estimation methods. [(a)] Equation reference where parameter can be found: [b] Dispersal data gathered in this study (see Chapter 4) are not representative of true dispersal distances (nor survival rates with increasing distance moved); [c] Extreme values of α (i.e. 0.05 and 5) represent dispersal distances over which survival probability approaches zero at about 100km and 1km respectively, with average dispersal distances of 20km and 0.2km respectively.

Parameter [(a)]	Description	Estimation method
b (3,12)	Scales the rate of change in local population size with patch area (or scales emigration rate by patch area).	Estimated from empirical data, by regressing observed population sizes (i.e. number of individuals/patch) against patch area.
α (3)	Determines the distribution of dispersal distances for the species, with $1/\alpha$ being the average migration distance.	It was not possible to estimate α independently[b] for these data, so a range of values from 0.05 to 5[c] were tested.
A_0 (8)	The approximate size of patch for which annual extinction probability equals unity.	Estimated from empirical data, relating to the size of the smallest currently occupied patch. This value is used to tease apart the values of e and y in the product $e' = ey^2$. See Equations (8) and (9) below.
x (1,6)	Scales extinction risk as strongly (>1) or weakly (<1) dependent upon patch area. This parameter can also be regarded as the species sensitivity to environmental stochasticity.	Estimated from model fitting.
e (1)	Constant, determining the average extinction risk.	$e = A_0^x$ (8)
y (2)	Scales the efficiency of colonization in relation to connectivity.	y can be disentangled from the composite parameter e' (estimated from model fitting), using the equation : $y = \sqrt{\frac{e'}{e}}$ (9)

5.3.3 Empirical data

A 2001 primate survey of all coastal forests within the Kwale District, Kenya (Chapter 2) provided the incidence function model with *C. a. palliatus* occupancy data for all forests patches (p_i) in the network. Of the 124 forests patches surveyed, *C. a. palliatus* inhabited 55, representing 44% patch occupancy in the District (Fig. 5.1). For all occupied patches in the system, local population sizes were also known (i.e. the total number of individuals per patch), and these were regressed against patch area to estimate the parameter *b* in the incidence function model.

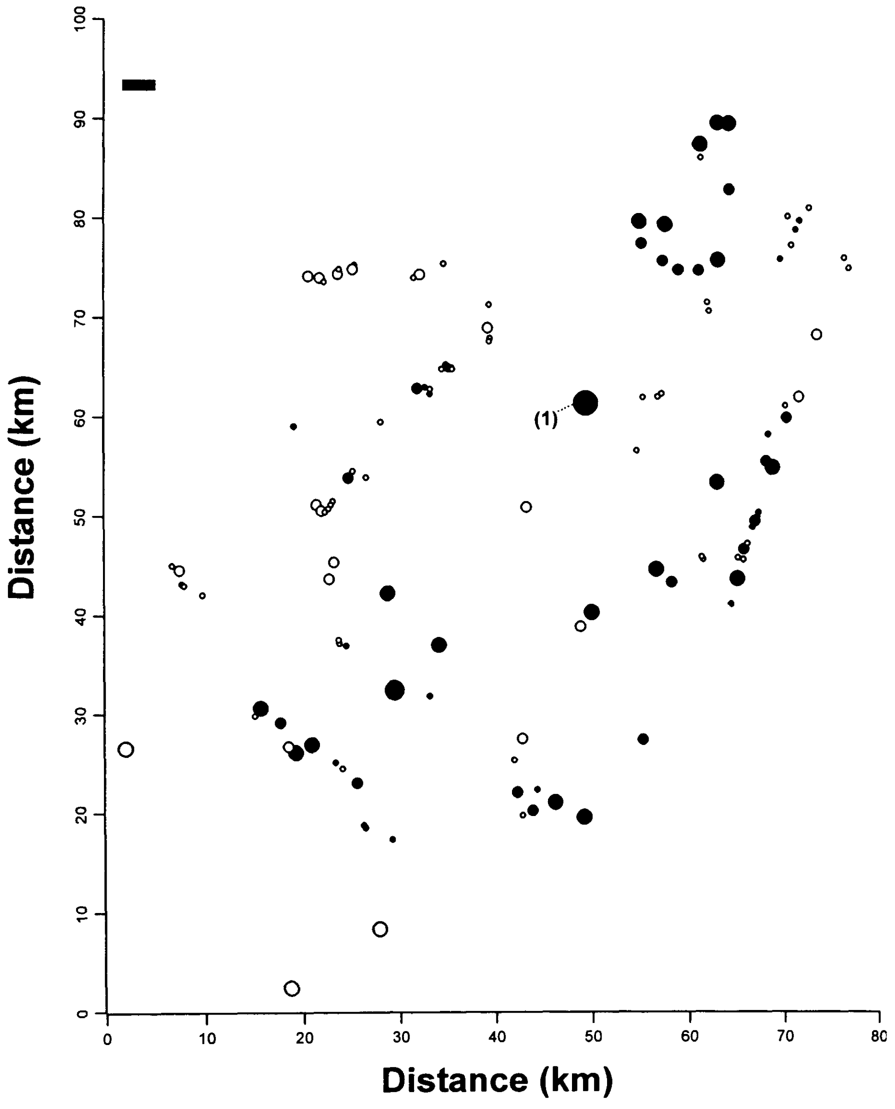


Fig. 5.1. Habitat patch structure of the *C. a. palliatus* metapopulation in Kwale District, Kenya. The figure shows the spatial distribution of patches; *Black circles* represent 'occupied' forest patches with known *C. a. palliatus* populations; *White circles* represent 'unoccupied' forest patches (derived from 2001 census data); *Grey circles*, represent occupied forest patches in Tanzania included in the incidence function model; (1) Indicates the Shimba Hills National Reserve (>150km^2 in area); *Circle size* represents relative patch area (km^2).

All forest areas and spatial locations were determined either from GPS forest boundary maps, gathered during the 2001 survey period, or digitised forest boundaries from a classified 2003 Landsat TM image of the study site (Chapters 2 & 4). The areas (A_i) of all 124 forest patches (km^2) were calculated via an ArcView geographical information system (ArcView GIS 3.2, ESRI Inc. 1999), using Xtools extension (Version 6.1, 2001). Fifty-four percent of patches were smaller than $0.1km^2$ in area, 29% were between $0.1\text{-}1km^2$, and 16% were between $1\text{-}15km^2$. The largest patch in the system, the Shimba Hills National Reserve, was over $150km^2$.

Given that the Kenyan *C. a. palliatus* metapopulation may not be geographically isolated from populations in northern Tanzania, the nearest three forest patches on the Tanzanian border were also digitised from Landsat TM data and were included in all model simulations to account for potential immigration into the system (Fig. 5.1). An optimal scenario was assumed, whereby all three Tanzanian forest patches (areas = $1.6km^2$, $1.4km^2$ and $1.2km^2$, respectively) were occupied, and thus had potential for supplying immigrants to the patches nearest the Kenyan border, and therefore the Kwale network as a whole.

To calculate the isolation or 'connectivity' value (S_i) of each patch, the shortest (Euclidean) isolation distances from the edges of each forest patch to the edges of all other 123 Kenyan (plus three Tanzanian) forest patches (d_{ij}) in the system had to be determined. To avoid the underestimation of isolation distance where Euclidean paths crossed the Indian Ocean, an ArcView 3.2 extension (Distance and Azimuth Matrix v.2:Jenness, 2005), was modified to define realistic paths. Hence, in those instances where exact (vector-based) isolation distances unrealistically entered the Indian Ocean, the algorithm discarded the straight line and resorted to a more realistic, cost-distance (raster-based) calculation. For more detailed information and extension illustration, see *Appendix VII).* The average distance from one Kwale forest patch to its nearest-neighbour was 0.77km ± 0.12 S.E. (median = 0.29km, range = 0.04 - 9.4km, n = 124). When considering all resident *C. a. palliatus* populations in the Kwale forest network however, isolation distances were greater: the average distance from one colobus population to its nearest-neighbour forest patch was 0.96km ± 0.23 S.E. (n = 55), whilst average distance from one colobus population to another colobus population was 1.54km ± 0.27 S.E. (n = 55).

5.3.4 Model simulations

To simulate the dynamics of the *C. a. palliatus* metapopulation, the incidence function model can be used to numerically simulate extinction-colonisation dynamics within the patch network, assigning area-dependent extinctions and isolation-dependent colonisations independently for each patch (Hanski, 1994b, 1998). One thousand simulation replicates were used, over 500 discrete time units, often referred to as 'generations'. The true time scale of one 'generation' is very difficult to define, however it is related to the minimum time required for an extinction or re-colonization event to occur (often associated with the reproductive generation time of the study species) (Hanski, pers. com). In the case of *C. a. palliatus* therefore, one 'generation' may be equivalent to between 1 to 4 years. Results were summarised after each generation as the median number of occupied patches (i.e. number of populations) within the network over the 1000 simulation replicates, referred to as the 'metapopulation size' (M_{pop}).

To test the influence of a possible link between the Kwale District *C. a. palliatus* metapopulation and forests within Tanzania, two models were compared. The first model, simulated colobus metapopulation dynamics using only the 124 habitat patches in Kenya. The second model simulated the dynamics of the same 124 habitat patches, however the areas and isolation distances of the three occupied Tanzanian forests were included within the connectivity measures (S_i) of each of the 124 Kenyan patches (Equation 3). Any positive influence of a Tanzanian connection would therefore be recorded as an increase in overall colobus metapopulation size (M_{pop}), or increased probability of occupancy (p_i^*) of each of the 124 Kenyan forest patches, after 500 generations. In the latter case, significance was tested using a Wilcoxon-signed ranks test.

To investigate the dynamic consequences of change in the spatial structure of the patch network a series of simulations looked at the effects of future forest loss and deforestation in the Kwale District. These were as follows: (1) the sequential removal of the smallest 10-50% of patches, (2) the sequential removal of the largest 10-50% of patches, (3) the removal of forests by protection status, and (4) the sequential 10-50% reduction in forest area by protection status. Within all of these simulations, connection to the Tanzanian coastal forests was maintained. For the latter simulation, loss in forest area was modelled as a uniform removal of forest from the patch edges, i.e. simulating habitat encroachment. As forest areas contract, the isolation distances between forest patches will inevitably increase. Therefore isolation distances were increased (d_{ij}^*) relative to reductions in forest radii, assuming forests were circular in geometry for simplicity:

$$d_{ij}^* = d_{ij} + \left(\sqrt{\frac{A_i}{\pi}} - \sqrt{\frac{lA_i}{\pi}}\right) + \left(\sqrt{\frac{A_j}{\pi}} - \sqrt{\frac{lA_j}{\pi}}\right) \tag{10}$$

where d_{ij}^* is the modified isolation distance (km), d_{ij} is the original isolation distance (km), A_i is the original patch area (km^2), and lA_i is the new patch area (km^2) following 10-50% loss of forest.

A final simulation explored the value of individual forest patches to the dynamics of the *C. a. palliatus* metapopulation as a whole. Ovaskainen and Hanski (2003b) provide a variety of measures to assess the value of individual habitat patches, including patch contribution to metapopulation capacity, colonisation events, metapopulation persistence, and metapopulation size. The latter measure had previously been calculated as the total number of occupied patches in the metapopulation (i.e. M_{pop}), however Ovaskainen and Hanksi suggest a more detailed estimate of metapopulation size based on the expected number of individuals in the metapopulation as a whole (M_{ind}), with more weight given to larger patches. Rather than view the equilibrium state of patches as either 0 or 1 in this analysis, the model also uses the precise probability of occupancy (p_i^*) of patches after each of the 1000 simulations. For example, if patch *i* was occupied for 560 out of 1000 simulations at equilibrium, the probability of occupancy would be 0.56 (p_i^*) rather than 1 (J_i). Therefore, the contribution of patch *i* to metapopulation size (U_i) would be derived from the following equations:

$$U_i = M_{ind} - M_{ind}^{-i} \tag{11}$$

Where the size of the metapopulation (M_{ind}) is defined as:

$$M_{ind} = \sum_{j \neq i} A_i^b p_i^* \tag{12}$$

M_{ind}^{-i}, is the size of the metapopulation in the network from which patch *i* has been removed. In this analysis, individual population sizes are dependent upon the scaling parameter *b*, similar to Equation 3 of the incidence function model (Table 5.1). Patch weight (A_i^b) is also dynamic, in the sense that it depends on the equilibrium state of the patch (p_i^*). For this analysis ten large patches (>4km^2), ten medium patches (between 0.1 – 2km^2) and ten small patches (<0.1km^2) were randomly chosen and individually removed from the Kwale forest network, comparing metapopulation size (M_{ind}) before and after removal (Equation 11). The initial simulations which compared the *C. a. palliatus* metapopulation with or without the Tanzanian forest connection (i.e. using M_{pop}), also measured metapopulation size in this way (M_{ind}) as a possible third indicator of connectivity influence.

5.3.5 Sensitivity analysis

To explore the incidence function model's sensitivity to biological uncertainty, two models were compared with varying parameter values of α : (1) the original 124 patch occupancy model (with Tanzanian connection), and (2) simulations with the Shimba Hills National Reserve removed. In these simulations α varied between 0.05, 0.1 and 0.5

5.3.6 Statistical analysis

In addition to incidence function model simulations, overall patterns of occupancy in all 124 Kenyan forest patches were examined in a stepwise generalised linear model (GLM) with binomial error structure (Crawley, 1993). The aim was to determine whether variance in occupancy could be explained by the independent effects of three spatial characteristics of patches: patch area (km^2); isolation distance (km) to the nearest geographical patch; or isolation distance (km) to the nearest *C. a. palliatus* population. Using the statistical software R, version 1.9.1 (www.r-project.org), each forest patch was entered as a unit, with presence or absence of populations coded as a binary response variable. All three spatial variables were entered into a full model and log-transformed to normalise the distributions. All non-significant variables were sequentially removed, least significant first, until a minimal adequate model was reached. Statistical significance was tested using deletion F-tests corrected for over-dispersion.

5.4 Results

5.4.1 Patterns of occupancy

Occupancy of forest patches by *C. a. palliatus* was positively related to forest area (GLM parameter co-efficient = 0.99 ± 0.19 S.E., F=56.5, $p<0.0001$) and negatively related to the isolation distance of the nearest colobus population (GLM parameter co-efficient = -0.52 ± 0.15 S.E., F=15.2, $p<0.0002$) (Fig 5.2). There was no significant influence of geographic isolation on population occupancy. The combination of these two factors explained 36% of the variance in occupancy of colobus populations observed in this study (null deviance = 170.32, residual deviance = 109.94, df = 121,1).

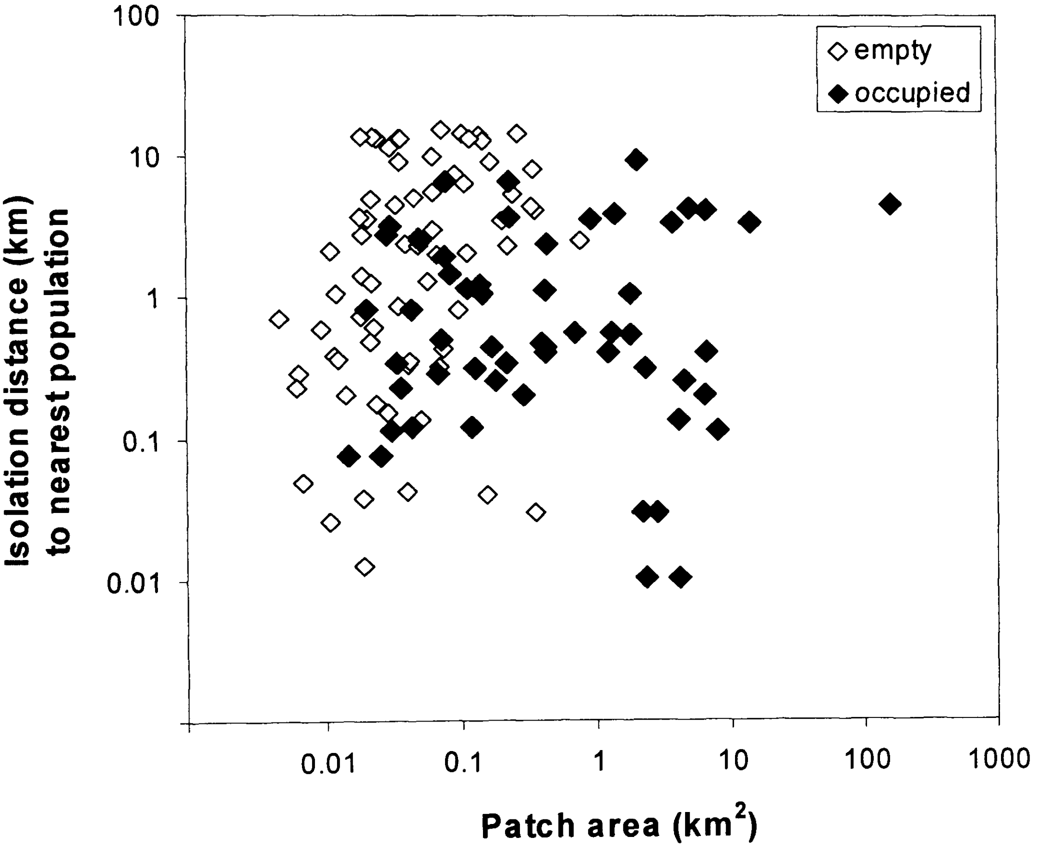


Fig. 5.2. Patch occupancy patterns of *C. a. palliatus* populations in relation to forest area and isolation distance to nearest populations.

5.4.2 Parameter estimation and model fitting

The scaling parameter *b*, defining the rate of change in local population size with patch area, was derived by regressing observed population sizes (the number of individuals per patch) against patch area ($b = 0.46 \pm 0.05$ S.E., $t=8.26$, $p<0.001$, $R^2_{adjusted} = 0.57$) (Fig. 5.3). For *C. a. palliatus*, there is a significant increase in population size with increasing patch area, but at a sub-proportional rate, indicating lower group densities in larger patches (see Chapter 3). The smallest occupied patch was 0.015km^2, leading to estimates of A_0 based on the next smallest patch area in the system where *C. a. palliatus* were absent: 0.014km^2.

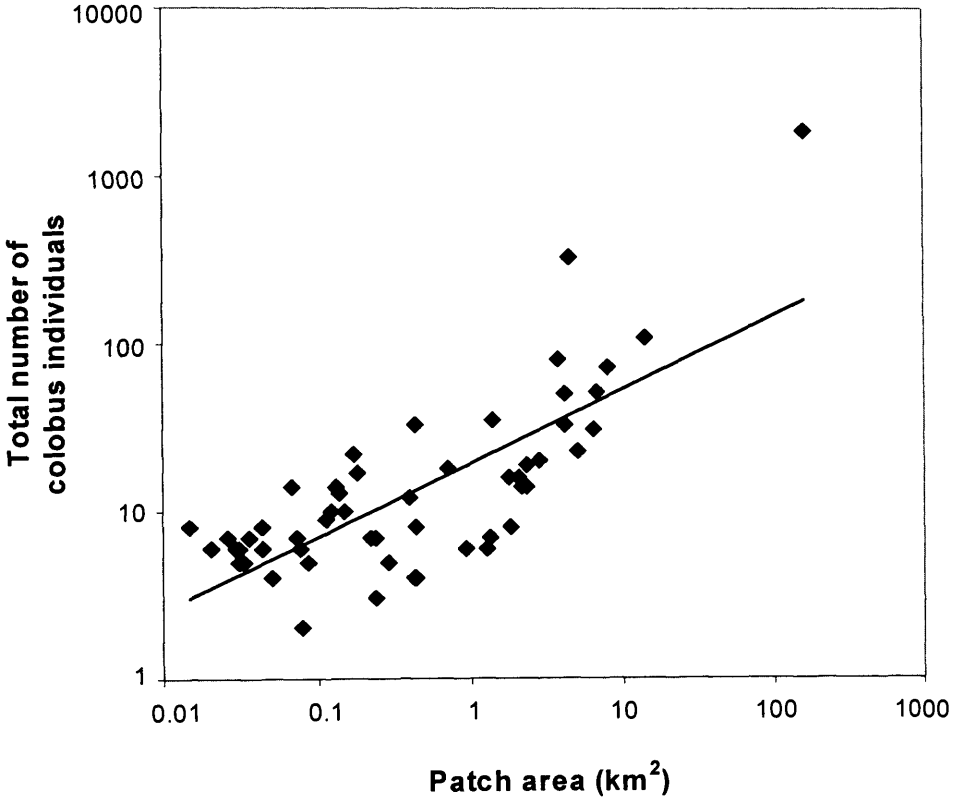


Fig. 5.3. Relationship between patch area (A) and *C. a. palliatus* population size (N). Solid line represents the linear regression $N = cA^b$ ($c = 2.62$, $b = 0.46 \pm 0.05$, $r^2 = 0.56$).

The results of fitting the incidence function model using a range of dispersal parameter values (α) are detailed in Table 5.2. For values of $\alpha \geq 0.5$ the fit of the model is clearly worse for the snapshot of 2001 *C. a. palliatus* occupancy data: $\alpha = 0.5$ produced similar Log(L) values to the null model, whilst $\alpha = 5$ failed to converge all together. The estimates for parameters *x, e,* and *y* were therefore obtained whilst $\alpha = 0.1$, as this model provided the best fit with the lowest log likelihood value when compared to the null model. The value of α translates to a *C. a. palliatus* survival probability (during dispersal) that approaches zero at approximately 50km, with capable average dispersal distances of 10km. Subsequent incidence function simulations of *C. a. palliatus* metapopulation dynamics used the parameter estimates detailed in Table 5.3.

Table 5.2. Parameter x , e', y and e estimates and log likelihood values with varying values of the dispersal parameter α .[a] Log(L) = log likelihood value; *NC* = non-convergence of model. Null model Log (L) = 83.55.

	Parameter values (lower-upper C.I.)				
α	*x*	**e'**	*y*	**e**	**Log (L)[a]**
0.05	0.92 (0.57-1.31)	3.98 (2.81-4.97)	51.24	0.02	60.37
0.1	0.96 (0.61-1.37)	2.32 (1.08-3.37)	24.13	0.017	59.25
0.5	1.81 (1.29-2.33)	-4.55 (-6.23-(-2.92))	4.73	0.0005	83.77
1	2.92 (2.24-3.68)	-9.99 (-12.34-(-7.92))	3.17	$4.51e^{-6}$	123.89
5	*NC*	*NC*	*NC*	*NC*	*NC*

Table 5.3. Final parameter values used in the incidence function model simulations.

Parameter	**Value**
b	0.463
α	0.1
A_o	0.014
x	0.959
e	0.017
y	24.139

5.4.3 Model simulations

Dynamics of the entire Kwale forest patch network (*n* =124) were simulated. There was no significant difference in model outputs whether the Kenyan patch network was isolated or connected to coastal forests in Tanzania, however a general increased trend was evident when the Tanzanian forests were included: M_{pop} increased by 1.7% (one additional occupied patch) and M_{ind} increased by 0.2% (i.e. $U_{i} = 0.13$). The probability of occupancy of all the Kenyan patches (p_i^*) did not significantly increase with such a connection (Wilcoxon-signed ranks test, *n* = 124, Z = -1.844, p = 0.065). However, since the latter result approached statistical significance, and there was an overall positive trend in all three measures, it remains possible that the Tanzanian patches have a positive influence of the Kenyan coastal forest network.

The *C. a. palliatus* metapopulation simulations, whether isolated or connected to Tanzania, showed quasi-stable dynamics (Fig. 5.4) in the sense that the number of occupied patches fluctuated relatively little, and the metapopulation typically persisted over 500 generations with no indication of patch extinction overtaking colonisation rates. The median number of occupied patches remained constant, regardless of the 60 or more patches originally 'empty' in the system, with median patch occupancy stabilising at 57 patches between 100 and 500 generations.

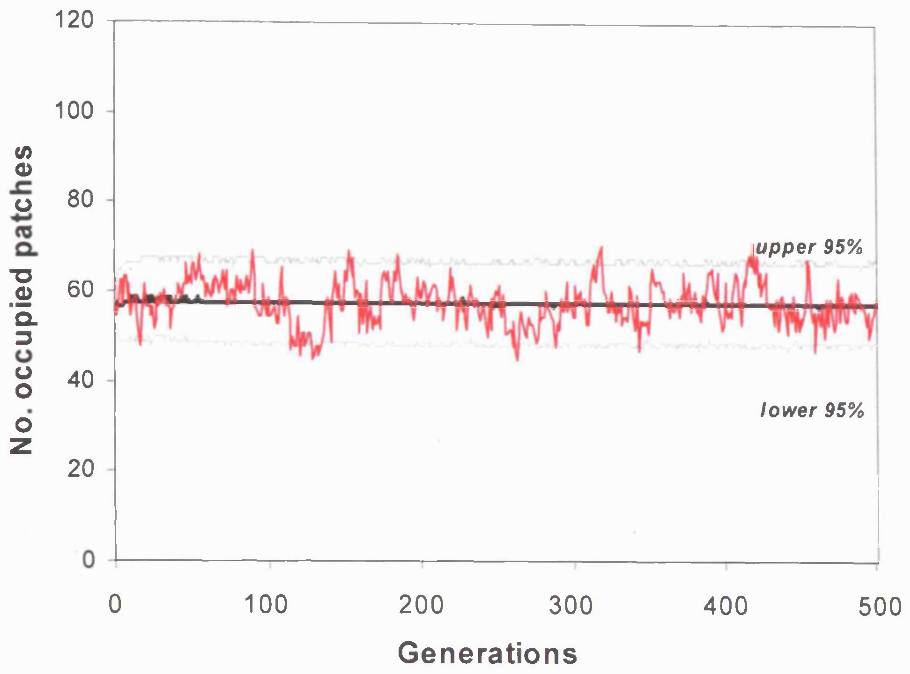


Fig. 5.4. Predicted trajectories of *C. a. palliatus* patch occupancy within 124 Kwale District forests, over 500 generations (iterating the patch network in Fig 5.1). The graph shows the median number of occupied patches after 1000 iterations (black line), 90% upper and lower confidence limits (grey lines), and an example of 1 iteration of the incidence model (red line).

Further incidence function simulations involving the five forms of forest loss highlighted the relative importance of specific habitat patches for *C. a. palliatus* metapopulation persistence. Removal of the smallest patches in the system had little effect on overall metapopulation persistence (Fig. 5.5a). This may be due to the fact that 10-20% of the smallest patches within the system were already empty or poorly connected at the onset of the simulation (Fig. 5.1 and 5.2). In addition, the smallest 50% of patches were all under 0.1km^2 in area. Within the incidence function model these small patches would all have high extinction probabilities and would rarely contribute dispersing migrants to the metapopulation as a whole, effectively acting as possible sinks in the system. In contrast, large forest patches were critical to future *C. a. palliatus* metapopulation persistence (Fig. 5.5b). Removing the largest patch in the system, the Shimba Hills National Reserve, significantly decreased the overall number of occupied patches in the metapopulation. Nineteen *C. a. palliatus* populations (including the National Reserve) went extinct in response to the loss of this individual habitat patch. However, the population still maintained a quasi-equilibrium state between 100 and 500 generations. This indicates that although the patch makes a significant contribution to the overall occupancy level of the metapopulation as a whole, the network may not be entirely dependent upon Shimba in a mainland-island sense. Simulating the loss of 10-20% of the largest forests was enough to cause metapopulation extinction within 340 and 128 generations, respectively. Due to the severity of the decline in metapopulation patch occupancy with this level of perturbation it was decided to simulate the removal of two, four, five and six of the largest patches to establish the critical threshold whereupon metapopulation equilibrium is lost. It was found that removing just five of the largest patches (4%); i.e. the Shimba Hills National Reserve, Marenji, Mwaluganje and Buda Forest Reserves, and Shimoni West (a presently unprotected forest), rendered the entire metapopulation highly unstable with no re-establishment of a quasi-equilibrium state (Fig. 5.5b).

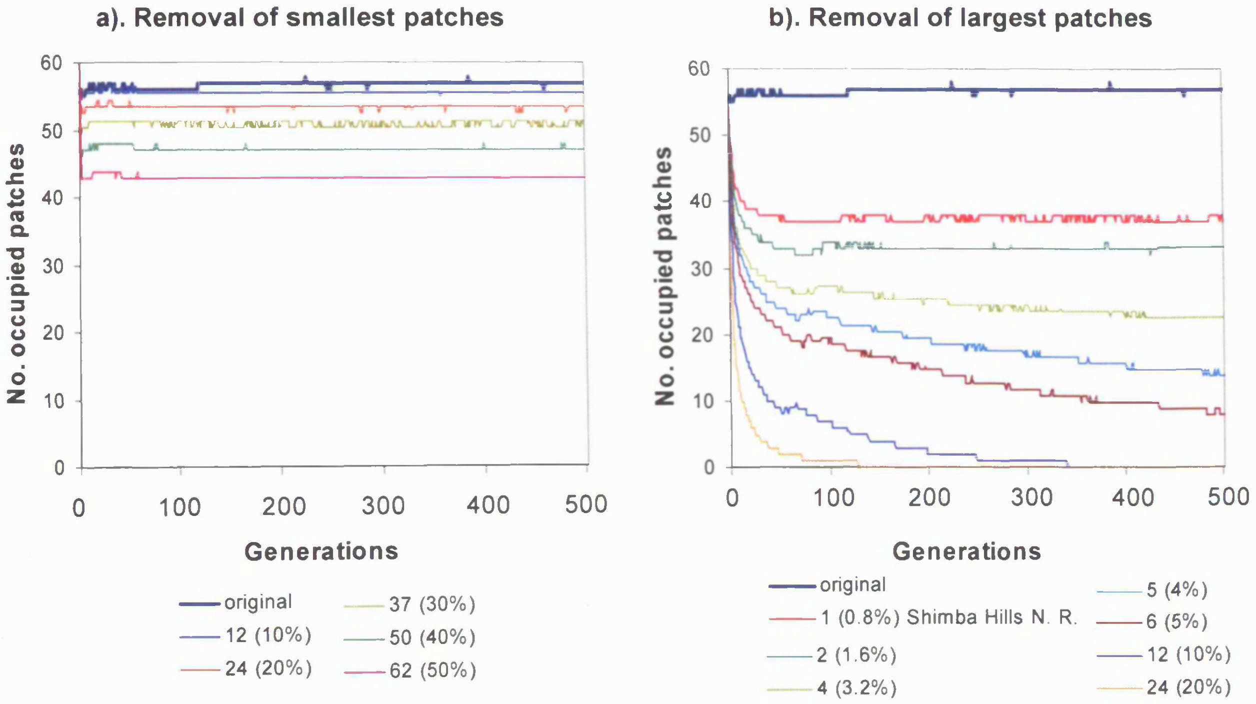


Fig. 5.5 Both figures a). and b). illustrate the long-term effects of removing forest patches from the system. Legends refer to the total number (and percentage) of patches removed from the initial network of 124 forests in Fig 5.1.

The long-term effects of removal of forests by protection status are illustrated in Figure 5.6.

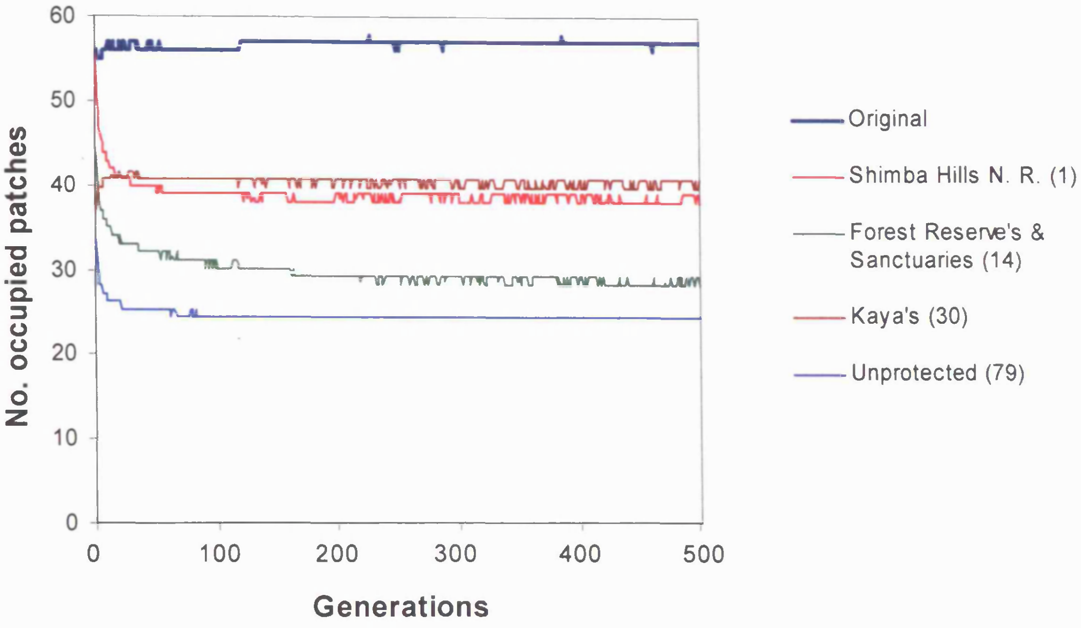


Fig. 5.6. The metapopulation dynamics of *C. a. palliatus* comparing the original 124 habitat patch network with loss of forests, removed by protection status: the Shimba Hills National Reserve, 14 Forest Reserves and Sanctuaries, 30 Kayas and 79 unprotected forests, over 500 generations.

Removal of the unprotected forests has the greatest long-term impact on the metapopulation, followed by Forest Reserves and the Shimba Hills National Reserve. However, the total number of occupied patches at equilibrium may also reflect the gross differences in the number of forests (and colobus populations) initially removed at the onset of each model simulation. Table 5.4 summarises the impact of removing forests by protection status in terms of both initial and ensuing population loss.

Table 5.4. Removal of forest patches by protection status and long-term impacts on the *C. a. palliatus* metapopulation. This table summarises the initial number and area of forest patches removed in the simulations illustrated in Figure 5.6. Impacts are expressed as: [a] the total number of populations removed at the onset of the simulation; [b] the total number of populations lost after forest removal, up until 500 generations; [c] the sum of both initial and ensuing population loss; [d] Removal of 30 Kayas with six re-colonizations of other patches after 500 generations. All figures in brackets express population loss as a proportion of the metapopulation size (number of populations) at 0 generations.

Protection	Initial patch loss		Initial	Ensuing	Total
Status	No.	Area (km^2)	popn loss[a]	popn loss[b]	popn loss[c]
National Reserve	1	158.90	1 (0.02)	18 (0.33)	19 (0.35)
Forest Reserve & sanctuary	14	54.93	12 (0.22)	15 (0.27)	27 (0.49)
Kaya	30	10.90	20 (0.36)	0 (0.00)	[d] 14 (0.25)
Unprotected	79	30.41	22 (0.40)	9 (0.16)	31 (0.56)

By removing the unprotected forests, the simulation is also permanently removing a large proportion of the metapopulation (i.e. 22 occupied patches, 40% of the original number of populations) at 0 generations, the largest perturbation to the network (in terms of population loss), compared to Kaya, Forest Reserve and the National Reserve removal, respectively. However, the long-term impact of removing the Forest Reserves or National Reserve are far greater, given the number of population extinctions occurring within 150 and 60 generations respectively (Table 5.4, Fig 5.6). The latter protected forests could provide key migrants to the network and may be critical with regards to rescue effects of smaller neighbouring patches. Removal of the Kayas had no effect on metapopulation occupancy patterns other than removing the existing populations within the Kayas themselves. In fact, occupancy of the remaining patches slightly increased with the removal of these forests. To discover if this was a true effect of Kaya removal or a symptom of the random stochastic process inherent in the incidence function model, the average occupancy (p_i^*) of all remaining patches were compared before and after each of these simulations (Fig. 5.7). It can be seen that in all cases, including the Kayas, patch removal by protection status significantly decreases average patch occupancy within the remaining forest patches.

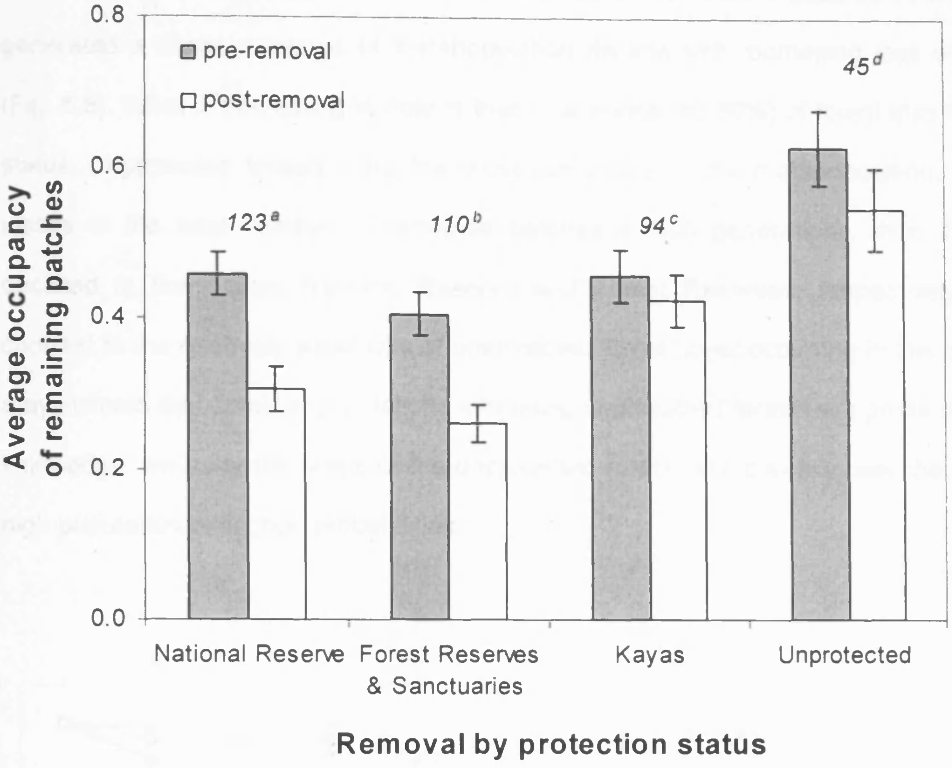


Fig. 5.7. The change in average occupancy of each forest patch at 500 generations when either the National Reserve, Forest Reserve's, Kaya's or unprotected forest patches are removed. Bars show the average occupancy before (grey) and after (white) each removal simulation; y-error bars = ± 1 S.E.; values above bars = *n*. Results of Wilcoxon signed ranks tests = ^{a} (n=123, Z = -9.612, p<0.000), ^{b} (n=110, Z = -9.093, p<0.000), ^{c} (n=94, Z = -7.386, p<0.000), ^{d} (n=45, Z = -5.667, p<0.000).

Reduction of forest area, without the complete removal of patches from the network, generated a linear response of metapopulation decline with increasing loss of forest area (Fig. 5.8). What is interesting to note is that in all levels (10-50%) of forest loss by protection status, unprotected forests were the most vulnerable in the metapopulation, with greater losses in the total number of occupied patches at 500 generations, than if forest area declined in the Kayas, National Reserve and Forest Reserves, respectively. This is in contrast to the relatively small loss of unprotected forest cover occurring in this process. This may indicate that colobus populations inhabiting unprotected forests are presently living on a knife-edge, whereby the areas of the unprotected forests are critically near the threshold for high population extinction probabilities.

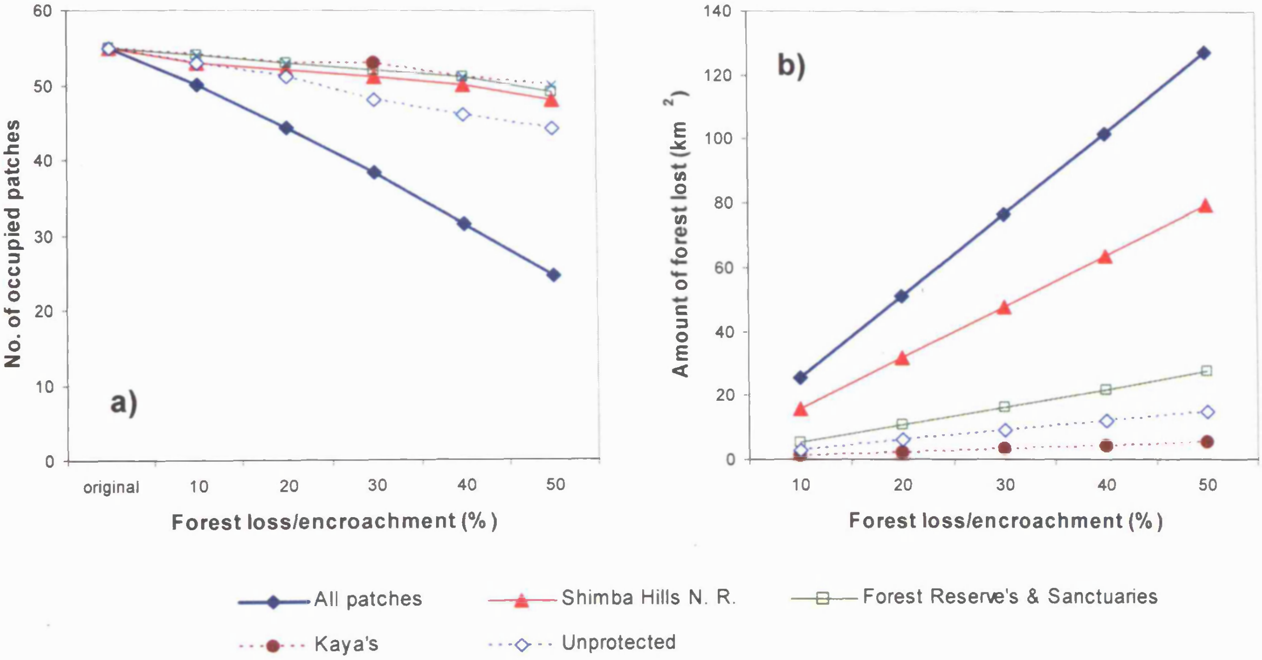


Fig. 5.8. Figure a): *C. a. palliatus* metapopulation size at 500 generations after 10%, 20%, 30%, 40% and 50% reductions in patch areas respectively. Forest loss was allocated to all forests in the network, or to forest patches by protection status only. Figure b) summarises the total amount of forest lost (km^2) in each of the simulations.

The contribution of individual habitat patches to overall metapopulation size (M_{ind}) are detailed in Figure 5.9.

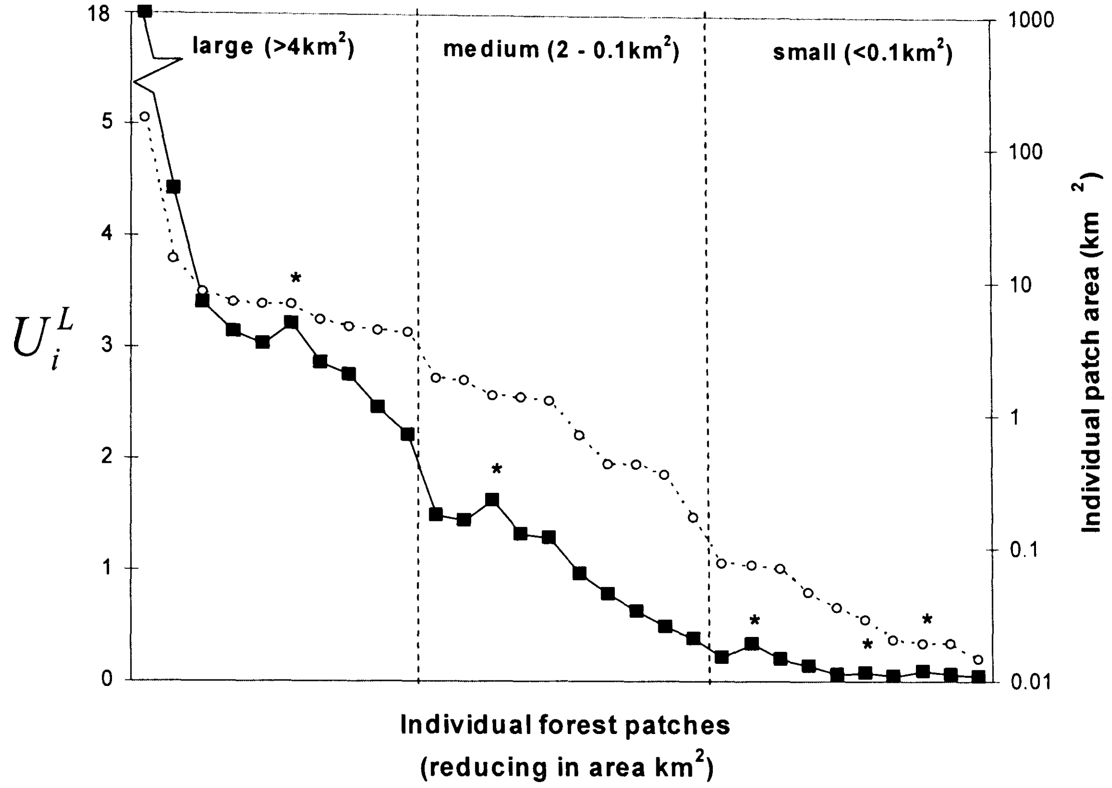


Fig. 5.9. The contribution of 30 individual forest patches to metapopulation size (M^{ind}). *Filled squares* = the contribution value (U_i^L) of individual patches to the metapopulation as a whole; *open circles* = the area (km^2) of individual patches; *asterisk* = patches where contribution values are greater than expected from the declining trend with patch area. Patches are arranged in order of decreasing patch size, whilst the figure shows the results of simulations involving 10 large (>4km^2), 10 medium (0.1-2km^2) and 10 small (<0.1km^2) forest patch removals.

Systematically removing individual patches and re-running the incidence function model (with 123 patches) can provide a good comparative measure of the importance of individual forest patches in the Kwale District, if patch contributions (U_i) *are* assessed via the lowered probabilities of patch occupancies and the reduction in the number of individuals within the metapopulation at equilibrium. The ten small patches made the lowest contributions to the capacity of the network as a whole when compared with the ten medium and ten large patches respectively. The Shimba Hills National Reserve has a markedly large U_i value to the *C. a. palliatus* metapopulation (U_i = 17.9) when compared with all other patches in the network. The progressive decline in magnitude of U_i values with decreasing patch area is no surprise given the weighting of population size with patch area. However, in five instances it was discovered that individual patch contributions were greater than expected, which may indicate that these habitat patches are better connected to the forest network and thus have greater value. Patch contribution was also found to be most relevant within the range of larger patches (>4km^2). Here, patches of relatively similar size displayed noticeably different U_i^L values, again potentially reflecting that habitat patches better connected to the forest network have the greater value.

5.4.4 Model sensitivity to uncertainty

Like all simulations, the incidence function model is numerically sensitive. Given the three parameters which provide the greatest degree of biological realism to the model, *b*, α and A_o, only α is unknown. Sensitivity analyses indicate that the metapopulation occupancy patterns of the original Kwale forest network showed no significant differences in quasi-equilibrium state with varying values of α (i.e. 0.05, 0.1 and 0.5) (Fig. 5.10a).

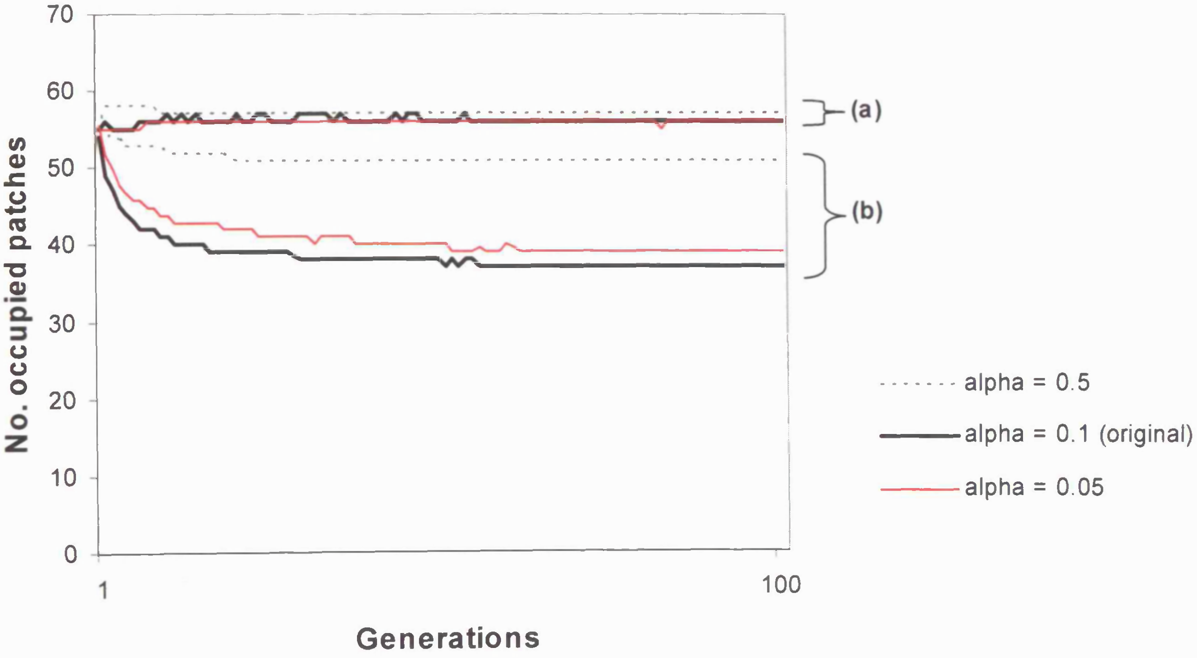


Fig. 5.10. Incidence function model sensitivity to values of α. (a) = three simulations of the original *C. a. palliatus* metapopulation (124 patches) varying the values of α, (b) three simulations of the *C. a. palliatus* metapopulation with Shimba Hills National Reserve removed (123 patches) varying the values of α.

However, when dynamic complexity was added to the model, e.g. by removing the Shimba Hills National Reserve (Fig. 5.10b), different values of α gave rise to quite divergent patterns of metapopulation persistence. Firstly, model outputs were not substantially different within an order of magnitude of α values, i.e. $\alpha = 0.1$ and 0.05. In these simulations, an α value of 0.05 only changed metapopulation occupancy by 5%. This may also be due to $\alpha = 0.05$ being the next closest fit of the incidence function model to the observed occupancy data (Table 5.2). It should also be noted, that when α values are changed, other parameters are modified during model fitting such as x, e, and y in response to changes in the underlying connectivity values S_i, (see Equation 3). For example, as alpha decreases from 0.1 to 0.05, the incidence function model compensates for the resultant increase in connectivity (S_i) by amplifying the number of turnover events, i.e. extinction risk e increases, together with an increase in the efficiency of colonisation y. Secondly, metapopulation occupancy (following the removal of the National Reserve) differed significantly with α at 0.5. In this simulation, the original occupancy at equilibrium (with α at 0.1) was raised by 37%. The dynamic response however, was still evident, confirming that the model's qualitative predictions, rather than quantitative outputs are still valid, regardless of the sensitivity to this parameter.

5.5 Discussion

5.5.1 Main study findings

The results of this study suggest that in the Kwale District of Kenya the spatial configuration of forest habitat plays an important role in the occurrence and potential metapopulation dynamics of the Angola black-and-white colobus. Both habitat patch area and isolation distance from neighbouring colobus populations had a significant effect on colobus occurrence, whilst the general fit of the incidence function model to present *C. a. palliatus* occupancy patterns also confirmed that habitat patch area, patch connectivity and the spatial distribution of populations are likely to play a major role in *C. a. palliatus* population dynamics. With regards to the incidence function model fit, average colobus dispersal distances of 10km (i.e. with α at 0.1) are certainly feasible given the medium body size of the subspecies; i.e. 7-10kg (Peters, 1983; Rowe, 1996; Sutherland *et al.*, 2000), and are consistent with the documented sightings of healthy colobus individuals moving 5km from the nearest forest edges (Chapter 4). These latter distances were purely based on straight-line calculations, therefore potential dispersal distances, accounting for more natural animal movement, could be much larger (Diffendorfer, Gaines & Holt, 1995; Johnson *et al.*, 1992; Ricketts, 2001; Schippers *et al.*, 1996). Values of α may also suggest that the non-habitat matrix, presently viewed as homogeneous and inhospitable in this model (Hanski, 1994b; Ricketts, 2001), could be facilitating long-distance dispersal between forest patches. Indeed, non-forest vegetation types found within the matrix of this region (e.g. mangrove, perennial and timber plantations) could be highly advantageous for arboreal colobine dispersal (Chapter 4), and may play a significant, yet presently overlooked, role in this network.

The metapopulation simulations in this study suggest that large patches in the Kwale forest network are critical to future *C. a. palliatus* persistence. In particular, there was a significant impact on metapopulation size and persistence when the Shimba Hills National Reserve was removed, especially in combination with other large forest losses that together represent 4% of all large patches (three Forest Reserves and the presently unprotected Shimoni forest). It could be feasible that sub-networks of forests are clustered together, with neighbouring smaller patches relying on these larger patches either for connectivity to the wider metapopulation, sources of immigrants, and/or rescue effects (Brown & Kodric-Brown, 1977). There may also be a degree of local source-sink dynamics within the network, i.e. the large habitat patches displaying net positive population growth (sources), supporting neighbouring patches with negative population growth (sinks) through immigration (Hanski & Simberloff, 1997; Pulliam, 1988; Pulliam & Danielson, 1991). However, source-sink dynamics are based on assumptions involving differences in patch quality, and forests surrounding 'source' patches are not necessarily 'sinks' because they are small. Present patterns of occupancy may also illustrate this effect, as there are a variety of adequately-sized patches near colobus populations that are presently unoccupied (Fig 5.2). Ideally, two or more surveys are required to establish whether these empty patches are symptomatic of the extinction-colonisation processes within the metapopulation network. Otherwise, differences in patch quality could also be influencing the present state of occupancy (see Chapter 3).

Habitat destruction in the Kwale District is likely to involve a combination of the future landscape scenarios simulated in this study. In the future, forest encroachment may be the driving force of future metapopulation occupancy patterns in the Kwale District (see Chapters 2 and 3), particularly within unprotected forests (Fig. 5.8). Metapopulation models may therefore provide a valuable conceptual framework in which to explore these processes, and the potential effectiveness of future conservation interventions in these areas.

Removal simulations involving individual forest patches (Fig. 5.9), combined with alternative measures of metapopulation size (Ovaskainen & Hanski, 2003b), provided a useful measure in which to assess patch contribution to the *C. a. palliatus* metapopulation as a whole. Such explorations are especially relevant in the context of conservation, when limited resources might be most effectively allocated towards the management of the most "valuable" pieces of habitat (Cabeza & Moilanen, 2003; Drechsler *et al.*, 2003; Ovaskainen & Hanski, 2003b; Turner, Arthaud & Engstrom, 1995). For example, in the simulation where 79 unprotected forests underwent 50% deforestation (Fig. 5.8.a) or were removed (Fig. 5.6), it is difficult to determine which patches in particular were decisive in the respective 20% and 56% declines in metapopulation occupancy. However, a comparison of U_i values for each of the unprotected forests (Fig. 5.9) may permit wildlife managers to determine the key patches, or combinations of patches, that prevent these declines, without the unrealistic expense of implementing conservation measures to preserve all 79 unprotected forests. Similarly, this method could be used to highlight (or rank) the most valuable patches within the entire forest network. It should be stressed however, that these models can only provide a conceptual framework in which to explore these ideas, and should not be used exclusively to implement conservation management directives. Rather, metapopulation models may be most effectively used as a component of other local or national site-selection methods for prioritising conservation, for example by adding regional scale, spatial detail and/or connectivity to existing quantitative population (and habitat) viability analyses (Akcakaya, 2000, 2001; Akcakaya, McCarthy & Pearce, 1995; 2004; Coulson *et al.*, 2001; Davies *et al.*, 2001; Lacy, 1993-1994), or by augmenting other conceptual, criteria-based evaluations such as 'site-selection' algorithms (Cabeza & Moilanen, 2003; Carroll *et al.*, 2003; Drechsler *et al.*, 2003).

5.5.2 Modelling uncertainties

When assessing the validity of *C. a. palliatus* metapopulation predictions for conservation management decisions, it is also useful to be clear about the uncertainties and assumptions inherent in the incidence function modelling approach. Outputs from the models themselves will be most useful if they are kept in context with the quality of biological data, confidence limits (Table 5.2) and sensitivity (Fig. 5.10) of model parameters.

There are a number of assumptions inherent in the incidence function modelling approach which wildlife managers should be made aware of. These assumptions specifically relate to parameter estimation and the errors that can occur in this process (Conroy *et al.*, 1995; Moilanen, 2002). In the case of this study, the regional population of *C. a. palliatus* fits well within most of the parameter estimate restrictions set by Hanski (1999b).

Firstly, Kenyan forest patches were discrete and numerous (at least 30 patches, 10 empty and 10 occupied, are advised), with substantial variation in patch area and/or isolation for good parameter estimation. All forest patches in the network were accounted for and areas were accurately measured. In contrast, crude measures of patch areas or missing patches could cause significant errors in parameter estimation and subsequent model predictions, e.g. extinction probabilities for large patches, migration distances, and colonisation ability of species are all overestimated by missing patches and poorly estimated areas (Moilanen, 2002).

Secondly, a complete survey of patch occupancy in 2001 (Chapter 2) eliminated 'false zeros' in the dataset (i.e. observed or assumed empty patches, when there truly were populations present), an additional source of bias that can cause anomalous parameter estimates (Hanski, 1994b, 1999b; Moilanen, 2002).

Lastly, the incidence function model assumes that the landscape and pattern of patch occupancy have been fairly stable, or, if the landscape has been recently altered, that sufficient time has passed for the population to reach an equilibrium state within the altered landscape (Hanski, 1994b, 1999b; Hokit, Stith & Branch, 2001; Moilanen, 2000). In the natural world only a handful of primate study sites exhibit a historical, equilibrium state of 'natural' forest fragmentation (Lawes *et al.*, 2000; Mbora, 2004; Tutin, 1999), unaffected by the dynamic changes of human land use. Even within these sites, and several of the modeled non-primate metapopulation networks, some degree of dynamic, anthropogenic habitat change is evident (for a recent review of the non-primate metapopulations, see Baguette, 2004). In Kenya, a history of 12-year forest loss was found to negatively influence the density of individual *C. a. palliatus* populations (Chapter 3). However, forest loss did not influence population occupancy of patches, and the total number of forest patches over this time remained constant. Compared with invertebrate and small mammal metapopulations (e.g. Hanski *et al.*, 1996b; Moilanen *et al.*, 1998), the long generation times and slow population turnover of colobus (Elmhagen & Angerbjorn, 2001; Newton & Dunbar, 1994) may cause populations to linger-on in small forest patches prior to true extinction (Tilman *et al.*, 1994), thus masking actual lowered equilibrium levels of occupancy in the Kenya forest network. By relying solely on a snapshot of patch occupancy data in this study without any temporal measures of either turnover events or increasing/decreasing trends in the metapopulation, the original incidence model (ie. without dynamic perturbation) may be overestimating the persistence of *C. a. palliatus* in Kenya, and should be viewed with caution (Clinchy, Haydon & Smith, 2002; Hokit *et al.*, 2001; Moilanen, 2000, 2004). The difficulty in tackling the equilibrium assumption is also highlighted by other primate studies. Chapman *et al.* (2003) used Hanski's incidence function model to fit data from two independent colobus surveys in the Kibale forest, Uganda. Of the 16 forest patches that were surveyed in 1995 which supported resident colobus populations, three had been cleared by the year 2000. Similarly in Los Tuxtlas, Mexico the fragmented forest habitat of a howler monkey metapopulation (*Allouatta palliata mexicana*) had undergone 4-7% annual deforestation rates since the 1960s (Mandujano *et al.*, in press).

Assuming equilibrium in the incidence function model should be highlighted as a further reason for viewing the quantitative outputs of such models with caution. Nevertheless, it is possible that even if metapopulations are not at equilibrium the qualitative predictions of future landscape scenarios are still likely to be comparable to a 'quasi-equilibrium' state as they may still provide a 'relative' index of patch importance to overall metapopulation stability (Hanski, 1999b; Ovaskainen & Hanski, 2001, 2003b).

5.5.3 Future development of a metapopulation approach

Assessment of the accuracy of a metapopulation approach is extremely difficult with only one 'snapshot' of occupancy data. However, future field studies in the Kwale District could be designed to gather further biological data for model parameterisation, monitor the success of model predictions, and continually improve the model in response to new understanding (Conroy *et al.*, 1995; Turner *et al.*, 1995). For example, at present the network has no data on population turnover events (Thomas, 1994) which could allow for measures of both colonisation and extinction processes within the metapopulation. Cowlishaw *et al* (in prep.) were able to successfully derive field-based quasi-equilibrium extinction and colonisation rates for the Tana River red colobus (*Procolobus badius rufomitratus*) metapopulation, using an incidence function model, but this required primate survey data over a 20-year period. Given the time-scale difficulties for tracking these processes in a species with slow population turnover (Elmhagen & Angerbjorn, 2001), *C. a. palliatus* population dynamics may have to be measured differently, e.g. looking for short-term trends such as differences in subpopulation growth rates (Coulson *et al.*, 1999; Dobson & Lyles, 1989).

Finally, it may also be useful to develop the degree of environmental realism in incidence function simulations, in order to help improve model fit to colobus occupancy data and to provide more opportunities to explore the impacts of alternative conservation management options for the subspecies, such as habitat restoration (MacMahon & Holl, 2001; Young, 2000) or the creation of dispersal corridors (Bennett, 1998; Laurance, 2004). This would involve the inclusion of measures such as habitat quality (Fleishman *et al.*, 2002; Thomas *et al.*, 2001) and matrix heterogeneity (Ricketts, 2001), which have largely been ignored in previous applications to other taxa. Results of previous studies (Chapters 3 and 4) have determined that habitat quality and matrix heterogeneity are important factors involved in *C. a. palliatus* subpopulation density, incidence and individual colobus movements within non-forested areas of the subspecies range. Additional research focusing on the frequency of colobus dispersal and survival in the 'matrix' could also provide more accurate measures of the parameter α, and subsequent levels of connectivity within the network. Further exploration of the effects of matrix heterogeneity on metapopulation dynamics will be presented in Chapter 6.

In essence, the incidence function model provides a good starting point from which it is possible to conceptualise colobus population dynamics in a spatial framework. A metapopulation exploration has opened up a valuable, landscape-level understanding of this subspecies persistence in a fragmented forest network, particularly where the impacts of future forest loss need to be addressed. It is currently difficult to predict which forest-dependent species will survive in forest fragments without adequately assessing the future impacts of habitat conversion (Chapman & Peres, 2001). The incidence function model may provide a valuable theoretical framework in which to explore such impacts.

6. Metapopulation dynamics of an arboreal primate and the influence of the matrix.

6.1 Abstract

In determining isolation effects in fragmented populations, the heterogeneity of the matrix is not often considered. This study uses data from an Angola black-and-white colobus (*Colobus angolensis palliatus*) metapopulation in East Africa, a detailed GIS land cover map of the region and Hanski's incidence function model to provide a case study for the exploration of matrix quality effects within a metapopulation framework. A relatively simple modification of the incidence function model was explored which incorporated a 'weighted' measure of isolation distance using estimates of inter-patch matrix quality. However, this measure was found to improve model fit by only 4%, suggesting either that the matrix may have a relatively small influence on metapopulation dynamics in the present system, or that this approach may only capture a small fraction of the true heterogeneity, quality and spatial configuration of land cover types in the matrix. The modified incidence function model was then used to explore colobus metapopulation dynamics under a range of future scenarios of matrix change. Simulations of future matrix degradation or improvement were found to substantially decrease or increase (respectively) the total number of *C. a. palliatus* populations in the fragmented network. Incidence function model usage in this context could provide a conceptual tool for wildlife managers to explore the best combination of (1) habitat preservation and (2) matrix preservation and/or enrichment initiatives that could best facilitate the persistence of metapopulations within fragmented forest networks.

6.2 Introduction

The spatial configuration of fragmented habitat plays a pivotal role in species population dynamics (Andren, 1994; Davies *et al.*, 2001; Fahrig, 2003; Fahrig & Merriam, 1994; Wiens, 1997; Wiens *et al.*, 1993a). Patch size, shape, number and connectivity have all been linked to patterns of species incidence, abundance, population growth and extinction (see Fahrig, 2003, for a recent review). Over the past decade in particular, metapopulation ecology has influenced both theoretical and empirical research of species population dynamics at the regional scale (Baguette, 2004; Hanski & Ovaskainen, 2003; Ricketts, 2001; Vandermeer & Carvajal, 2001), focusing primarily upon the influences of habitat patch size and connectivity within fragmented landscapes (Hanski, 1994b; Hanski & Gilpin, 1997). In this approach, spatially subdivided populations are modelled within a binary landscape of habitat and 'matrix', i.e. the non-habitat surrounding the native habitat of interest. The critical factor maintaining metapopulation persistence in these fragmented networks is the movement of individuals between habitat patches, either 'rescuing' subpopulations from extinction or re-colonizing empty patches in the network. Migration of individuals is assumed to be distance dependent (see Chapter 5 for more details on metapopulation assumptions and a full description of Hanski's incidence function model, Hanski, 1994b).

Habitat patch 'connectivity' in the metapopulation sense is largely modelled using the shortest (Euclidean) isolation distances to all possible source populations in the fragmented network (Moilanen & Nieminen, 2002), whilst the matrix is assumed to be homogeneous and ecologically unimportant (Murphy & Lovett-Doust, 2004; Ricketts, 2001; Vandermeer & Carvajal, 2001). However, true 'connectivity' in nature is undoubtedly more complex, as the landscape between habitat fragments is often composed of a wide variety of natural or human-modified land cover types (Forman, 1997).

Field studies have found that differences in the heterogeneity, quality and fine-scale spatial distribution of matrix can significantly influence the occurrence, richness and abundance of bird and small mammal assemblages within fragmented forest remnants (Antongiovanni & Metzger, 2005b; Gascon *et al.*, 1999; Jokimaki & Huhta, 1996; Pardini, 2004; Pardini *et al.*, 2005; Wethered & Lawes, 2003). At an individual level, matrix heterogeneity has also been found to influence the movement behaviour of dispersing individuals (Cook *et al.*, 2004; Doncaster, Rondinini & Johnson, 2001; Goodwin & Fahrig, 2002) and consequently, dispersal success between habitat fragments (Bonte *et al.*, 2003; Ferreras, 2001; Pither & Taylor, 1998; Ricketts, 2001). In some instances, there are clear species-specific differences in the ability to tolerate or exploit the matrix (Develey & Stouffer, 2001; Laurance, 1994; Laurance & Yensen, 1991; Nupp & Swihart, 2000) whilst in some rainforest species, the inability to use the matrix is the main factor cited for population declines and extinctions (Diamond & Bishop, 1987; Laurance, 1994; Viveiros de Castro & Fernandez, 2004).

In a metapopulation context, both the structural characteristics of the matrix (structural connectivity), and the specific mobility and behaviour of the dispersing individuals (functional connectivity), will greatly influence effective isolation distances between habitat patches (Tischendorf, Bender & Fahrig, 2003; Tischendorf & Fahrig, 2000, 2001). The origins of both 'structural' and 'functional' concepts of connectivity are more frequently addressed in the discipline of landscape ecology (Tischendorf & Fahrig, 2000; Wiens, 1997; With, Gardner & Turner, 1997). Here, connectivity is principally viewed by the degree to which the landscape facilitates or impedes individual movement amongst resource patches (Taylor *et al.*, 1993). Although there has been an obvious acknowledgement of the importance of matrix complexity, and landscape-level ecological processes, within the metapopulation literature (Baguette & Mennechez, 2004; Hanski & Gilpin, 1997; Hanski & Ovaskainen, 2003; Moilanen & Hanksi, 2001) metapopulation models have yet to firmly incorporate a more structural and/or functional (landscape ecology) approach to patch connectivity (Ricketts, 2001; Shreeve *et al.*, 2004; Tischendorf & Fahrig, 2000, 2001; Vandermeer & Carvajal, 2001; Wiens, 1997).

Some authors have discussed the possibility of 'weighting' isolation distances between habitat patches by the quality of matrix habitat comprising this distance. In this simple modification of connectivity, both the structure and coverage of matrix types are critical, as they could either impede or facilitate dispersal along original isolation distances (i.e. 'functional distance', Petit & Burel, 1998; 'matrix resistence', Ricketts, 2001; 'migration filter', Vandermeer & Carvajal, 2001; e.g. 'matrix permeability', Wiens, 1997). To date, only one attempt has been made to explore the applicability of this approach in empirical metapopulation networks. Moilanen and Hanksi (1998) weighted patch isolation metrics in an incidence function model of a Granville fritillary butterfly metapopulation in Finland. They found that adding additional complexity beyond the effects of habitat patch area and isolation distance did not significantly improve the predictive power of the model. However, further research is required to establish the generality of this finding across other systems.

Given the need for further empirical explorations of matrix effects within differing metapopulation networks, this study explores the significance of a simple matrix-weighted measure of patch connectivity using the incidence function model for a forest-dependent primate species in Kenya, the Angola black-and-white colobus (*Colobus angolensis palliatus*). The metapopulation dynamics of this taxon have previously been modelled using shortest isolation distance measures of connectivity within an incidence function model approach (see Chapter 5). Survey data on the presence of *C. a. palliatus*, a spatially-explicit database of all habitat patches in the region, and a matrix land cover map (derived from Landsat TM data) will provide the framework to further explore matrix heterogeneity and its relevance to the metapopulation dynamics in this case study.

In addition, the incidence function model has been found to be an extremely useful tool for investigating impacts of future habitat change in fragmented landscapes (Hanski, 1998; Hanski & Simberloff, 1997). A more detailed incidence function approach which incorporates the effects of matrix quality may hence provide additional scope for the exploration of future changes in the land cover types surrounding fragmented forest networks. Therefore, the two main aims of this study were to (1) determine whether a simple, matrix-related modification of inter-patch distance in the incidence function model can improve model predictive power, and (2) explore the influence of future changes in the matrix on *C. a. palliatus* metapopulation persistence.

6.3 Methods

6.3.1 Study site, species and prior research

The Kwale District in the Coastal Province of Kenya lies between Mombasa and the border of North Eastern Tanzania (3°30', 4°45'S; 38°31' and 39°31'E). The District is roughly 8,300km^2 in area and encompasses a heterogeneous mix of both indigenous and agricultural land cover types (Chapter 4). Of primary conservation interest is the 124 coastal forest patches (total area: 255km^2) remaining within this District (Chapter 2). Along with the Eastern Arc Mountains and coastal forests of northern Tanzania and northern Kenya (Clarke, 2000), the Kwale District coastal forests are a core component of one of 25 global diversity hotspots (Myers *et al.*, 2000), and are listed as one of 11 priority regions for international conservation investment (Brooks *et al.*, 2002). The Kwale District forests also provide habitat for the entire Kenyan population of Angola black-and-white colobus (*Colobus angolensis palliatus*). This primate taxon is 'data deficient' in current IUCN red listings (IUCN, 2004) and the need for more comprehensive information regarding the species status in Kenya has previously been highlighted (Oates, 1996a). Steps towards this assessment have already been made, with a recent, 2001 primate survey of all 124 forests in the District. Fifty-five *C. a. palliatus* populations were found during this survey, (44% habitat patch occupancy), with an estimated national population estimate of 3,100 – 5,000 individuals (Chapter 2). Colobus occurrence in this forest network has also been significantly linked with the quality (i.e. canopy cover) and spatial characteristics (i.e. patch area and isolation distance from source populations) of habitat patches (Chapters 3 and 5), whilst the future population dynamics of *C. a. palliatus* have also been modelled in a metapopulation framework using Hanski's incidence function model (Chapter 5). In this model, exact patch areas and shortest (Euclidean) isolation distances were used. The spatial characteristics of the habitat network were determined using a geographical information system (GIS) (ArcView GIS 3.2, ESRI Inc. 1999) and a database describing the spatial locations and forest boundaries of all 124 habitat patches in the Kwale District. Within model simulations however, matrix quality was not considered, as the intervening landscape between habitat patches was assumed to be homogeneous.

However, the matrix in the Kwale District is extremely varied (Chapter 4). Indigenous matrix vegetation is comprised of mangrove, coastal shrubland, and shrub or wooded grassland areas, which can also contain small clusters of indigenous (forest) tree species (too small in area to warrant a 'forest habitat' classification). Historical human land use in the region has transformed coastal forest and other types of indigenous matrix vegetation into pastoral grasslands, perennial plantations (i.e. coconut, cashew nut, mango), timber plantations, annual croplands (e.g. maize, rice, sugarcane and root vegetable crops) and areas of human development/settlement (CEPF, 2003; Muchoki, 1990; Nzoika *et al.*, 2003).

Differences in the structure and quality of the matrix within the Kwale District have also been found to potentially aid or hinder colobus dispersal between habitat patches (Chapter 4). *C. a. palliatus* is primarily arboreal in nature (Davies, 1994), therefore dispersal movements could be energetically costly through matrix types that require terrestrial locomotion (Aronsen, 2004b). This could result in colobus individuals avoiding more open matrix types in preference for closed, canopy-like matrix. This hypothesis is supported from recently documented reports of colobus individuals and groups moving through closed-canopy matrix types in the Kwale District such as mangroves and perennial plantations, whilst more open matrix types such as annual croplands, grasslands and shrub grasslands are generally avoided (Chapter 4).

6.3.2 Matrix characteristics

Using a 2003 land cover map of the Kwale District (derived from Landsat TM data: 25m x 25m resolution) (see *Appendix IV*) and GPS-derived maps of the boundaries of all habitat patches in the network, all existing matrix land cover types (i.e. surrounding habitat patches) were re-classified to a species-specific matrix classification using ArcGIS Spatial Analyst (ArcInfo 9.0, ESRI Inc. 2002), as detailed in Table 6.1. In this process, each of the 17 identifiable matrix types were allocated a 'quality' rank based on the hypothesis that colobus movement through the matrix would be facilitated when the vegetation structure was similar to that of habitat fragments (Pearson, 1993; Stouffer & Bierregaard, 1995). If beneficial matrix structure also had a high proportional coverage of colobus food trees, general colobus locomotion and foraging efficiency were assumed to improve during inter-patch dispersal (Aronsen, 2004b; McGraw, 1998a). The matrix 'quality' ranks were therefore as follows; 0, matrix type offers no benefit to arboreal locomotion and may even hinder primate dispersal; 1, matrix type offers limited access to arboreal locomotion with limited occurrence of colobus food trees; 2, matrix type offers dense tall canopy and unhindered arboreal locomotion with limited occurrence of colobus food trees; 3, matrix type offers closed tall canopy, unhindered arboreal locomotion and high occurrence of colobus food trees. In all cases, the proportion of tall vegetation cover was viewed as the most important factor influencing dispersal, whilst colobus food trees were viewed as an additional benefit only. The resultant matrix 'quality' map for the Kwale District (raster format: 25m x 25m resolution) is shown in Figure 6.1.

Table 6.1. Characteristics of matrix types and their suitability for *C. a. palliatus* dispersal within the Kwale District, Kenya. [a] Coverage of tall (>6m) vegetation and colobus food trees = *closed* (80-100%), *dense* (50-79%), *open* (20-49%), *sparse* (2-19%), *none* (0%) (Grunblatt *et al.*, 1989); [b] predicted locomotion of colobus individuals within matrix given the variation in tall canopy cover; [c] Reflects the quality of each matrix type in facilitating arboreal dispersal between forest patches.

Matrix type	Matrix characteristics [a]		Predicted [b] locomotion	Quality [c] rank
	> 6m trees	food trees		
Indigenous				
Indigenous coastal forest vegetation	closed	dense	unhindered arboreal	3
Mangrove	closed	open	unhindered arboreal	3
Wooded shrubland	open	open	intermediate arboreal	1
Wooded grassland	open	sparse	intermediate arboreal	1
Shrubland	sparse	sparse	intermediate arboreal	1
Shrub grassland	sparse	sparse	terrestrial	0
Bare ground	none	none	terrestrial	0
Sand	none	none	terrestrial	0
Swamp	none	none	none	0
Water	none	none	none	0
Human land use / other				
Perrenial plantation	dense	sparse	unhindered arboreal	2
Timber plantation	dense	sparse	unhindered arboreal	2
Annual cropland <1m	sparse	none	terrestrial	0
Annual cropland 1-3m	sparse	none	terrestrial	0
Grassland	sparse	none	terrestrial	0
Human development	none	none	terrestrial	0
Quarry	none	none	terrestrial	0

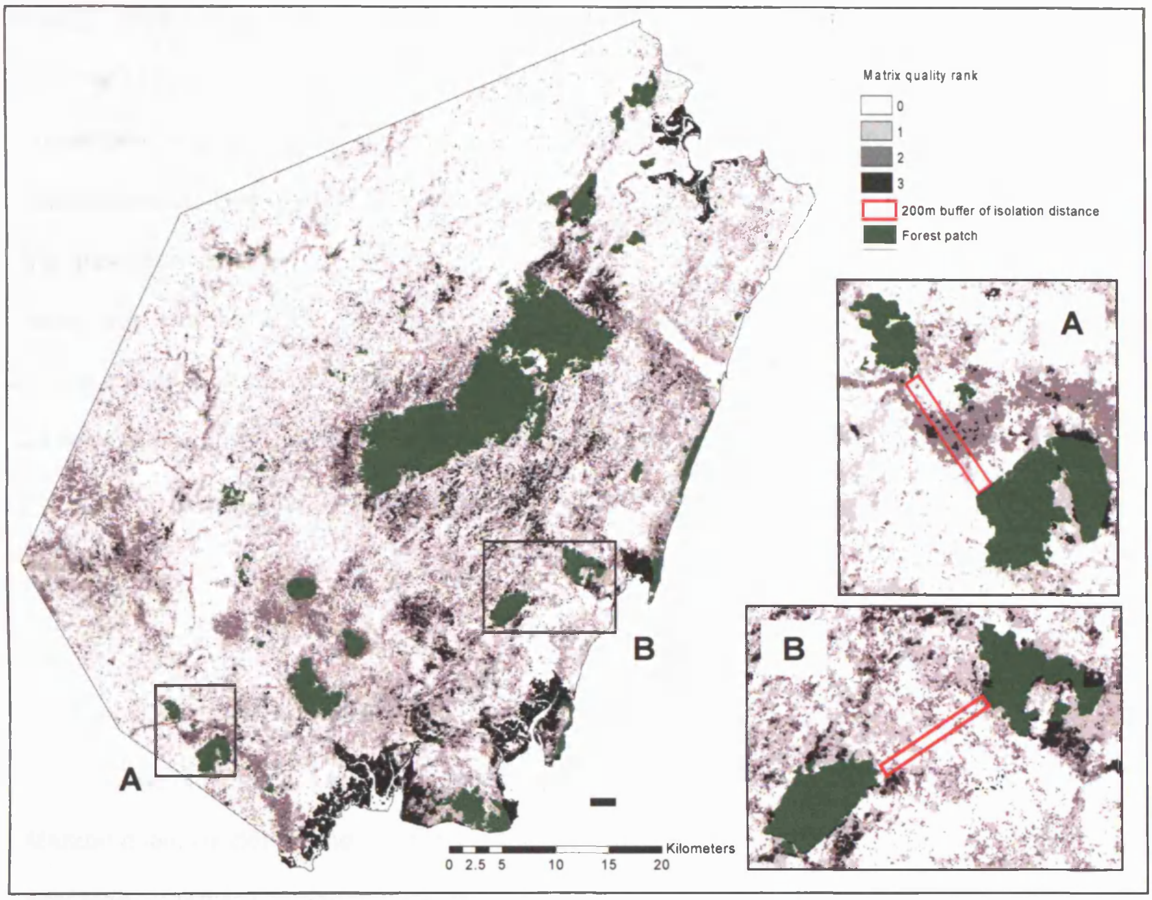


Fig. 6.1. Matrix quality in the Kwale District, Kenya. Both figures A and B illustrate 200m flat-ended buffers of the shortest (Euclidean) isolation distances, between pair-wise comparisons of habitat patches.

6.3.3 Weighing isolation distance by matrix quality

Using ArcView 3.2 and a Distance and Azimuth Matrix v.2 (Jenness, 2005) it was possible to calculate the shortest (Euclidian) isolation distances between all pair-wise habitat patch combinations in the forest network (i.e. $n*(n-1)/2 = 7,626$ comparisons, where n, total number of patches, is 124). These isolation distances (km) were calculated from habitat patch edge-to-edge and accounted for the Indian Ocean coastline (see *Appendix VII*). The GIS analysis also created a shapefile of all pair-wise isolation lines (trajectories). To account for variation in matrix quality over these isolation distances, 50m-, 100m- and 200m-width flat-ended buffers were superimposed along all 7,626 isolation lines (ArcToolbox proximity buffer extension: ArcInfo 9.0, ESRI Inc. 2004). Each of the three resultant buffer shapefiles were then overlaid onto the matrix quality map (Fig. 6.1) and the average (mean) matrix quality value (range 0-3) of all 25m x 25m matrix cells beneath each buffer zone were summarised using Spatial Analyst Zonal Statistics (ArcInfo 9.0, ESRI Inc. 2004). Buffer zones were averaged over land only. Any Indian Ocean matrix cells were excluded from the zonal statistics. This calculation gave an estimate of the average quality of matrix for each of the pair-wise isolation distances. A Pearson's correlation analysis was then used to determine whether 50m, 100m and 200m buffer methods produced similar estimates of matrix quality. The results indicated a strong correlation between matrix quality estimates for all three buffer methods (Pearson's correlation values ranged from 0.992 to 0.998, $n = 7{,}626$, $p < 0.001$). A single buffer width, of 200m, was therefore selected for use in all subsequent analyses.

6.3.4 Incidence function model

The incidence function model (Hanski, 1994b) is based on a first-order, linear Markov chain model for the changes in the state of one habitat patch, which may be either occupied or empty. Changes in the state of patch i are determined by extinction and colonization probabilities E_i and C_i, which are calculated independently for every patch i in each time unit, using patch areas A_i and patch connectivity measures S_i as variables. Specifically, the area of a patch is assumed to determine the extinction probability, $E_i = e / A_i^x$, where e and x are parameters determining the shape of the response. The colonization probability of patch i is defined by a sigmoid function $C_i = S_i^2 / (S_i^2 + y^2)$, where parameter y determines the shape of the reponse. In the standard incidence function model (Hanski, 1994b, 1998), patch connectivity (S_i) is defined as:

$$S_i = \sum_{j \neq i} p_i \exp(-\alpha d_{ij}) A_j^b \qquad (1)$$

where p_i is the observed incidence of the patch (simply a 'snapshot' of data, resulting in the input of species presence = 1, or absence = 0), and d_{ij} is the distance between patches i and j. The parameter α determines the rate of decline in survival of a migrant with increasing distance moved. Since the size of neighbouring populations could affect the number of migrants reaching the focal patch i, A_j is included in Equation (1), whilst parameter b scales expected population size with patch area.

Using the independent extinction (E_i) and colonization (C_i) probabilities for each patch in the fragmented network, and including a rescue effect (a population may be rescued from extinction by immigration enhancing local population sizes, Brown & Kodric-Brown, 1977; Hanski, 1994b), predicted patch incidence J_i is given by:

$$J_i = \frac{C_i}{C_i + E_i - E_i C_i} = \left[1 + \frac{e'}{S_i^2 A_i^x}\right]^{-1} \tag{2}$$

where $e' = ey^2$ (for methods on how to separate the values e and y from the composite parameter e', see Chapter 5).

The model parameters x, y, e, b, and α can be estimated from the snapshot of field data by fitting equation 2 to the observed occupancy patterns. The best fit between the observed incidence data (p_i) and the model's predicted incidence (J_i) can be found by minimizing the likelihood estimator:

$$-\sum p_i \ln J_i + (1 - p_i)\ln(1 - J_i) \tag{3}$$

If matrix quality is introduced into the incidence function model's connectivity measure detailed in Equation (1), one might hypothesise that poor-quality matrix might mimic the 'inhospitable' matrix of the original metapopulation assumption, corroborating an unmodified isolation distance. In contrast, good quality matrix could facilitate dispersal (via low dispersal costs through structurally similar, habitat-like matrix), resulting in an effective shortening of patch isolation distances. To insert a modifier of the isolation distance component (d_{ij}) of the connectivity variable to incorporate such matrix effects gives a modified connectivity index S_i^{MQ}:

$$S_i^{MQ} = \sum_{j \neq i} p_i \exp\left(-\alpha d_{ij} \left[1 - \frac{m_{ij}}{m_{\max}}\right]^w \right) A_j^b \tag{4}$$

where m_{ij} is the average matrix quality between habitat patches i and j, and m_{max} is the maximum matrix quality (i.e. 3). In effect, this equation transforms matrix quality into a measure of matrix permeability (Wiens, 1997), in which higher matrix quality scores will decrease the isolation distances between habitat patches. An additional parameter w scales matrix permeability to the matrix quality score, where a high value of w indicates high matrix permeability.

Using the likelihood estimator fitting procedure detailed in Equation (3), the best fit between the observed incidence data (p_i) and predicted incidence (J_i) was found for the modified incidence function model accounting for variability in matrix quality (S_i^{MQ}), i.e. Equation (4).

A range of dispersal parameter values, namely α = 0.05, 0.1 and 0.5 (Chapter 5), and matrix permeability scales, namely w = 0.1, 0.5, 1, 2, 3, 4, and 5, were explored during model fitting. The results of model fitting for Equation (4) were compared with those obtained for Equation 1 (see Chapter 5). Direct comparisons were possible, despite the additional parameter w in the modified incidence function model, as the likelihood fitting procedure used in this analysis (Equation 4) uses the connectivity values S_i and S_i^{MQ}, and not parameters α, b, and w, directly. All the equation symbols used in this chapter are summarised in *Appendix VI*.

6.3.5 Model simulations

To test whether this modification of the incidence function model had any impact on model predictions, two models were compared: (1) the original incidence function model (for future simplicity, referred to as IF) and (2) the modified (matrix) incidence function model (referred to as MIF), both of which simulated future *C. a. palliatus* metapopulation dynamics. One thousand simulation replicated were used, over 500 generations (see Chapter 5). In addition, the MIF model was used to simulate the effects of future forest loss by removing habitat patches by protection status: loss of one National Reserve, 14 Forest Reserves & Sanctuaries, 30 Kaya's (sacred forests protected by the local community) and 79 unprotected forests. These future habitat loss scenarios had previously been modelled using the IF model approach (see also Chapter 5 for more detailed methods), therefore a comparison of the two model outputs was feasible.

To explore the influence of matrix quality on future *C. a. palliatus* metapopulation dynamics, two MIF model simulations looked at the effects of either degrading or increasing the quality of the matrix in the Kwale District. In these simulations, the existing matrix quality measures (m_{ij}) were systematically increased or decreased by 0.2, 0.4, 0.6, 0.8 and 1.0, respectively. The upper and lower limits of matrix quality (i.e. 3 and 0), were maintained throughout each of the two modification procedures. Again, one thousand replicate simulations over 500 generations were used. Results were summarised as the total number of occupied patches in the network i.e. metapopulation size (M_{pop}), following matrix quality change. The new level of metapopulation size was recorded when the metapopulation re-established a quasi-equilibrium state (i.e. between 1 and 500 generations). In addition, the number of generations the *C. a. palliatus* metapopulation required to reach this new equilibrium was also noted. During all simulations, habitat patch area was assumed to be constant. Finally, the model's sensitivity to the matrix scaling parameter in Equation (4) was also tested using a variety of values of w = 1, 2, 3, and 4.

6.4 Results

6.4.1 Matrix quality and incidence function model fit

The average matrix quality between habitat patches ranged from land cover types that provided no structural benefit to arboreal primate locomotion (i.e. minimum matrix quality = 0.04), to land cover which closely matched the closed, tall canopy of habitat fragments (i.e. maximum matrix quality = 2.81) (Fig. 6.2). However, most paths had low average matrix quality, and overall average inter-patch matrix quality was 0.92.

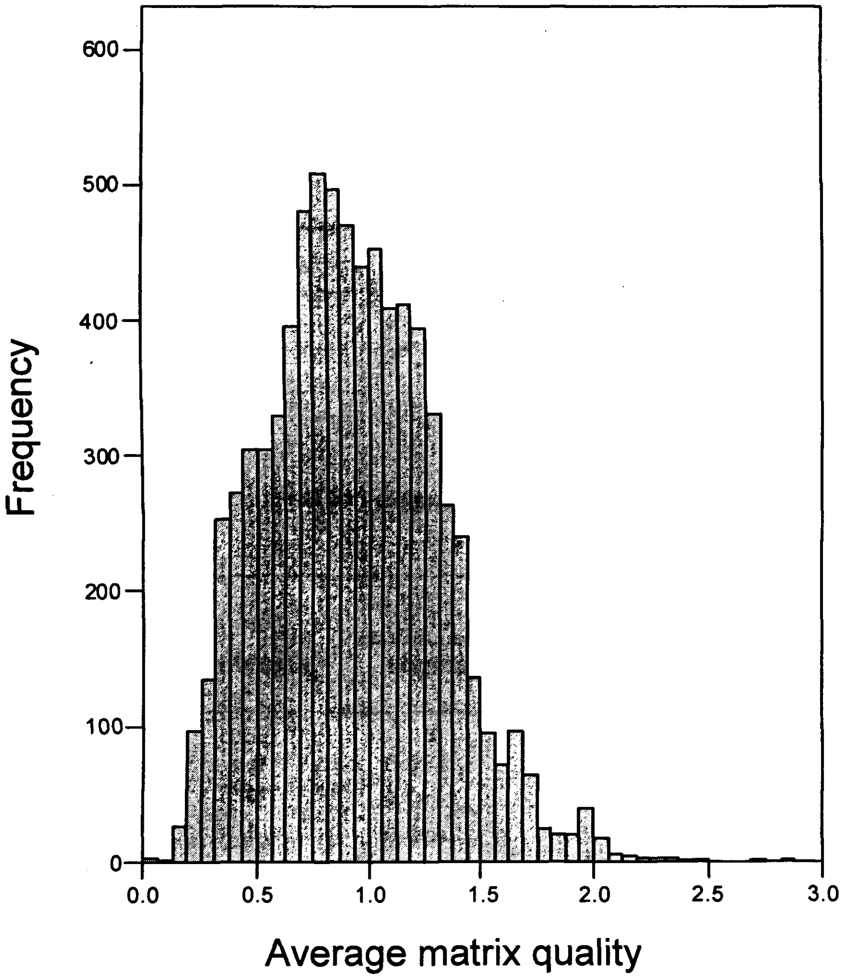


Fig. 6.2. Variation in average matrix quality (m_{ij}) between habitat patches in the Kwale District, Kenya.

The goodness of fit of the MIF model, i.e. accounting for variance in inter-patch matrix quality, is detailed for different values of α and w in Table 6.2. The model with α at 0.1 consistently provided a better fit than models with α at 0.5 or 0.05. When compared with the original IF model however, the greatest improvement in model fit was only a 2.53 reduction (4.3%) in the likelihood estimator, with α at 0.1 and w at 4. The model parameters used in subsequent metapopulation simulations are detailed in Table 6.3.

Table 6.2. Likelihood estimator values (Log(L)) for model fit when the incidence function model was modified for inter-patch matrix quality. Results of models with varying values of the dispersal parameter α and the matrix scaling parameter w. Original incidence function model Log (L) = 59.25; Null model Log (L) = 83.55. The best fit is highlighted in bold.

	w						
α	0.1	0.5	1	2	3	4	5
0.05	60.24	59.79	59.30	58.63	58.36	58.40	58.62
0.1	59.12	58.68	58.25	57.50	56.94	**56.72**	56.82
0.5	82.89	79.82	79.32	70.57	60.30	62.17	58.79

Table 6.3. Comparison of original and expanded (matrix) incidence function model parameters

	Values	
Parameter	**original IF**	**IF with matrix**
b	0.463	0.463
α	0.1	0.1
A_o	0.014	0.014
x	0.959	0.884
e	0.017	0.024
y	24.139	91.227
w	-	4

6.4.2 Model expansion and its effects on metapopulation predictions

Under present day conditions, the IF model and the MIF model produced analogous outputs of the metapopulation dynamics of *C. a. palliatus*, over 500 generations, when there was no change to the fragmented forest network (Fig 6.3). Likewise, in future scenarios involving forest patch removal by protection status, the predicted metapopulation dynamics of *C. a. palliatus* from both models were qualitatively similar. In this case, the MIF model varied to within 4-17% of the predicted occupancy levels generated from the IF model. These results suggest that variation in matrix-related connectivity between habitat patches may be sufficient to exert a distinct but relatively minor effect on metapopulation dynamics under different patch removal scenarios.

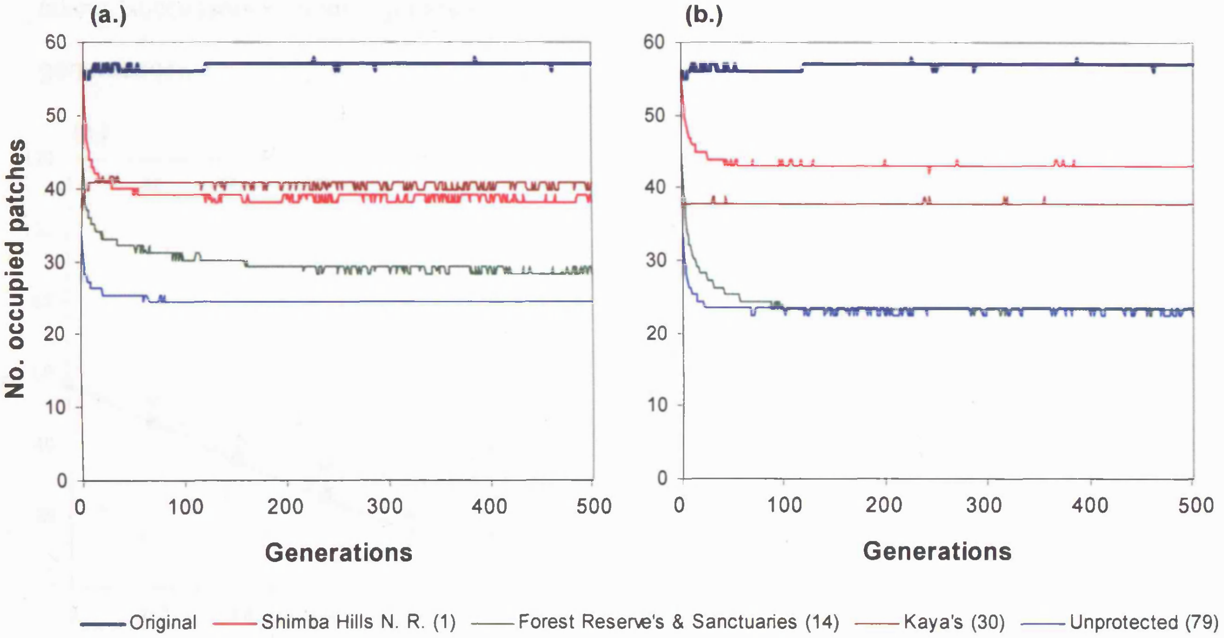


Fig. 6.3. Comparison of (a.) original and (b.) matrix incidence function model simulations. This figure illustrates the qualitative differences in the projected metapopulation dynamics of *C. a. palliatus*, comparing original dynamics with the loss of forest by management category over 500 generations: the Shimba Hills National Reserve, 14 Forest Reserves & Sanctuaries, 30 Kayas and 79 unprotected forests.

The *C. a. palliatus* metapopulation was found to be highly responsive to future changes in the quality of the Kwale District matrix (Fig. 6.4). Systematic degradation of the matrix resulted in a near-linear decline in patch occupancy, however the magnitude of this decline was strongly dependent upon the value of the parameter *w* (e.g. a 0.2 decline in average matrix quality decreased the expected number of patches occupied at equilibrium by between 7 and 19%). Conversely, even small improvements in matrix were sufficient to raise occupancy levels of the metapopulation (e.g. a 0.2 increase in matrix quality was enough to raise the equilibrium number of patches by about 10%, regardless of the value of *w*). The response times to all levels of improvement (0.2 – 1.0) were also relatively rapid, with increases in metapopulation size taking place within 9 to 13 generations. Not surprisingly, matrix degradation was more disruptive to connectivity with the metapopulation taking successively longer generations to re-establish equilibrium (i.e. from 46 to 331 generations).

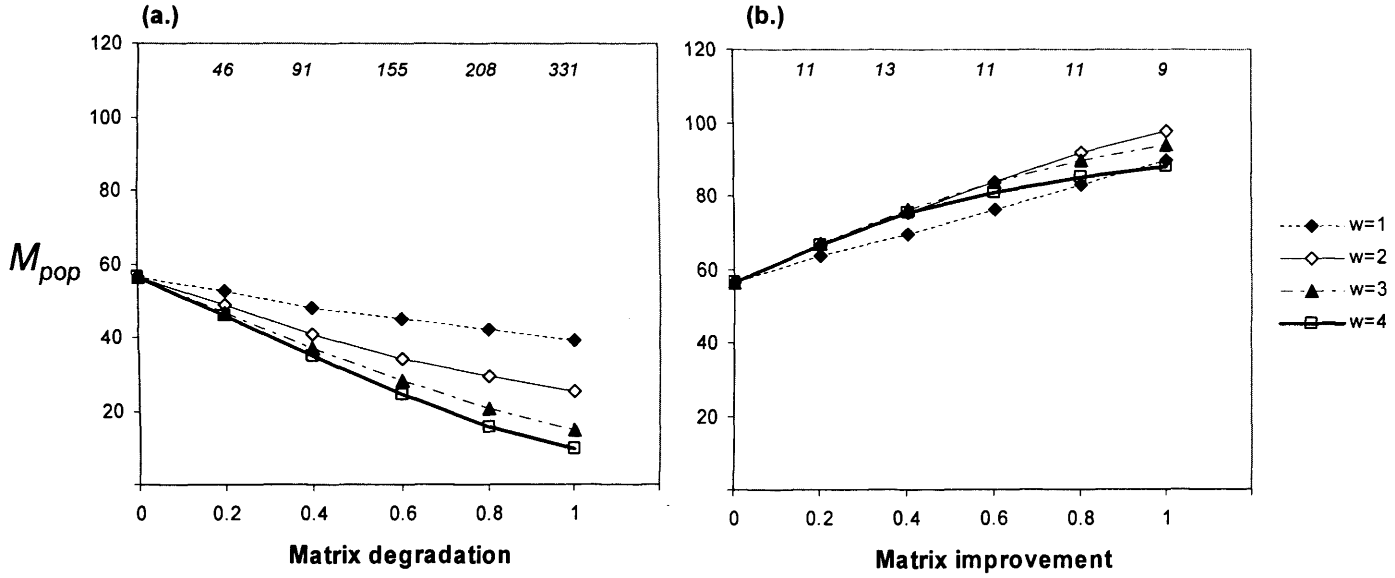


Fig 6.4. Effects of future (a.) degradation and (b.) improvement of the Kwale District matrix, on future *C. a. palliatus* metapopulation dynamics. Each figure illustrates the total metapopulation size M_{pop} at equilibrium. Italicized numbers are the average number of generations (for all four parameter *w* estimates = 1, 2, 3, 4) taken to re-establish the equilibrium state.

6.5 Discussion

6.5.1 Metapopulation model predictive power and the influence of the matrix

Given the relative importance of differing matrix land cover types for *C. a. palliatus* movement in the Kwale District (Chapter 4), it was unexpected that inclusion of GIS data into the incidence function model failed to improve model fit to any substantial degree. These results are in accordance with Moilanen & Hanski's findings (1998) who used a slightly more complex, parameter-rich method of matrix 'weighted' isolation distance in the simulation of Glanville fritillary butterfly metapopulation dynamics. However, these findings do not necessarily indicate that the matrix is unimportant, but rather that it may be difficult to characterise matrix quality in a simple yet realistic way. It is extremely difficult to find a simple but realistic patch connectivity measure in metapopulation theory given the sheer complexity of real landscapes found in nature (Gutzwiller, 2002; Ricketts, 2001; Tischendorf & Fahrig, 2001; Wiens *et al.*, 1993a).

In the case of *C. a. palliatus* the spatial configuration of matrix types in the Kwale District may be of key importance to the metapopulation network. A value of matrix quality averaged over shortest (Euclidean) isolation distances may therefore present too crude a measure of matrix heterogeneity, as this measure fails to take account of the spatial arrangement of important matrix land cover types relative to habitat patches in the network (Andren, 1994; Fahrig & Merriam, 1994; Wiens *et al.*, 1993a). For example, in Figure 6.1(A) the true connectivity of two patches in the Kwale forest network could be strongly influenced by the s-shaped corridor of perennial plantation and indigenous trees found in the matrix (offering a high-quality dispersal corridor), rather than the matrix composition of the straight-line shortest distance between the two respective patches. Animals tend to exhibit habitat preferences and thus seldom move randomly (Dunning *et al.*, 1995; Hastings, 1996; Verbeylen *et al.*, 2003). Therefore a more species-specific 'functional' approach to connectivity may be required which incorporates the movement behaviour of dispersing individuals (Tischendorf & Fahrig, 2000).

'Least-cost' modelling, for example, may be an appropriate avenue of further exploration (Adriaensen *et al.*, 2003; Chardon, Adriaensen & Matthysen, 2003; Ferreras, 2001; Graham, 2001; Gustafson & Gardner, 1996; Schippers *et al.*, 1996; Verbeylen *et al.*, 2003). In this approach, it is assumed that focal species will avoid matrix habitats that are energetically costly, risky or a barrier to movement, preferring to move within beneficial, less-costly matrix or corridors (Hansson, 1991; Johnson *et al.*, 1992). By allocating resistance values to differing matrix cover types within a GIS environment the least-cost paths between habitat patches could be calculated, based on movement routes through the most beneficial matrix types. Results of such models may give a more realistic measure of isolation distance between habitat patches, often referred to as 'effective' isolation distance (Adriaensen *et al.*, 2003; Ferreras, 2001; Verbeylen *et al.*, 2003), whilst allowing wildlife managers to visualise existing dispersal corridors or barriers within the matrix (Gustafson & Gardner, 1996)

6.5.2 Future changes in the matrix and C. a. palliatus metapopulation persistence

Further to Moilanen & Hanski's (1998) exploration of the influence of matrix quality, this study also used the MIF model to simulate the impacts of future habitat and landscape change on *C. a. palliatus* metapopulation dynamics. The MIF model produced qualitatively similar results to the IF model when either the original (stable) patch network or future patch loss scenarios were simulated. However, the MIF approach also facilitated an exploration of the effects of future changes in the quality of the Kwale matrix. These effects were found to be substantial. Only small levels of matrix degradation were required to delay the recovery of the *C. a. palliatus* metapopulation in response to this change (i.e. to delay the time required to reach equilibrium) and to lower the total number of occupied patches in the network at equilibrium. Such matrix degradation could be comparable to anthropogenic matrix conversion from woodland and shrubland to pastoral grasslands or annual cropland, for example. In contrast, colobus metapopulation occupancy patterns responded positively, and relatively rapidly, to small increments of structural improvement of the Kwale District matrix. These changes were equivalent to matrix enrichment schemes such as the creation the planting of trees in the existing matrix or the transformation of cropland to perennial plantation. Both these responses indicate a need for integrated landscape-habitat management in this fragmented network (Saunders *et al.*, 1991; Wiens, 1997).

The higher levels of matrix improvement simulated in Figure 6.4 would certainly be unrealistic on a practical conservation management level. By increasing the entire connectivity of the network towards a matrix structure that is similar to that of habitat patches you would effectively make the entire fragmented landscape a single element (in which case metapopulation theory is no longer applicable) (Hanski & Gilpin, 1997; Wiens, 1997). Additional arguments against the excessive improvement of connectivity (and possible increase in dispersal rates between populations) include the spread of disease between subpopulations (Hess, 1996), the proliferation of competitive or predatory species in the matrix (Rich, Dobkin & Niles, 1994; Simberloff & Cox, 1987), and the increased synchronicity between populations. The latter effect is important as it may increase the chance of simultaneous extinctions in the metapopulation network as a whole (Heino & Hanksi, 2001).

More appropriately, the MIF model provides the conceptual flexibility to explore both (1) the optimal combination of habitat patches required for future metapopulation persistence (see Chapter 5), and (2) the optimal matrix land cover preservation (or enrichment) between pairs or groups of habitat patches which may enhance such persistence. In addition, MIF model simulations could be used to predict the impacts of future changes in the landscape (incorporating matrix change), and/or predict the effectiveness of landscape-level management initiatives between particular habitat patches.

It is presently difficult to answer the practical question of whether, given a limited conservation budget, improving habitat or building corridors (or perhaps a combination of the two) is the best option for metapopulation management (Etienne & Heesterbeek, 2001). The MIF model may provide a starting point from which to explore such issues. Also, in light of current concerns regarding the conservation 'cost-effectiveness' of (man-made) linear corridors in the landscape (Beier & Noss, 1998; Bennett, 1998; Crome, 1997; Simberloff & Cox, 1987) it may be more feasible, as this study has shown, to maintain or increase connectivity in a fragmented landscape by preserving, enriching or altering the management practices (e.g. present agricultural production regimes) of the surrounding matrix than to reconnect them with expensive purpose-built corridors (Baum *et al.*, 2004; Ricketts, 2001).

Whilst the simple measure of matrix quality used here was clearly unlikely to have captured the true complexity of a heterogeneous landscape, it has nonetheless permitted an exploration of the possible impact of future change in the landscape surrounding habitat fragments. These results thus provide a starting point from which to develop more comprehensive measures of metapopulation connectivity, for example by exploring the explanatory power of effective (least cost) migration paths rather than shortest isolation distances. Such an understanding would increase our ability to spatially prioritise landscape preservation and enrichment, both in and around existing habitat patches.

7. Discussion

In a paper concerning the population dynamics and conservation of primates, Dobson & Lyles (1989) stated that, "Unfortunately, most primate field studies last for about as long as it takes to satisfy doctoral research requirements". The authors were trying to highlight the inadequacies of short-term data collection and its limitations for practical primate conservation. However, the results of this study illustrate that within a relatively short period of time and with limited funding, a significant amount of practical information can be gathered concerning the national status of a tropical forest-dependent primate species, and its habitat requirements, ecological flexibility and response to anthropogenic disturbance, both within and beyond the boundaries of forest fragments. This study has also illustrated that short-term species presence/absence data can be combined with remotely sensed data, a geographical information system (GIS) and a conceptual metapopulation model, to provide a simple yet powerful tool to understand the spatial geometry and heterogeneity of the regional landscape and its direct relevance to species metapopulation dynamics and conservation.

7.1 The regional-landscape scale

Effective conservation programs promoting species preservation in fragmented tropical forest networks must determine the priority areas for habitat management, often at the regional, national or biogeographical scale (Bibby, 1998; Cowlishaw & Dunbar, 2000a; Sutherland, 1998). In order to identify such conservation priorities, it is critical to establish the a species' status and distribution and the factors that regulate its occurrence and/or density within these areas (Chapman, Struhsaker & Lambert, 2005). In the case of the Angola black-and-white colobus (*Colobus angolensis palliatus*) in East Africa, this study dealt with the national (Kenyan) extent of the subspecies' geographical range. A 'national' survey level was appropriate since forest habitat and wildlife management/protection would ultimately be administered at the same scale, via governmental Forest Departments, local NGOs and the Kenya Wildlife Service.

The national primate survey presented in this study established a Kenyan *C. a. palliatus* population estimate of between 3,100 and 4,900 individuals (570 – 900 groups). Fifty-five subpopulations were distributed within 124 coastal forest fragments (total forested area = 255km^2). All surveyed forest patches occurred entirely within the south coast Kwale District of Kenya. The largest forest patches in the network provided habitat for the largest colobus populations in the District, including: (1) the Shimba Hills National Reserve (>150km^2 area, 2,436 ± 458 S. E. colobus individuals), (2) six of the Forest Reserves, (3) Kaya Muhaka and (4) the Diani and Shimoni unprotected forests, highlighting the importance of these sites for species protection. The survey was also valuable in highlighting that 12% of the District's coastal forest cover (i.e. 3,000ha, 79 forest patches) still remains unprotected and (including the Diani and Shimoni colobus populations) provides habitat for over 17% of the national *C. a. palliatus* population.

Furthermore, by focusing on forest fragment comparisons it was possible to disentangle some of the underlying ecological processes that influence species persistence in such fragmented landscapes. At the *within-fragment* scale, forest area was found to be the most influential of all habitat variables, influencing both population density and occupancy patterns of *C. a. palliatus*. The quality of individual habitat patches was also found to be important. Colobus occurrence was positively associated with canopy cover, whilst colobus density in the occupied forest patches was attributable to the proportion of forest loss over the preceding 12 years and the basal area of 14 major food tree species. It seems that *C. a. palliatus* can exhibit a high degree of dietary flexibility, as it exploits more than 100 indigenous tree species. This may allow populations to occupy forest patches when resource quality is relatively low. However once a patch is occupied, key local food resources must play an important role in supporting high colobus population densities. Folivorous primate biomass has been positively associated with high-quality (high protein-to-fibre ratio) food plants (Chapman *et al.*, 2002; Oates *et al.*, 1990; Wasserman & Chapman, 2003), and further study might usefully explore the nutrient quality of *C. a. palliatus* food plants, particularly for the major food tree species.

At the *between-fragment* scale, the spatial distribution of the 124 habitat patches and the heterogeneity of the surrounding landscape were found to play a significant role in *C. a. palliatus* occurrence, dispersal and metapopulation dynamics. Isolation distances from neighbouring colobus populations were significant indicators of population occurrence in the forest network. The use of a spatially explicit metapopulation model, the incidence function model, confirmed the importance of habitat patch area, patch isolation and the spatial distribution of occupied patches.

By expanding the focus of ecological thinking towards the spatial, landscape-level of *C. a. palliatus* population processes, the 'matrix' became an important (yet previously overlooked) avenue for research. Information concerning species dispersal movements can be difficult and time-consuming to collect (Bennett, 1998; Bowne & Bowers, 2004). However, this study illustrates that valuable qualitative and quantitative data can be gathered within a short time period, drawing on local community knowledge. *C. a. palliatus* dependency upon closed-canopy forest habitat also corresponded well with the reports of colobus movement through matrix land cover types which were structurally similar to that of forest habitat. For *C. a. palliatus* in the Kwale District of Kenya, matrix land cover types such as mangrove, timber plantations and perennial plantations are likely to have the potential to facilitate colobus movement between habitat patches. *C. a. palliatus* showed great flexibility in utilising these, and other more open matrix types (e.g. wooded shrubland, wooded grassland and shrubland), traveling over 4km from the nearest boundaries of forest habitat. It was also evident that colobus groups and individuals exploited certain matrix types for their availability of food resources. Tree species found within indigenous mangrove, wooded shrubland and wooded grassland areas were targeted, as well as indigenous coastal trees persisting within perennial plantations. The dense canopy of coconut palms, cashew nut and mango trees present in the latter matrix type facilitated colobine locomotion and access to such food resources.

The overall importance of mangrove as a facilitator of inter-patch dispersal, and as a potentially important foraging habitat, for *C. a. palliatus* has important implications for colobus conservation. Studies of two other colobines, the Zanzibar red colobus (*Procolobus kirkii*) (Siex, 2003), and Temminck's red colobus (*Procolobus badius temminckii*) (Galat-Luong & Galat, 2005), have also documented colobine use of mangrove areas as additional foraging sites and refuges from human disturbance. These results suggest that conservationists should consider the benefits of classifying mangrove as 'suitable' habitat for colobines, particularly when prioritising important areas for future preservation. For *C. a.*

palliatus this would also challenge the metapopulation assumptions incorporated within this study, as the present spatial distribution of habitat patches incorporates closed-canopy coastal forest only. If mangrove were to be included within the habitat management strategy for this subspecies, both the areas and connectivity measures used in the metapopulation model would need to be adjusted, and the resultant metapopulation dynamics of the species re-explored.

It is extremely difficult to identify the precise mechanisms underlying the variety of responses of primates to fragmented landscapes (Chapman *et al.*, 2005; Marsh, 2003b). However, the regional-landscape approach used in this study will certainly provide wildlife managers in Kenya with a more comprehensive, holistic understanding of *C. a. palliatus* habitat requirements and response to forest fragmentation than would have been obtained from an individual, patch-specific study on a much smaller scale.

7.2 The future of forest fragments

Human population growth and development within tropical forest biomes leads to the appropriation of extensive areas of land for settlement, agriculture, and resource extraction; in addition, the infrastructure to support these ongoing activities can cause further loss, fragmentation and degradation (Balmford *et al.*, 1998a; Mace & Baillie, 2001). To assess the ecological impacts of current human disturbance within the regional scale of this study, it was useful to understand: (1) the effectiveness of current forest protection (Struhsaker *et al.*, 2005), (2) the current and future threats to colobus persistence, including community utilisation of forest fragments and the surrounding landscape (Balmford, Mace & Ginsberg, 1998b; Chapman *et al.*, 2003), and (3) the possible consequences of alternative scenarios of future landscape change, using predictive models to explore the future persistence of *C. a. palliatus* (Dunning *et al.*, 1995; Turner *et al.*, 1995).

7.2.1 Current forest protection

The coastal forest fragments of Kwale District were either protected as National Reserves (1: the Shimba Hills National Reserve), Forest Reserves (14) or sacred Kayas (30). Seventy-nine forests in the District remained unprotected and were under heavy exploitation. The Forest Reserves protected some of the largest remaining forest habitats (and colobus populations) in the District, however they were also found to be under similar levels of anthropogenic threat to the unprotected forests. In contrast, the sacred Kayas (which were jointly protected by the local Mijikenda communities and the National Museums of Kenya) exhibited relatively lower levels of exploitation. Forest loss, logging, hunting and charcoal-producing activities in these forests were all at significantly lower levels than the unprotected forests. The failing infrastructure/capacity for wildlife protection and poor law enforcement within the Forest Reserves, compared with the local community involvement in the protection of the sacred Kayas, may explain the contrasting levels of effectiveness of these two protection strategies.

7.2.2. Community utilisation of forest fragments and future threats

A major degree of resource overlap was found within coastal forest fragments between human extraction practices in the Kwale District and *C. a. palliatus* food resource requirements. Over 45% of local tree extraction targeted just 10 species of indigenous tree. Nine of these species were food trees of the colobus, whilst four were major food trees. Local needs for these forest resources included fuel wood, charcoal-production, wood-carving for the tourism industry, building poles, and in particular, hardwood trees (such as *Millettia usamensis, Combretum schumannii* and *Lecaniodiscus fraxinifolius*) for construction. Left unaddressed, the permanent removal of such major food resources will reduce colobus densities in remnant forests, as well as further degrade forest canopies and ultimately reduce forest area. The latter two effects are known within this study to significantly predict the occurrence of colobus populations within forest fragments.

Historical research into the past distribution of *C. a. palliatus* in the north coast forests of Kenya also highlighted a possible future threat to the colobus, namely cultural differences within subdivisions of the indigenous coastal tribe (Mijikenda), which may have led to extinction of remnant populations of colobus in north coast forests through hunting for bushmeat (a major threat more commonly cited for colobine declines in west and central Africa, Davies, 1987; Lahm, 1993; Martin & Asibey, 1979; Oates, 1996b; Waltert *et al.*, 2002). As coastal development increases in the Kwale District, influxes of north coast or other Kenyan ethnic groups (Hoorweg, 2000) may bring such hunters into an area where hunting is currently rare, thus introducing a new and serious threat to the survival of the remaining south coast colobus populations.

As the area and quality of the Kwale District coastal forests decline (particularly in small <10ha fragments) through continued anthropogenic disturbance, *C. a. palliatus* populations inhabiting such fragments may also have to increase their dependency on food resources from the surrounding matrix (Cowlishaw & Dunbar, 2000b). In agricultural areas such as Vanga (the southernmost region of the Kwale District), colobus crop-raiding and the resultant human wildlife conflict (Naughton-Treves, 1998) may become an additional problem that requires attention in future *C. a palliatus* conservation initiatives.

7.2.3 Exploring future persistence

Spatially explicit metapopulation models, such as Hanski's incidence function model (Hanski, 1994b), can provide an additional conceptual framework in which to assess future scenarios of habitat loss or alternative habitat management strategies (Turner *et al.*, 1995; Wahlberg *et al.*, 1996). Using limited data and simple assumptions, the incidence function model approach used in this study confirmed the importance of large forests for *C. a. palliatus* metapopulation persistence. The metapopulation was not entirely dependent upon the largest patch in the forest network (the Shimba Hills Forest Reserve), although the removal of this forest in combination with 4% of the other large forests in the District significantly decreased the long-term occupancy, stability and persistence of the entire metapopulation. Simulations of future forest loss scenarios also highlighted that many of the colobus populations inhabiting unprotected forests may be particularly vulnerable: reductions in area of 10-50% of these forests had a greater impact on the metapopulation than similar percentage losses in all other forest management categories. The incidence function model could also rank individual habitat patches in the District by their contribution to *C. a. palliatus* metapopulation persistence. Similarly, this method could be used to rank the relative contribution of alternative habitat management (e.g. habitat protection scenarios, increasing forest areas) or species management (e.g. translocation) strategies. In all cases, transparency regarding model assumptions and sensitivity to uncertainty is essential, and a degree of realism (for example the original incidence function model does not consider the effects of matrix heterogeneity, habitat quality or underlying subpopulation demography) is essential. Such an understanding will help to clarify the context of model predictions and assist in identifying future field research required to fill the gaps in our knowledge.

Future impacts of landscape change may also include changes in the matrix surrounding habitat fragments (Bennett, 1998; Wiens, 1997). Using a modified incidence function model which accounted for variance in matrix quality between habitat patches, this study simulated the future degradation of the Kwale District matrix. Only small levels of matrix degradation were required to lower *C. a. palliatus* metapopulation occupancy in the network. In contrast, colobus occupancy patterns responded positively, and relatively rapidly, to small levels of improvement of the matrix. By adopting a regional scale and metapopulation outlook to the assessment of *C. a. palliatus* persistence in southern Kenya, the need for integrated landscape-habitat management in this fragmented network has been usefully highlighted (Saunders *et al.*, 1991; Wiens, 1997).

7.3 The practicalities of conservation

How useful are the approaches used in this study for the practical conservation of the Angola black-and-white colobus and its coastal forest habitat in Kenya?

The national primate survey undertaken here provides a baseline of *C. a. palliatus* status and distribution data to assist wildlife managers with the prioritisation of conservation efforts, namely the protection of both key *C. a. palliatus* populations and presently undervalued or unprotected forest fragments in the Kwale forest network (e.g. the Shimoni and Diani forests). Focusing on a forest-dependent species also necessitated the development of an objective means of determining the location, size and spacing of coastal forest coverage in the District. This was facilitated by the usage of GPS mapping and a simple geographical information system (GIS). It is hoped that both the GIS of 2001 coastal forest cover and the spatially-explicit *C. a. palliatus* subpopulation database (the latter including detailed information on subpopulation occurrence, density and size, as well as the average group size and group demography per patch, geo-referenced in ArcView 3.2 GIS) will form the basis of future coastal forest, *C. a. palliatus* and biodiversity monitoring in the

District. Arrangements have already been made for this database to be managed by a local conservation organisation based in Diani Beach, Kwale District: Wakuluzu, Friends of the Colobus Trust. In collaboration with the Kenya Wildlife Service, Kenya Forest Department and Coastal Forest Conservation Unit (National Museums of Kenya), the Colobus Trust will continue to monitor future *C. a. palliatus* populations and forest change in the District. More specifically, the database will also form a baseline from which the Colobus Trust can monitor the effectiveness of its ongoing primate conservation, forest conservation and local education programs (Cunneyworth & Rhys-Hurn, 2004).

A comparison of *C. a. palliatus* occurrence and abundance patterns within 46 forest fragments identified the key external factors (spatial, structural, resource and disturbance) that were most likely to be critical to the continued survival of the subspecies. Most important was the quality of coastal forest habitat, especially large, closed-canopy forest, preferably with good coverage of key food resources such as indigenous coastal hardwood species. Wildlife managers need this information in order to effectively prioritise habitat preservation or enrichment initiatives to curb future declines in colobus density. Understanding the degree of overlap between colobus food resources and human utilisation also helps to target conservation efforts towards current and future threats, for example hardwood logging, which may necessitate a response involving increased collaborative efforts or capacity building with rangers in the Forest Reserves, and the woodcarving industry, which may involve education campaigns targeting 'good wood' use by tourists, and research into alternative timber species for this purpose.

The landscape-based approach combining semi-structured interviews, remote-sensing and GIS techniques provided key information about the influences of the surrounding matrix and its importance for *C. a. palliatus* conservation. Local interviews proved a highly valuable resource for information regarding colobus use of the matrix. Results of this study will provide wildlife managers with additional non-forest habitats to monitor, protect and enrich. Land cover (GIS) maps will help to visualise and monitor temporal changes in the spatial configuration of important matrix types, natural corridors (Hess & Fischer, 2001) and stepping stones (Baum *et al.*, 2004) in the Kwale District landscape.

An incidence function model approach, simulating the future metapopulation dynamics of C. *a. palliatus* was a useful heuristic tool which could: (1) rank the relative contribution of habitat patches to metapopulation persistence; (2) explore the impacts of future scenarios of habitat and/or matrix change, and (3) explore the best options for metapopulation management, e.g. optimising habitat preservation or corridor placement (Etienne & Heesterbeek, 2001; Hanski & Thomas, 1994; Turner *et al.*, 1995). In addition to these specific benefits, the application of metapopulation theory also emphasies more generally the importance of research on a region-landscape level, whilst also bringing attention to species' dispersal capabilities and extinction risks in the region (Doak & Mills, 1994).

This study focused on a 'single-species' approach to the population ecology and future conservation management of *C. a. palliatus*. Whilst the topic of whether to conserve biodiversity at the species level is hotly debated (Bowen-Jones & Entwistle, 2002; Caro, 2003; Caro *et al.*, 2004; Franklin, 1993, 1994; Lindenmayer, 1999; Olden, 2003; Towns & Williams, 1993; Walpole & Leader-Williams, 2002) the results of this study should indicate that the concept is potentially important in southern Kenya, given the impossibility of managing the wide array of taxa that inhabit the coastal forests of this region. *C. a. palliatus* is a textbook example of a 'charismatic vertebrate' (Heywood, 1995; Leader-Williams & Dublin, 2000) that can serve as a 'flagship species' for coastal forest conservation (Bowen-Jones & Entwistle, 2002; Towns & Williams, 1993; Walpole & Leader-Williams, 2002). The fact that this taxon can also be integrally linked to the quality and spatial characteristics of coastal forest fragments, and the surrounding (human-dominated) landscape and its associated pressures, adds further to its relevance as an 'indicator species' for detrimental changes in the fragmented forest network (Heywood, 1995; Meffe & Carroll, 1997). Conservation efforts in the northern coastal forests of Kenya have previously highlighted the importance of the Tana River forests (associated with the Tana River red colobus *Procolobus badius rufomitratus*: Mbora & Meikle, 2004) and the Arabuko Sokoke Forest (associated with the Sokoke scops owl *Otus ireneae*, and the Golden-rumped Elephant Shrew *Rhynchocyon chrysopygus*: Muriithi & Kenyon, 2002) however the southern coastal forests are presently lacking an attractive focal species to encourage habitat protection. *C. a. palliatus* has the potential to focus both national and international interest (and ultimately financial support) towards further conservation efforts, which would benefit both the focal species and wider biodiversity across the region (Meffe & Carroll, 1997).

Whilst flagship species are usually identified to appeal especially to western donors (Entwhistle, Mickleburgh & Dunstone, 2000), in the case of the colobus in Kwale District there is also great potential to focus local interest in habitat conservation. The sacred Kaya forests are a key example where the local community actively preserve forest fragments and Kaya elders remember taboos, songs and stories about the '*mbega*' (*C. a. palliatus*) in their forests (pers. obs.). Moreover, *C. a. palliatus* is not regarded as a pest species by the local community, in contrast to other crop-raiding diurnal primates in the District. Therefore local conservation efforts could also focus on preserving the cultural significance of the species (Bowen-Jones & Entwistle, 2002), with the aim of generating local pride in the preservation of the colobus and its habitat (particularly in Kaya and unprotected forests). The Kayas and unprotected forests surrounding many of the tourist areas in Kwale District have the additional potential for successful habitat protection based on the economic value in terms of tourism of the colobus and the rich biodiversity of the coastal forests (Hackel, 1999; Navrud & Mungatana, 1994).

In conclusion, this study will provide a sound ecological baseline of information upon which to implement future *C. a. palliatus* and coastal forest conservation initiatives in the Kwale District of Kenya.

7.4 Recommendations

There now follows a brief summary of the possible areas for future colobus research and habitat conservation that have arisen from the results of this study:

- Establish the current status and distribution of *C. a. palliatus* in coastal forests and Eastern Arc Mountains of Tanzania. Update subspecies' current 'data deficient' status on the IUCN Red List of Threatened Species (IUCN, 2004)
- Promote *C. a. palliatus* as a 'flagship' and 'indicator' species for coastal forest and biodiversity conservation in southern Kenya
- Prioritise conservation effort towards large forest patches and large *C. a. palliatus* populations: the Shimba Hills National Reserve, Forest Reserves, Kaya Muhaka, and Shimoni and Diani forests (currently unprotected)
- Improve current forest protection efforts in the Forest Reserves and unprotected forests of the Kwale District (for detailed practical recommendations, see Marshall & Jenkins, 1994)
- Include coastal mangrove within existing habitat preservation and *C. a. palliatus* conservation strategies
- Promote alternative wood resources, especially in the hardwood and woodcarving industries and increase tourist awareness of ecological woodcarvings
- Increase community involvement in local forest conservation efforts
- Emphasise and encourage existing cultural values of *C. a. palliatus* and its habitat through community education
- Preserve existing indigenous wooded shrubland, shrubland, timber plantation and perennial plantations surrounding small coastal forest remnants
- Initiate long-term monitoring of *C. a. palliatus* populations and coastal forest status in the Kwale District
- Initiate research in the Vanga region of Kwale District to establish *C. a. palliatus* usage of forest, mangrove and agricultural mosaics (to include studies of colobus movement patterns, resource use, mortality risks and regional comparisons of crop-raiding)
- Compare the feeding ecology of *C. a. palliatus* populations within differing forest fragments and include research into the nutrient quality (in particular, protein-to-fibre content) of colobus food trees

- Promote research into alternative tree planting schemes in the matrix which could benefit both *C. a. palliatus* foraging and the local community, e.g. '*Neem*' (*Azadirachta indica*)

- Assess the impacts of enriching the matrix between habitat fragments (e.g. perennial or timber plantations), both for future connectivity of the *C. a. palliatus* metapopulation and the risk of increasing human-wildlife conflict (this should also consider the impacts of other crop-raiding wildlife species)

Aberg, J., Jansson, G., Swenson, J.E., & Angelstam, P. (1995) The effect of matrix on the occurence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. *Oecologia*, **103**, 265-269.

Adamson, J. (1967) *The Peoples of Kenya* Collins & Harvill Press, London, UK.

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.P., Richardson, J.S., & A., S.D. (1987) Ecological neighbourhoods: scaling environmental patterns. *Oikos*, **49**, 340-346.

Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003) The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning*, **64**, 233-247.

Akcakaya, H.R. (2000) Viability analyses with habitat-based metapopulation models. *Population Ecology*, **42**, 45-53.

Akcakaya, H.R. (2001) Linking population-level risk assessment with landscape and habitat models. *Science of the Total Environment*, **274**, 283-291.

Akcakaya, H.R., Atwood, J.L., Breininger, D., Collins, C.T., & Duncan, B. (2003) Metapopulation dynamics of the California Least Tern. *Journal of Wildlife Management*, **67**, 829-842.

Akcakaya, H.R., McCarthy, M.A., & Pearce, J.L. (1995) Linking landscape data with population viability analysis - management options for the Helmeted Honeyeater (*Lichenostomus Melanops Cassidix*). *Biological Conservation*, **73**, 169-176.

Akcakaya, H.R., Radeloff, V.C., Mlandenoff, D.J., & He, H.S. (2004) Integrating landscape and metapopulation modeling approaches: Viability of the sharp-tailed grouse in a dynamic landscape. *Conservation Biology*, **18**, 526-537.

Andren, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat - a review. *Oikos*, **71**, 355-366.

Antongiovanni, M. & Metzger, J.P. (2005a) Influence of matrix habitats on the occurence of insectivorous bird species in Amazonian forest fragments. *Biological Conservation*, **122**, 411-451.

Antongiovanni, M. & Metzger, J.P. (2005b) Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest framents. *Biological Conservation*, **122**, 441-451.

Arnold, G.W., Steven, D.E., Weeldenburg, J.R., & Smith, E.A. (1993) Influences of remnant size, spacing pattern and connectivity on population-boundaries and demography in Euros (*Macropus-Robustus*) living in a fragmented landscape. *Biological Conservation*, **64**, 219-230.

Aronsen, G.P. (2004a) The energetics of positional behaviour and support use in arboreal primates: conservation implications. *Folia Primatologica*, **75**, 233.

Aronsen, G.P. (2004b) *Positional behaviour and support use in three arboreal monkeys of Kibale Forest, Uganda: The influences of forest structure, microhabitats and energetics.* PhD. thesis, Yale University, New Haven, CT.

Arosen, G.P. (2004) The Energetics of Positional Behaviour and Support Use in Arboreal Primates: Conservation Implications. *Folia Primatologica*, **75**, 233.

Baguette, M. (2004) The classical metapopulation theory and the real, natural world: a critical appraisal. *Basic and Applied Ecology*, **5**, 213-224.

Baguette, M. & Mennechez, G. (2004) Resource and habitat patches, landscape ecology and metapopulation biology: a consensual viewpoint. *Oikos*, **106**, 399-403.

Baguette, M. & Schtickzelle, N. (2003) Local population dynamics are important to the conservation of metapopulations in highly fragmented landscapes. *Journal of Applied Ecology*, **40**, 404-412.

Balmford, A., Mace, G.M., & Ginsberg, J., eds. (1998a) *Conservation in a changing world.* Cambridge University Press, Cambridge.

Balmford, A., Mace, G.M., & Ginsberg, J.R. (1998b). The challengest to conservation in a changing world: putting processes on the map. In *Conservation in a changing world.* (eds G.M. Mace, A. Balmford & J.R. Ginsberg), pp. 1-29. Cambridge University Press, Cambridge.

Baum, K.A., Haynes, K.J., Dillemuth, F.P., & Cronin, J.T. (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology*, **85**, 2671-2676.

Beentje, H. (1994) *Kenya trees, shrubs and lianes*, Nairobi, Kenya.

Beier, P. & Noss, R.F. (1998) Do habitat corridors provide connectivity? *Conservation Biology*, **12**, 1241-1252.

Bélichon, S., Clobert, J., & Massot, M. (1996) Are there differences in fitness components between philopatric and dispersing individuals? *Acta Oecologica-International Journal of Ecology*, **17**, 503-517.

Bender, D.J., Contreras, T.A., & Fahrig, L. (1998) Habitat loss and population decline: A meta-analysis of the patch size effect. *Ecology*, **79**, 517-533.

Bennett, A.F. (1998). Movements of animals through linkages. In *Linkages in the landscape: The role of corridors and connectivity in wildlife conservation.* (ed A.F. Bennett), pp. 67-91. IUCN, Gland, Switzerland.

Bennett, E.L. & Robinson, J.G. (2000) *Hunting of wildlife in tropical forests: implications for biodiversity and forest peoples.* International Bank for Reconsruction/The World Bank, Washington, D. C.

Berggren, A., Carlson, A., & Kindvall, O. (2001) The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crickets (*Metrioptera roeseli*). *Journal of Animal Ecology*, **70**, 663-670.

Bernard, H.R. (2002) *Research methods in anthropology: Qualitative and quantitative approaches*, 3rd edn. Altemira Press, Walnut Creek, CA.

Beyer, H.L. (2004) Hawth's analysis tools for ArcGIS. http://www.spatialecology.com/htools.

Bibby, C.J. (1998). Selecting areas for conservation. In *Conservation science in action.* (ed W.J. Sutherland), pp. 176-201. Blackwell Science Ltd., Oxford.

Bicca-Marques, J.C. & Calegaro-Marques, C. (1994) Exotic plant species can serve as staple food resources for wild howler populations. *Folia Primatologica*, **63**, 209-211.

Bierregaard, R.O., Gascon, C., Lovejoy, T.E., & Mesquita, R.C.G., eds. (2001) *The ecology and conservation of a fragmented forest: lessons from Amazonia.* CT:Yale University Press, New Haven.

Bocian, C.M. (1997) *Niche Separation of Black-and-White Colobus Monkeys (Colobus angolensis and C. guereza) in the Ituri Forest.*, PhD program in Biology, Graduate Centre, City University of New York.

Bonte, D., Lens, L., Maelfait, J.P., Hoffmann, M., & Kuijken, E. (2003) Patch quality and connectivity influence spatial dynamics in a dune wolfspider. *Oecologia*, **135**, 227-233.

Bowen-Jones, E. & Entwistle, A. (2002) Identifying appropriate flagship species: the importance of culture and local contexts. *Oryx*, **36**, 189-195.

Bowne, D.R. & Bowers, M.A. (2004) Interpatch movements in spatially structured populations: a literature review. *Landscape Ecology*, **19**, 1-20.

Brooks, T.M., Mittermeier, R.S., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., & Hilton-Taylor, C. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, **16**, 909-923.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology*, **58**, 445-449.

Brugiere, D. & Fleury, M.C. (2000) Estimating primate densities using home range and line transect methods: A comparative test with the black colobus monkey *(Colobus satanas). Primates*, **41**, 373-382.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., & Thomas, L. (2001) *Introduction to Distance Sampling: Estimating abundance of biological populations.* Oxford University Press Inc., Oxford.

Bullock, J. (1996). Plants. In *Ecological Census Techniques. A handbook* (ed G.D. Sutherland), pp. 111-137. Cambridge University Press, Cambridge.

Burgess, N.D. (2000). Global importance and patterns in the distribution of coastal forest species. In *The coastal forests of Eastern Africa* (eds N.D. Burgess & G.P. Clarke), pp. 235-249. IUCN, Glans, Switzerland & Cambridge, U.K.

Burgess, N.D., Clarke, G.P., Madgwick, J., & Robertson, S.A. (2000). Distribution and status. In *Coastal Forest of Eastern Africa* (eds N.D. Burgess & G.P. Clarke). IUCN, Gland, Switzerland and Cambridge, UK.

Burgess, N.D., Clarke, G.P., & Rodgers, W.A. (1998) Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society*, **64**, 337-367.

Burgman, M.A., Ferson, S., & Akcakaya, H.R. (1993) *Risk assessment in conservation biology* Chapman and Hall, London.

Butynski, T. & Mwangi, G. (1994). Conservation status and distribution of the Tana River red colobus and crested mangabey. Zoo Atlanta / Kenya Wildlife Service / National Museums of Kenya / Institute of Primate Research / East African Wildlife Society, Nairobi.

Cabeza, M. & Moilanen, A. (2003) Site-selection algorithms and habitat loss. *Conservation Biology*, **17**, 1402-1413.

Caro, T.M. (2003) Umbrella species: critique and lessons from East Africa. *Animal Conservation*, **6**, 171-181.

Caro, T.M., Engilis, A., Fitzherbert, E., & Gardner, T. (2004) Preliminary assessment of the flagship species concept at a small scale. *Animal Conservation*, **7**, 63-70.

Carroll, C., Noss, R.E., Paquet, P.C., & Schumaker, N.H. (2003) Use of population viability analysis and reserve selection algorithms in regional conservation plans. *Ecological Applications*, **13**, 1773-1789.

Caughley, G. & Gunn, A. (1996). Risks faced by small populations. In *Conservation biology in theory and in practice.* (eds G. Caughley & A. Gunn), pp. 166-189. Blackwell Science Ltd., Oxford.

CEPF (2003). Critical Ecosystem Partnership Fund, Ecosystem Profile: Eastern Arc Mountains and Coastal Forests of Tanzania and Kenya. Conservation International and International Centre of Insect Physiology and Ecology.

Chapman, C.A., Balcomb, S.R., Gillespie, T.R., Skorupa, J.P., & Struhsaker, T.T. (2000) Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conservation Biology*, **14**, 207-217.

Chapman, C.A. & Chapman, L.J. (1999) Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates*, **40**, 215-231.

Chapman, C.A. & Chapman, L.J. (2002) Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. *Comparative Biochemistry and Physiology - Part A: Molecular and Integrative Physiology*, **133**, 861-875.

Chapman, C.A., Chapman, L.J., Bjorndal, K.A., & Onderdonk, D.A. (2002) Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. *International Journal of Primatology*, **23**, 283-310.

Chapman, C.A., Chapman, L.J., Naughton-Treves, L., Lawes, M.J., & McDowell, L.R. (2004) Predicting folivorous primate abundance: Validation of a nutritional model. *American Journal of Primatology*, **62**, 55-69.

Chapman, C.A. & Lambert, J.E. (2000) Habitat alteration and the conservation of African primates: Case study of Kibale National Park, Uganda. *American Journal of Primatology*, **50**, 169-185.

Chapman, C.A., Lawes, M.J., Naughton-Treves, L., & Gillespie, T.R. (2003). Primate survival in community-owned fragments: are metapopulation models useful amidst instensive use? In *Primates in Fragments* (ed L.K. Marsh), pp. 63-76. Kluwer Academic/Plenum Publishers, New York.

Chapman, C.A. & Peres, C.A. (2001) Primate conservation in the new millennium: The role of scientists. *Evolutionary Anthropology*, **10**, 16-33.

Chapman, C.A., Struhsaker, T.T., & Lambert, J.E. (2005) Thirty Years of Research in Kibale National Park, Uganda, Reveals a Complex Picture for Conservation. *International Journal of Primatology*, **26**, 539-555.

Chardon, J.P., Adriaensen, F., & Matthysen, E. (2003) Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (*Pararge aegeria L.*). *Landscape Ecology*, **18**, 561-573.

Clarke, G.P. (1998). A new regional centre of endemism in Africa. In *Chorology, Taxonomy ad Ecology of the Floras of Africa and Madagascar* (eds C.R. Huxley, J.M. Lock & D.F. Cutler), pp. 53-65. Royal Botanical Gardens, Kew.

Clarke, G.P. (2000). Defining the eastern African Coastal Forests. In *Coastal Forests of Eastern Africa* (eds N.D. Burgess & G.P. Clarke), pp. 9-27. IUCN, Gland, Switzerland & Cambridge, UK.

Clinchy, M., Haydon, D.T., & Smith, A.T. (2002) Pattern does not equal process: What does patch occupancy really tell us about metapopulation dynamics? *American Naturalist*, **159**, 351-362.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305-335.

Colyn, M.M. (1991) *Zoogeographical importance of the Zaire River basin for speciation: L'importance zoogéographique du Bassin du Fleurve Zaire pour la spéciation: le cas des Primates simiens.* Koninklijk Museum voor Midden-Afrika, Tervuren, Belgie.

Congalton, R.G. (1991) A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sensing of Environment*, **37**, 35-46.

Connor, E.F., Courtney, A.C., & Yoder, J.M. (2000) Individuals-Area Relationships: The relationship between animal population density and area. *Ecology*, **81**, 734-748.

Conroy, M.J., Cohen, Y., James, F.C., Matsinos, Y.G., & Maurer, B.A. (1995) Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications*, **5**, 17-19.

Cook, W.M., Anderson, R.M., & Schweiger, E.W. (2004) Is the matrix really inhospitable? Vole runway distribution in an experimentally fragmented landscape. *Oikos*, **104**, 5-14.

Coulson, T., Albon, S., Pilkington, J., & Clutton-Brock, T.H. (1999) Small-scale spatial dynamics in a fluctuation ungulate population. *Journal of Animal Ecology*, **68**, 658-671.

Coulson, T., Mace, G.M., Hudson, E., & Possingham, H. (2001) The use and abuse of population viability analysis. *Trends in Ecology & Evolution*, **16**, 219-221.

Cowlishaw, G. (1999) Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. *Conservation Biology*, **13**, 1183-1193.

Cowlishaw, G. & Dunbar, R. (2000a). Conservation strategies. In *Primate Conservation Biology* (eds G. Cowlishaw & R. Dunbar), pp. 289-329. The University of Chicago Press, Chicago.

Cowlishaw, G. & Dunbar, R. (2000b). Habitat disturbance. In *Primate Conservation Biology* (eds G. Cowlishaw & R. Dunbar), pp. 191-241. The University of Chicago Press, Chicago.

Cowlishaw, G. & Dunbar, R. (2000c). Population biology. In *Primate conservation biology* (eds G. Cowlishaw & R. Dunbar), pp. 119-157. The University of Chicago Press, Chicago.

Cowlishaw, G., Rowcliffe, J.M., & Anderson, J. (in prep.) A preliminary analysis of the metapopulation dynamics of the Tana River primates.

Crawley, M.J. (1993) *GLIM for Ecologists.* Blackwell Scientific Publications, Oxford.

Crawley, M.J. (2002). Model simplification. In *Statistical computing: An introduction to data analysis using S-Plus.*, pp. 449-465. John Wiley & Sons Ltd, Chichester.

Crome, H.J. (1997). Researching tropical forest fragmentation: shall we keep on doing what we are doing? In *Tropical forest remnants: ecology, management, and conservation of tropical forest fragments.* (eds W.F. Laurance & R.O. Bierregaard), pp. 485-501. University of Chicago Press., Chicago.

Cuaron, A.D. (2000) A global perspective on habitat disturbance and tropical rainforest mammals. *Conservation Biology*, **14**, 1574-1579.

Cunneyworth, P. & Rhys-Hurn, A. (2004). Wakuluzu, Friends of the Colobus Trust: Four year programme overview and development plan 2004-2007., Diani Beach, Kenya.

Davies, A.G. (1987). The Gola Forest Reserves, Sierra Leone: Wildlife conservation and forest management. IUCN, Gland, Switzerland.

Davies, A.G. (1994). Colobine populations. In *Colobine monkeys: their ecology, behaviour and evolution* (eds A.G. Davies & J.F. Oates), pp. 285-310. Cambridge University Press, Cambridge.

Davies, A.G., Oates, J.F., & Dasilva, G.L. (1999) Patterns of frugivory in three West African colobine monkeys. *International Journal of Primatology*, **20**, 327-357.

Davies, K.F., Gascon, C., & Margules, C.R. (2001). Habitat fragmentation: consequences, management and future research priorities. In *Conservation biology: research priorities for the next decade* (eds M.E. Soule & G.H. Orians), pp. 81-97. Island Press, Washington, D. C.

Decker, B.S. (1989) *Effects of habitat disturbance on the behavioural ecology and demographics of the Tana River red colobus (Colobus badius rufomitratus)* PhD Thesis, Emory University, Atlanta, Georgia.

Decker, B.S. (1994) Effects of habitat disturbance on the behavioral ecology and demographics of the Tana river red colobus (*Colobus badius rufomitratus*). *International Journal of Primatology*, **15**, 703-737.

Develey, P.F. & Stouffer, P.C. (2001) Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conservation Biology*, **15**, 1416-1422.

Diamond, J.M. & Bishop, K.D. (1987) Bird survival in an isolated Javan woodland: island or mirror? *Conservation Biology*, **1**, 132-142.

Didham, R.K. & Lawton, J.H. (1999) Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica*, **31**, 17-30.

Diffendorfer, J.E., Gaines, M.S., & Holt, R.D. (1995) Habitat fragmentation and movements of three small mammals *(Sigmodon, Microtus, and Peromyscus)*. *Ecology*, **76**, 827-839.

Doak, D.F. & Mills, L.S. (1994) A Useful Role for Theory in Conservation. *Ecology*, **75**, 615-626.

Dobson, A.P. & Lyles, A.M. (1989) The population dynamics and conservation of primate populations. *Conservation Biology*, **3**, 362-380.

Doncaster, C.P., Rondinini, C., & Johnson, P.C.D. (2001) Field test for the environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. *Journal of Animal Ecology*, **70**, 33-46.

Drechsler, M., Frank, K., Hanski, I., O'Hara, R.B., & Wissel, C. (2003) Ranking metapopulation extinction risk: From patterns in data to conservation management decisions. *Ecological Applications*, **13**, 990-998.

Dunbar, R.I.M. (1987) Habitat Quality, Population-Dynamics, and Group Composition in Colobus Monkeys (Colobus-Guereza). *International Journal of Primatology*, **8**, 299-329.

Dunning, J.B.J., Danielson, B.J., Noor, B.R., & Root, T.L. (1995) Spatially explicit population models: current forms and future uses. *Ecological Applications*, **5**, 3-11.

Ellis, S. (1997) Primate conservation and the IUCN/SCC conservation breeding specialist group: Tools, models, and processes. *Primate Conservation*, **17**, 41-45.

Elmhagen, B. & Angerbjorn, A. (2001) The applicability of metapopulation theory to large mammals. *Oikos*, **94**, 89-100.

Entwhistle, A.C., Mickleburgh, S., & Dunstone, N. (2000). Mammal conservation: current contexts and opportunities. In *Priorities for the conservation of mammalian diversity.* (eds A. Entwhistle & N. Dunstone), pp. 1-7. Cambridge University Press, Cambridge.

ERDAS (1999) *Field Guide: revised and expanded* 1999 ERDAS Inc., Atlanta, USA.

Estrada, A. & Coates-Estrada, R. (1996) Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *International Journal of Primatology*, **17**, 759-783.

Estrada, A., Coates-Estrada, R., Meritt, D.J., Montiel, S., & Curiel, D. (1993) Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. *Vegetatio*, **107/108**, 245-257.

Etienne, R.S. & Heesterbeek, J.A.P. (2001) Rules of thumb for conservation of metapopulations based on a stochastic winking-patch model. *American Naturalist*, **158**, 389-407.

Eudey, A.A. (1987). Action plan for Asian primate conservation, 1987 - 1991. IUCN, Gland, Switzerland.

Fahrig, L. (2001) How much habitat is enough? *Biological Conservation*, **100**, 65-74.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, **34**, 487-515.

Fahrig, L. & Merriam, G. (1994) Conservation of fragmented populations. *Conservation Biology*, **8**, 50-59.

Fashing, P.J. & Cords, M. (2000) Diurnal primate densities and biomass in the Kakamega Forest: An evaluation of census methods and a comparison with other forests. *American Journal of Primatology*, **50**, 139-152.

Fashing, P.J., Plumptre, A.J., Mullindahabi, F., Gakima, J.B., Masozera, M., Munanura, I., & Nguyen, N. (2004) Ranging patterns of an unusually large *Colobus angolensis* group in Rwanda. *Folia Primatologica*, **75**, 23.

Ferreras, P. (2001) Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian lynx. *Biological Conservation*, **100**, 125-136.

Field, M.Y. & Guatelli-Steinberg, D. (2003) Dispersal and the inbreeding avoidance hypothesis. *Primate Report*, **67**, 7-60.

Fimbel, C., Vedder, A., Dierenfeld, E., & Mulindahabi, F. (2001) An ecological basis for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. *African Journal of Ecology*, **39**, 83-92.

Fitzgibbon, C.D., Mogaka, H., & Fanshawe, J.H. (1995) Subsistence hunting in Arabuko-Sokoke Forest, Kenya, and Its effects on mammal populations. *Conservation Biology*, **9**, 1116-1126.

Fleishman, E., Ray, C., Sjogren-Gulve, P., Boggs, C.L., & Murphy, D.D. (2002) Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology*, **16**, 706-716.

Forman, R.T.T. (1997) *Land mosaics: The ecology of landscapes and regions.* Cambridge University Press., Cambridge.

FRA (2000). The Global Forest Resources Assessment 2000. FAO Forestry Papers 140.

Franklin, J.F. (1993) Preserving Biodiversity - Species, Ecosystems, or Landscapes. *Ecological Applications*, **3**, 202-205.

Franklin, J.F. (1994) Preserving Biodiversity - Species in Landscapes - Response. *Ecological Applications*, **4**, 208-209.

Freckleton, R.P. & Watkinson, A.R. (2002) Large-scale spatial dynamics of plants:metapopulations, regional ensembles and patchy populations. *Journal of Ecology*, **90**, 419-434.

Galat-Luong, A. & Galat, G. (2005) Conservation and Survival Adaptations of Temminck's Red Colobus (*Procolobus badius temmincki*), in Senegal. *International Journal of Primatology*, **26**, 585-603.

Ganade, G. (2001). Forest restoration in abandoned pastures of central Amazonia. In *Lessons from Amazonia* (eds R.O. Bierregaard, C. Gascon, T.E. Lovejoy & R.C.G. Mesquita), pp. 313-324. Yale University Press, New Haven & London.

Ganzhorn, J.U. (1985) Utilization of eucalyptus and pine plantations by brown lemurs in the eastern rainforest of Madagascar. *Primate Conservation*, **6**, 34-35.

Ganzhorn, J.U. (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology*, **76**, 2048-2096.

Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., & Borges, S. (1999) Matrix habitat and species richness in tropical forest remnants. *Biological Conservation*, **91**, 223-229.

Gebo, D.L. & Chapman, C.A. (1995) Habitat, annual, and seasonal effects on positional behavior in red colobus monkeys. *American Journal of Physical Anthropology*, **96**, 73-82.

Githitho, A.N. (1998). Institutional challenges in conservation: The case of the sacred kaya forests of the Kenya coast. NMK/CFCU, Kenya.

Glander, K.E. (1992) Dispersal patterns in Costa Rican mantled howling monkeys. *International Journal of Primatology*, **13**, 415-436.

Goheen, J.R., Swihart, R.K., Gehring, T.M., & Miller, M.S. (2003) Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity. *Oikos*, **102**, 95-103.

Goodwin, B.J. & Fahrig, L. (2002) Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, *Trirhabda borealis*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **80**, 24-35.

Graham, C.H. (2001) Factors influenceing movement patterns of Keel-billed toucans in a fragmented tropical landscape in Southern Mexico. *Conservation Biology*, **15**, 1789-1798.

Grieg-Smith, P. (1983) *Quantitative plant ecology*, 3rd edn. Blackwell Scientific Publications.

Grimes, K. & Paterson, J.D. (2000) *Colobus guereza* and exotic plant species in the Entebbe Botanical Gardens. *American Journal of Primatology*, **51**, 59-60.

Groves, C. (2001) *Primate taxonomy.* Smithsonian Institution Press, Washingston.

Grubb, P., Butynski, T.M., Oates, J.F., Bearder, S.K., Disotell, T.R., Groves, C.P., & Struhsaker, T.T. (2003) Assessment of the diversity of African primates. *International Journal of Primatology*, **24**, 1301-1357.

Grunblatt, J., Ottichilo, W.K., & Sinange, R.K. (1989) A heirarchical approach to vegetation classification in Kenya. *African Journal of Ecology*, **27**, 45-51.

Gustafson, E.J. & Gardner, R.H. (1996) The effect of landscape heterogeneity on the probability of patch colonization. *Ecology*, **77**, 94-107.

Gutzwiller, K.J., ed. (2002) *Applying landscape ecology in biological conservation.* Springer-Verlag, New York.

Hackel, J.D. (1999) Community conservation and the future of Africa's wildlife. *Conservation Biology*, **13**, 726-734.

Hacker, J.E., Cowlishaw, G., & Williams, P.H. (1998) Patterns of African primate diversity and their evaluation for the selection of conservation areas. *Biological Conservation*, **84**, 251-262.

Hanski, I. (1994a) Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology & Evolution*, **9**, 131-135.

Hanski, I. (1994b) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 151-162.

Hanski, I. (1997). Metapopulation dynamics: from concepts and observations to predictive models. In *Metapopulation Biology: Ecology, Genetics and Evolution.* (eds I. Hanski & M.E. Gilpin), pp. 69-92. Academic Press, London., London.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41-49.

Hanski, I. (1999a) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos*, **87**, 209-219.

Hanski, I. (1999b). The incidence function model : applications. In *Metapopulation Ecology.* (ed I. Hanksi), pp. 233-260. Oxford University Press, Oxford.

Hanski, I., Alho, J., & Moilanen, A. (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology*, **81**, 239-251.

Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics - brief-history and conceptual domain. *Biological Journal of the Linnean Society*, **42**, 3-16.

Hanski, I. & Gyllenberg, M. (1993) Two general metapopulation models and the Core-Satellite species hypothesis. *American Naturalist*, **142**, 17-41.

Hanski, I., Moilanen, A., & Gyllenberg, M. (1996a) Minimum viable metapopulation size. *American Naturalist*, **147**, 527-541.

Hanski, I., Moilanen, A., Pakkala, T., & Kuussaari, M. (1996b) The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology*, **10**, 578-590.

Hanski, I. & Ovaskainen, O. (2002) Extinction debt at extinction threshold. *Conservation Biology*, **16**, 666-673.

Hanski, I. & Simberloff, D. (1997). The metapopulation approach, its history, conceptual domain and application to conservation. In *Metapopulation biology: ecology, genetics and evolution.* (eds I. Hanski & M.E. Gilpin), pp. 5-26. Academic Press., San Diego.

Hanski, I. & Thomas, C.D. (1994) Metapopulation Dynamics and Conservation - a Spatially Explicit Model Applied to Butterflies. *Biological Conservation*, **68**, 167-180.

Hanski, I.A. & Gilpin, M.E., eds. (1997) *Metapopulation biology: ecology, genetics, and evolution.* Academic Press Ltd., London.

Hanski, K. & Ovaskainen, O. (2003) Metapopulation theory for fragmented landscapes. *Theoretical Population Biology*, **64**, 119-127.

Hanski, L. (2004) Metapopulation theory, its use and misuse. *Basic and Applied Ecology*, **5**, 225-229.

Hansson, L. (1991) Dispersal and connectivity in metapopulations. *Biological Journal of the Linnean Society*, **42**, 89-103.

Harcourt, A. (1998). Ecological Indicators of Risk for Primates, as Judged By Species' Susceptibility to Logging. In *Behavioural Ecology and Conservation Biology* (ed T. Caro), pp. 56-79. Oxford University Press, Oxford.

Harcourt, A.H. (1995) Population Viability estimates - theory and practice for a wild gorilla population. *Conservation Biology*, **9**, 134-142.

Harcourt, A.H. (2002) Empirical estimates of minimum viable population sizes for primates: tens to tens of thousands? *Animal Conservation*, **5**, 237-244.

Harcourt, A.H. & Parks, S.A. (2003) Threatened primates experience high human densities: adding an index of threat to the IUCN Red List criteria. *Biological Conservation*, **109**, 137-149.

Harrison, S. (1997). Empirical evidence for metapopulation dynamics. In *Metapopulation biology: Ecology, genetic, and evolution.* (eds I.A. Hanski & M.E. Gilpin). Academic Press Ltd., London.

Hastings, A. (1996) Models of spatial spread: a synthesis. *Biological Conservation*, **78**, 143-148.

Hawthorne, W.D. (1993). East African Coastal Forest botany. In *Biogeography and Ecology of the Rain forests of Eastern Africa* (eds J.C. Lovett & S.K. Wasser), pp. 57-99. Cambridge University Press, Cambridge.

Heino, M. & Hanksi, I. (2001) Evolution of migration rate in a spatially realistic metapopulation model. *American Naturalist*, **157**, 495-511.

Heino, M. & Hanski, I. (2001) Evolution of migration rate in a spatially realistic metapopulation model. *American Naturalist*, **157**, 495-511.

Hess, G. (1996) Disease in metapopulation models: Implications for conservation. *Ecology*, **77**, 1617-1632.

Hess, G.R. & Fischer, R.A. (2001) Communicating clearly about conservation corridors. *Landscape and Urban Planning*, **55**, 195-208.

Heywood, V.H., ed. (1995) *Global biodiversity assessment.* Cambridge University Press, Cambridge.

Hill, M.F. & Caswell, H. (2001) The effects of habitat destruction in finite landscapes: a chain-binomial metapopulation model. *Oikos*, **93**, 321-331.

Hokit, D.G., Stith, B.M., & Branch, L.C. (2001) Comparison of two types of metapopulation models in real and artificial landscapes. *Conservation Biology*, **15**, 1102-1113.

Hoopes, M.F. & Harrison, S. (1998). Metapopulation, source-sink and disturbance dynamics. In *Conservation science and action* (ed W.J. Sutherland), pp. 135-151. Blackwell Science Ltd., Oxford.

Hoorweg, J. (2000) *Kenya coast handbook. Culture, resources and development in the East African littoral.* Munster, Lit, Hamburg.

HSEDCO (1998). Environmental baseline data report of Kwale prospecting area and ship loading facility. Human Settlements, Environment and Development Collaborative, Nairobi.

Isbell, L.A. & VanVuren, D. (1996) Differential costs of locational and social dispersal and their consequences for female group-living primates. *Behaviour*, **133**, 1-36.

IUCN (1996). African Primates. Status Survey and Conservation Action Plan. Revised Edition., Gland, Switzerland.

IUCN (2001) *IUCN Red List Categories and Criteria version 3.1.*

IUCN (2004) IUCN Red List of Threatened Species. <*www.redlist.org*>.

IUCN (2005). Primates in peril: The world's 25 most endangered primates 2004 - 2006. IUCN/SCC Primate Specialist Group (PSG) / International Primatological society (IPS) / Conservation International (CI).

Jaetzold, R. & Schmidt, H. (1983) *Farm management handbook of Kenya. Voll II : Natural conditions and farm management information. Part C - East Kenya.*, Ministry of Agriculture, Kenya and GTZ, Germany.

Janzen, D.H. (1986). The eternal external threat. In *Conservation biology: The science of scarcity and diversity.* (ed M.E. Soule). Sinauer Associates, Sunderland, Massachusetts.

Jenness, J. (2005) Distance Matrix (dist_mat_jen.avx) extension for ArcView 3.x, v. 2. Jenness Enterprises. Available at: http://www.jennessent.com/arcview/dist_matrix.htm.

Johns, A.D. (1985) Differential detectability of primates between primary and selectively logged habitats and implications for population surveys. *American Journal of Primatology*, **8**, 31-36.

Johns, A.D. (1987) Long-term responses of a west Malaysian primate community to selective logging. *International Journal of Primatology*, **8**, 511-511.

Johns, A.D. & Skorupa, J.P. (1987) Responses of rainforest primates to habitat disturbance - a review. *International Journal of Primatology*, **8**, 157-191.

Johnson, A.R., Wiens, J.A., Milne, B.T., & Crist, T.O. (1992) Animal movements and population-dynamics in heterogeneous landscapes. *Landscape Ecology*, **7**, 63-75.

Jokimaki, J. & Huhta, E. (1996) Effects of landscape matrix and habitat structure on a bird community in northern Finland: A multi-scale approach. *Ornis Fennica*, **73**, 97-113.

Kahumbu, P. (1997) The decline of Angolan colobus monkeys *Colobus angolensis palliatus* in Diani. *Bulletin of the EANHS*, **27**, 2-4.

Kallimanis, A.S., Kunin, W.E., Halley, J.M., & Sgardelis, S.P. (2005) Metapopulation extinction risk under spatially autocorrelated disturbance. *Conservation Biology*, **19**, 534-546.

Kanga, E.M. (2000) Survey of the Angolan black-and-white colobus monkey *(colobus angolensis palliatus)* in the Diani forests, Kenya. *African Primates*, **4**, 50-54.

Kanga, E.M. (2001) Survey of black and white colobus monkeys (*Colobus angolensis palliatus)* in Shimba Hills National Reserve and Maluganji Sanctuary, Kenya. *ASP Bulletin*, **25**, 8-9.

Karere, G.M., Oguge, N.O., Kirathe, J., Muoria, P.K., Moinde, N.N., & Suleman, M.A. (2004) Population sizes and distribution of primates in the lower Tana River forests, Kenya. *International Journal of Primatology*, **25**, 351-365.

Keymer, J.E., Marquet, P.A., Velasco-Hernandez, J.X., & Levin, S.A. (2000) Extinction thresholds and metapopulation persistence in dynamic landscapes. *American Naturalist*, **156**, 478-494.

Kingdon, J. (1981) Where have the colonists come from ? A zoogeographical examination of some mammalian isolates in eastern Africa. *African Journal of Ecology*, **19**, 115-124.

Kingdon, J. (1997) *The Kingdon Field Guide to African Mammals* Academic Press, London.

Korstjens, A.H. & Schippers, E.P. (2003) Dispersal patterns among olive colobus in Tai National Park. *International Journal of Primatology*, **24**, 515-539.

Lacy, R.C. (1993-1994) What is population (and habitat) viability analysis? *Primate Conservation*, **14-15**.

Lahaye, W.S., Gutierrez, R.J., & Akcakaya, H.R. (1994) Spotted owl metapopulation dynamics in southern California. *Journal of Animal Ecology*, **63**, 775-785.

Lahm, S.A. (1993) *Ecology and economics of human/wildlife interaction in northeastern Gabon.*, PhD thesis, New York University., New York.

Laidlaw, R.K. (2000) Effects of habitat disturbance and protected areas on mammals of peninsular Malaysia. *Conservation Biology*, **14**, 1639-1648.

Laurance, S.G. (1994) Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. *Biological Conservation*, **69**, 23-32.

Laurance, S.G. & Laurance, W.F. (1999) Tropical wildlife corridors: use of linear rainforest remnants by arboreal mammals. *Biological Conservation*, **91**, 231-239.

Laurance, S.G.W. (2004). Landscape connectivity and biological corridors. In *Agroforestry and biodiversity conservation in tropical landscapes.* (eds S. G., G.A.B. da Fonseca, C.A. Harvey, C. Gascon, H.L. Vasceoncelos & A.N. Isac), pp. 50-63. Island Press, Washington.

Laurance, W.F. & Vasceoncelos, H.L. (2004). Ecological effects of habitat fragmentation in the tropics. In *Agroforestry and biodiversity conservation in tropical landscapes.* (eds G. Schroth, G.A.B. da Fonseca, C.A. Harvey, C. Gascon, H.L. Vasceoncelos & A.N. Izac), pp. 33-49. Island Press, Washington, D. C.

Laurance, W.F. & Yensen, E. (1991) Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation*, **55**, 77-92.

Lawes, M.J., Mealin, P.E., & Piper, S.E. (2000) Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented afromontane forest in South Africa. *Conservation Biology*, **14**, 1088-1098.

Leader-Williams, N. & Dublin, H.T. (2000). Charismatic megafauna as 'flagship species'. In *Priorities for the conservation of mammalian diversity.* (eds A. Entwhistle & N. Dunstone), pp. 53-85. Cambridge University Press, Cambridge.

Levins, R. (1969a) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237-240.

Levins, R. (1969b) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237-240.

Levins, R. (1970). Extinction. In *Some mathematical problems in biology.* (ed M. Gertenhaber), pp. 75-107. American Mathematical Society, Providence, RI.

Li, Y.M. (2004) The effect of forest clear-cutting on habitat use in Sichuan snub-nosed monkey *(Rhinopithecus roxellana)* in Shennongjia Nature Reserve, China. *Primates*, **45**, 69-72.

Lillesand, T.M. & Kiefer, R.W. (2000) *Remote Sensing and Image Interpretation*, 4th edn. John Wiley & Sons, New York.

Lindenmayer, D.B. (1999) Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. *Forest Ecology and Management*, **115**, 277-287.

Lindenmayer, D.B., McCarthy, M.A., & Pope, M.L. (1999) Arboreal marsupial incidence in eucalypt patches in south eastern Australia: a test of Hanski's incidence function metapopulation model for patch occupancy. *Oikos*, **84**, 99-109.

Lopez, J.E. & Pfister, C.A. (2001) Local population dynamics in metapopulation models: Implications for conservation. *Conservation Biology*, **15**, 1700-1709.

Lovett, J.C. & Wasser, S.K. (1993) *Biography and Ecology of the Rainforests of Eastern Africa* Cambridge University Press, Cambridge, UK.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoography. *Evolution*, **17**, 373-387.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography* Princeton University Press, Princeton, New Jersey, USA.

Mace, G.M. & Baillie, J.E.M. (2001). Assessment and management of species at risk. In *Conservation biology: research priorities for the next decade* (eds M.E. Soule & G.H. Orians), pp. 11-31. Island Press, Washington, D. C.

Mace, G.M. & Balmford, A. (2000). Patterns and processes in contemporary mammalian extinctions. In *Priorities for the conservation of mammalian biodiversity.* (eds A. Entwhistle & N. Dunstone). Cambridge University Press, Cambridge.

MacMahon, J.A. & Holl, K.D. (2001). Ecological restoration: A key to conservation biology's future. In *Conservation biology: research priorities for the next decade.* (eds M.E. Soule & G.H. Orians), pp. 245-270. Island Press, Washington.

Mandujano, S., Escobedo-Morales, L.A., & Palacios-Silva, R. (2004) Brief report on *Alouatta palliata* movements among fragments in Los Tuxtlas, Mexico. *Neotropical Primates*, **12**.

Mandujano, S., Escobedo-Morales, L.A., Palacios-Silva, R., Arroyo, V., & Rodriguez-Toledo, E.M. (in press). A metapopulation approach to conserving the howler monkey in a highly fragmented landscape in Los Tuxtlas, Mexico. In *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behaviour and conservation.* (eds A. Estrada, P.A. Garber, M. Pavelka & L. LeAndra). Kluwer, New York.

Marsh, C.W. (1979) Female transference and mate choice amongh Tana River red colobus. *Nature*, **281**, 568-569.

Marsh, C.W. (1986) A re-survey of the Tana River primates and their habitat. *Primate Conservation*, **7**, 72-81.

Marsh, C.W., Johns, A.D., & Ayres, J.M. (1987). Effects of habitat disturbance on rain forest primates. In *Primate Conservation in the Tropical Rain Forest.* (ed A.L.I. Riss), pp. 83-107.

Marsh, L.K. (2003a). The nature of fragmentation. In *Primates in Fragments: Ecology and Conservation* (ed L.K. Marsh). Kluwer Academic / Plenum Publishers, New York.

Marsh, L.K., ed. (2003b) *Primates in Fragments. Ecology and Conservation.* Kluwer Academic/Plenum Publishers, New York.

Marsh, L.K., Chapman, C.A., Norconk, M.A., Ferrari, S.F., Gilbert, K.A., Bicca-Marques, J.C., & Wallis, J. (2003). Fragmentation: Specter of the future or the spirit of conservation? In *Primates in fragments:ecology and conservation.* (ed L.K. Marsh). Kluwer Academic/Plenum Publishers, New York.

Marshall, A.R., Topp-Jorgensen, J.E., Brink, H., & Fanning, E. (2005) Monkey abundance and social structure in two high elevation forest reserves in the Udzungwa Mountains of Tanzania. *International Journal of Primatology*, **26**, 127-145.

Marshall, N.T. & Jenkins, M. (1994). Hard times for hardwood: indigenous timber and the timber trade in Kenya. TRAFFIC International, Cambridge, United Kingdom.

Martin, C. & Asibey, E.O.A. (1979) Effect of timber exploitation on primate population and distribution in the Bia rainforest area of Ghana. In 7th Congress of the International Primatological Society, Bangalore, India.

Mate, C., Colell, M., & Escobar, M. (1995) Preliminary observations on the ecology of forest *cercopithecidae* in the Lokofe-Ikomaloki region (Ikela, Zaire). *Folia Primatologica*, **64**, 196-200.

Maundu, P.M., Ngugi, G.W., & Kabuye, C.H.S. (1999) *Traditional food plants of Kenya.* Kenya Resource Centre for Indigenous Knowledge (KENRIK): National Museums of Kenya, Nairobi.

Mbora, D.N.M. (2004) Forest fragmentation and the distribution, abundance and conservation of the Tana River Red Colobus (*Procolobus rufomitratus*). *Biological Conservation*, **118**, 67-77.

Mbora, D.N.M. & McGrew, W.C. (2003) Extra-group sexual consortship in the Tana River red colobus *(Procolobus rufomitratus)*. *Folia Primatologica*, **74**, 58-58.

Mbora, D.N.M. & Meikle, D.B. (2004) The value of unprotected habitat in conserving the critically endangered Tana River red colobus (Procolobus rufomitratus). *Biological Conservation*, **120**, 91-99.

McCarthy, M.A. & Lindenmayer, D.B. (2000) Spatially-correlated extinction in a metapopulation model of Leadbeater's Possum. *Biodiversity and Conservation*, **9**, 47-63.

McCullough, D.R. (1996) *Metapopulations and wildlife conservation.* Island Press, Washington D.C., USA.

McGraw, W.S. (1998a) Comparative locomotion and habitat use of six monkeys in the Tai forest, Ivory Coast. *American Journal of Physical Anthropology*, **105**, 493-510.

McGraw, W.S. (1998b) Posture and support use of old world monkeys *(Cercopithecidae)*: The influence of foraging strategies, activity patterns, and the spatial distribution of preferred food items. *American Journal of Primatology*, **46**, 229-250.

Medellin, R.A. & Equihua, M. (1998) Mammal species richness and habitat use in rainforest and abandoned agricultural fields in Chiapas, Mexico. *Journal of Applied Ecology*, **35**, 13-23.

Medley, K.E. (1993) Primate conservation along the Tana river, Kenya - an examination of the forest habitat. *Conservation Biology*, **7**, 109-121.

Meffe, G.K. & Carroll, C.R. (1997) *Principles of conservation biology.* Sinauer Associates.

Mesquita, R.C.G., Delamonica, P., & Laurance, W.F. (1999) Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation*, **91**, 129-134.

Mittermeier, R.A. (1973) Colobus monkeys and the tourist trade. *Oryx*, **12**, 113-117.

Mittermeier, R.A. (1996). Introduction. In *The pictorial guide to the living primates.* (ed N. Rowe), pp. 1. Pogonias Press, East Hampton, New York.

Mittermeier, R.A. & Cheney, D.L. (1987). Conservation of primates and their habitats. In.

Mittermeier, R.A., Konstant, W.R., Nicoll, M.E., & Langrand, O. (1992). Lemurs of Madagascar: An action plan for their conservation, 1993-1999. IUCN, Gland, Switzerland.

Moilanen, A. (2000) The equilibrium assumption in estimating the parameters of metapopulation models. *Journal of Animal Ecology*, **69**, 143-153.

Moilanen, A. (2002) Implications of empirical data quality to metapopulation model parameter estimation and application. *Oikos*, **96**, 516-530.

Moilanen, A. (2004) SPOMSIM : Software for stochastic patch occupancy models of metapopulation dynamics. *Ecological Modelling*, **179**, 533-550.

Moilanen, A. & Hanksi, I. (2001) On the use of connectivity measures in spatial ecology. *Oikos*, **95**, 147-151.

Moilanen, A. & Hanski, I. (1998) Metapopulation dynamics: Effects of habitat quality and landscape structure. *Ecology*, **79**, 2503-2515.

Moilanen, A. & Nieminen, M. (2002) Simple connectivity measures in spatial ecology. *Ecology*, **83**, 1131-1145.

Moilanen, A., Smith, A.T., & Hanski, I. (1998) Long-term dynamics in a metapopulation of the American pika. *American Naturalist*, **152**, 530-542.

Moreno-Black, G.S. & Bent, E.F. (1982) Secondary compounds in the diet of *Colobus angolensis. African Journal of Ecology*, **20**, 29-36.

Moreno-Black, G.S. & Maples, W.R. (1977) Different habitat utilization of four *Cercopithecidae* in a Kenyan forest. *Folia Primatologica*, **27**, 85-107.

Muchoki, C.H.K. (1990). Land use in Kwale district. Department of Resource Surveys and Remote Sensing, Ministry of Planning and National Development, Kenya., Nairobi.

Muoria, P.K., Karere, G.M., Moinde, N.N., & Suleman, M.A. (2003) Primate census and habitat evaluation in the Tana delta region, Kenya. *African Journal of Ecology*, **41**, 157-163.

Muriithi, S. & Kenyon, W. (2002) Conservation of biodiversity in the Arabuko Sokoke Forest, Kenya. *Biodiversity and Conservation*, **11**, 1437-1450.

Murphy, H.T. & Lovett-Doust, J. (2004) Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? *Oikos*, **105**, 3-14.

Mwalonya, J., Nicolle, A., Nicolle, S., & Zimbu, J. (2004) *Mgombato: Digo – Swahili – English Dictionary.*, Nairobi.

Myers, N. (1988). Tropical forests and their species: going, going...? In *Biodiversity* (eds E.O. Wilson & F.M. Peter), pp. 28-35. National Academy Press, Washington D. C.

Myers, N. (1991) Tropical forests:present status and future outlook. *Climatic Change*, **19**, 3-32.

Myers, N. (1994). Tropical deforestation: Rates and patterns. In *The causes of tropical deforestation* (eds K. Brown & D.W. Pearce), pp. 27-40. University College London Press, London.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853-858.

Napier, P.H. (1995) Catalogue of Primates in the British Museum (Natural History) and elsewhere in the British Isles. Part III : Family *Cercopithecidae*, subfamily *Colobinae. London: British Museum (Natural History).*

Naughton-Treves, L. (1998) Predicting patterns of crop damage by wildlife around Kibale National Park. *Conservation Biology*, **12**, 156-168.

Navrud, S. & Mungatana, E. (1994) Environmental valuation in developing countries: the recreation value of wildlife viewing. *Ecological Economics*, **11**, 135-151.

Newton, P.N. & Dunbar, R.I.M. (1994). Colobine monkey society. In *Colobine monkeys:their ecology, behaviour and evolution.* (eds A.G. Davies & J.F. Oates), pp. 311-346. Cambridge University Press, Cambridge.

Nishida, T., Itani, J., Hiraiwa, M., & Hasegawa, T. (1981) A newly-discovered population of *Colobus angolensis* in East Africa. *Primates*, **22**, 557-563.

Nobis, M. & Wohlgemuth, T. (2004) Trend words in ecological core journals over the last 25 years. *Oikos*, **106**, 411-420.

Nupp, T.E. & Swihart, R.K. (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy*, **81**, 512-526.

Nzoika, B., Ojiambo, L., & Gang, P. (2003). Impacts of landuse/land cover changes on terrestrial and marine biodiversity in Kwale District. Department of Resource Surveys and Remote Sensing (DRSRS), Nairobi.

Oates, J.F. (1977a). The guereza and its food. In *Primate Ecology* (ed T.H. Clutton-Brock), pp. 275-321. Academic Press, New York.

Oates, J.F. (1977b). The guereza and man. In *Primate Conservation.* Academic Press, eds : H. S. H. Prince Rainier & G. H. Bourne. New York.

Oates, J.F. (1977c) The social Life of a black-and-white colobus monkey, *(Colobus guereza). Z. Tierpsychol*, **45**, 1-60.

Oates, J.F. (1996a) *African Primates. Status Survey and Conservation Action Plan. Revised ed.* IUCN/SSC Primate Specialist Group, Gland, Switzerland.

Oates, J.F. (1996b) Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Australian Journal of Ecology*, **21**, 1-9.

Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Dasilva, G.L., & Mole, S. (1990) Determinants of variation in tropical forest primate biomass - new evidence from West Africa. *Ecology*, **71**, 328-343.

Olden, J.D. (2003) A species-specific approach to modeling biological communities and its potential for conservation. *Conservation Biology*, **17**, 854-863.

Olupot, W. & Waser, P.M. (2001) Activity patterns, habitat use and mortality risks of mangabey males living outside social groups. *Animal Behaviour*, **61**, 1227-1235.

Onderdonk, D.A. & Chapman, C.A. (2000) Coping with forest fragmentation: The primates of Kibale National Park, Uganda. *International Journal of Primatology*, **21**, 587-611.

Opdam, P. (1990). Dispersal in fragmented populations: the key to survival. In *Species dispersal in agricultural habitat.* (eds R.G.H. Bunce & D.C. Howard), pp. 3-18. Belhaven Press, London, New York.

Ovaskainen, O. & Hanski, I. (2001) Spatially structured metapopulation models: Global and local assessment of metapopulation capacity. *Theoretical Population Biology*, **60**, 281-302.

Ovaskainen, O. & Hanski, I. (2002) Transient dynamics in metapopulation response to perturbation. *Theoretical Population Biology*, **61**, 285-295.

Ovaskainen, O. & Hanski, I. (2003a) Extinction threshold in metapopulation models. *Annales Zoologici Fennici*, **40**, 81-97.

Ovaskainen, O. & Hanski, I. (2003b) How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? *Theoretical Population Biology*, **64**, 481-495.

Paradis, E., Baillie, S.R., & Sutherland, W.J. (2002) Modeling large-scale dispersal distances. *Ecological Modelling*, **151**, 279-292.

Paradis, E., Baillie, S.R., Sutherland, W.J., & Gregory, R.D. (1999) Dispersal and spatial scale affect synchrony in spatial population dynamics. *Ecology Letters*, **2**, 114-120.

Pardini, R. (2004) Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. *Biodiversity and Conservation*, **13**, 2567-2586.

Pardini, R., de Souza, S.M., Braga-Neto, R., & Metzger, J.P. (2005) The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biological Conservation*, **124**, 253-266.

Pearson, S.M. (1993) The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecology*, **8**, 3-18.

Peltonen, A. & Hanski, I. (1991) Patterns of island occupancy explained by colonization and extinction rates in shrews. *Ecology*, **72**, 1698-1708.

Percival, A.B. (1928) *A game ranger on safari* Nisbet & Co., Ltd, London.

Peres, C.A. (1999) General guidlines for standardizing line-transect surveys of tropical forest primates. *Neotropical Primates*, **7**, 11-16.

Peters, R.H. (1983) *The ecological implications of body size.* Cambridge University Press, Cambridge.

Petit, S. & Burel, F. (1998) Effects of landscape dynamics on the metapopulation of a ground beetle (*Coleoptera carabidea*) in a hedgerow network. *Agriculture, Ecosystems and Environment*, **69**, 243-252.

Pimm, S.L. & Raven, P. (2001) Extinction by numbers. *Nature*, **403**, 843-845.

Pither, J. & Taylor, P.D. (1998) An experimental assessment of landscape connectivity. *Oikos*, **83**, 166-174.

Plumptre, A.J. (2000) Monitoring mammal populations with line transect techniques in African forests. *Journal of Applied Ecology*, **37**, 356-368.

Plumptre, A.J. & Reynolds, V. (1994) The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *Journal of Applied Ecology*, **31**, 631-641.

Possingham, H.P., Andelman, S.J., Noon, B.R., Trombulak, S., & Pulliam, H.R. (2001). Making smart conservation decisions. In *Conservation biology: research priorities for the next decade.* (eds M.E. Soule & G.H. Orians), pp. 225-244. Island Press, Washington.

Pozo-Montuy, G. & Serio-Silva, J.C. (2003) Locomotion and feeding on the ground by black howler monkeys (*Alouatta pigra*) in a very fragmented habitat of Rancheria Leona Vicario, Balancan Tabasco, Mexico. *American Journal of Primatology*, **60**, 65.

Pratt, W.K. (1991) *Digital Image Processing* John Wiley & Sons, Inc., New York.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652-661.

Pulliam, H.R. & Danielson, B.J. (1991) Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist*, **137**, S50-S66.

Pusey, A.E. & Packer, C. (1986). Dispersal and Philopatry. In *Primate Societies* (eds B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker), pp. 250-266. The University of Chicago Press, Chicago.

Quintana-Ascencio, R.F. & Menges, E.S. (1996) Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. *Conservation Biology*, **10**, 1210-1219.

Rahm, U.H. (1970). Ecology, zoogeography and systematics of some East African forest monkeys. In *Old world Monkeys* (eds T.H. Napier & P.H. Napier), pp. 589-626. Academic Press, London.

Rajpurohit, L.S., Sommer, V., & Mohnot, S.M. (1995) Wanderers between harems and bachelor bands - male hanuman langurs *(Presbytis-Entellus)* at Jodhpur in Rajasthan. *Behaviour*, **132**, 255-299.

Ratsimbazafy, J.H. (2002) The role of exotic plant species in the diet of ruffed lemurs (*Varecia variegata*) at Manombo Forest in Madagascar. *American Journal of Primatology*, **57**, 30.

Reunanen, P., Monkkonen, M., & Nikula, A. (2000) Managing boreal forest landscapes for flying squirrels. *Conservation Biology*, **14**, 218-226.

Reynolds, V., Wallis, J., & Kyamanywa, R. (2003). Fragments, sugar, and chimpanzees in Masindi District, Western Uganda. In *Primates in fragments: Ecology and conservation* (ed L.K. Marsh), pp. 309-319. Kluwer Academic, New York.

Rich, A.C., Dobkin, D.S., & Niles, L.J. (1994) Defining forest fragmentation by corridor width: the influence of narrow forest dividing corridors on forest-nesting birds in southern New Jersey. *Conservation Biology*, **8**, 1109-1121.

Richmond, M.D. (1997) *A Guide to the Seashores of Eastern Africa and Western Indian Ocean Islands.* Sida/Department for Research Cooperation, SAREC.

Ricketts, T.H. (2001) The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist*, **158**, 87-99.

Ries, L., Fletcher, R.J., Battin, J., & Sisk, T.D. (2004) Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology Evolution and Systematics*, **35**, 491-522.

Robertson, S.A. & Luke, W.R.Q. (1993). Kenya Coastal Forests: The report of the NMK/WWF Coast Forest Survey, National Museums of Kenya, Nairobi.

Robinson, J.G., Redford, K.H., & Bennett, E.L. (1999) Wildlife harvest in logged tropical forests. *Science*, **284**, 595-593.

Rodgers, W.A. (1981) The distribution and conservation status of colobus monkeys in Tanzania. *Primates*, **22**, 33-45.

Rodgers, W.A. & Homewood, K.M. (1982) Biological values and conservation prospects for the forests and primate populations of the Uzungwa mountains, Tanzania. *Biological Conservation*, **24**, 285-304.

Rodgers, W.A., Owen, C.F., & Homewood, K.M. (1982) Biogeography of East African forest mammals. *Journal of Biogeography*, **9**, 41-54.

Rodriguez, A. & Delibes, M. (2003) Population fragmentation and extinction in the Iberian lynx. *Biological Conservation*, **109**, 321-331.

Rodriguez-Toledo, A.M., Mandujano, S., & Garcia-Orduna, F. (2003). Relationships between forest fragments and hower monkeys (*Aloutta palliata mexicana*) in Southern Veracruz, Mexico. In *Primates in Fragments* (ed L.K. Marsh), pp. 79-97. Kluwer Academic/Plenum Publishers, New York.

Ross, C. & Srivastava, A. (1994) Factors influencing the population density of the hanuman langur (*Presbytis entellus*) in Sariska tiger reserve. *Primates*, **35**, 361-367.

Rowe, N. (1996) *The pictorial guide to the living primates.* Pogonias Press., East Hampton, New York.

Rylands, A., Rodriguez-Luna, E., & Cortés-Ortiz, L. (1997) Neotropical primate conservation: The species and the IUCN/SCC primate specialist group network. *Primate Conservation*, **17**, 46-69.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770-1774.

Saunders, D.A., Hobbs, R.J., & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation - a review. *Conservation Biology*, **5**, 18-32.

Sayer, J.A., Harcourt, C.S., & Collins, N.M. (1992) *The conservation atlas of tropical forests: Africa* Macmillan, London.

Schipper, J. & Burgess, N.D. (2004). Ecoregion descriptions. In *Terrestrial ecoregions of Africa and Madagascar: A conservation assessment.* (eds N.D. Burgess, J. D'Amico Hales, E. Underwood, E. Dinerstein, D.K. Olson, I. Itoua, J. Schipper, T.H. Ricketts & K.B. Newman), pp. 252-254. Island Press, Washington, D. C.

Schippers, P., Verboom, J., Knaapen, J.P., & vanApeldoorn, R.C. (1996) Dispersal and habitat connectivity in complex heterogeneous landscapes: An analysis with a GIS-based random walk model. *Ecography*, **19**, 97-106.

Schtickzelle, N. & Baguette, M. (2003) Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. *Journal of Animal Ecology*, **72**, 533-545.

Shreeve, T.G., Dennis, R.L.H., & Van Dyck, H. (2004) Resources, habitats and metapopulations - whither reality? *Oikos*, **106**, 404-408.

Siegel, S. & Castellan, N.J.J. (1988) *Nonparametric statistics for the behavioral sciences.* McGraw-Hill Brook Co., Singapore.

Siex, K.S. (2003) *Effects of population compression on the demography, ecology, and behaviour of the Zanzibar red colobus monkey (Procolobus kirkii).* Duke University, Durham, North Carolina.

Siex, K.S. & Struhsaker, T.T. (1999) Colobus monkeys and coconuts: a study of perceived human- wildlife conflicts. *Journal of Applied Ecology*, **36**, 1009-1020.

Simberloff, D. (1998). Small and declining populations. In *Conservation Science and Action.* (ed W.J. Sutherland), pp. 116-135. Blackwell Science Ltd, Oxford.

Simberloff, D. & Cox, J. (1987) Consequences and costs of conservation corridors. *Conservation Biology*, 63-71.

Sjogren-Gulve, P. (1994) Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae. Ecology*, **75**, 1357-1367.

Skorupa, J.P. (1986). Responses of rainforest primates to selective logging in Kibale forest, Uganda: A summary report. In *Primates: The road to self-sustaining populations* (ed K. Benirshcke), pp. 57-70. Springer, Berlin.

Smith, M.A. & Green, D.M. (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography*, **28**, 110-128.

Smith, T.B., Bruford, M.W., & Wayne, R.K. (1993) The preservation of processes: The missing element of conservation programmes. *Biodiversity Letters*, **1**, 164-167.

Soule, M.E. (1987) *Viable populations for conservation* University of Cambridge, Cambridge.

Soule, M.E. & Orians, G.H., eds. (2001) *Conservation biology: research priorities for the next decade.* Island Press, Washington D. C.

Spear, T.T. (1978) *The Kaya complex* Kenya Literature Bureau, Nairobi, Kenya.

Sterck, L. (1995) *Females, foods and fights : A socioecological comparison of the sympatric Thomas Langur and Long-Tailed Macaque.* PhD thesis. Faculteit Biologie. Universiteit Utrecht, Utrecht.

Stigand, C.H. (1909) *The game of British East Africa* Horace Cox, London.

Stouffer, P.C. & Bierregaard, R.O. (1995) Use of Amazonian forest fragments by understorey insectivorous birds. *Ecology*, **76**, 2429-2445.

Strasser, E. (1992) Hindlimb proportions, allometry, and biomechanics in Old World monkeys (Primates, *Cercopithecidae*). *American Journal of Physical Anthropology*, **87**, 187-213.

Struhsaker, T.T. (1981a). Census methods for estimating densities. In *Techniques for the Study of Primate Population Ecology*, pp. 36-80. National Academy Press, Washington, DC.

Struhsaker, T.T. (1981b) Forest and primate conservation in East Africa. *African Journal of Ecology*, **19**, 99-114.

Struhsaker, T.T. (2000). The effects of predation and habitat quality on the socioecology of African monkeys: lessons from the islands of Bioko and Zanzibar. In *Old World Monkeys* (eds P.F. Whitehead & C.J. Jolly). Cambridge University, Cambridge.

Struhsaker, T.T. & Leakey, M. (1990) Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. *Behavioral Ecology and Sociobiology*, **26**, 435-43.

Struhsaker, T.T. & Siex, K.S. (1998) The Zanzibar red colobus: conservation status of an endangered island endemic. *Primate Conservation*, **18**, 51-58.

Struhsaker, T.T., Struhsaker, P.J., & Siex, K.S. (2005) Conserving Africa's rain forests: problems in protected areas and possible solutions. *Biological Conservation*, **123**, 45-54.

Sutherland, G.D., Harestad, A.S., Price, K., & Lertzman, K.P. (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology*, **4**, 16 [online] URL : http//www.consecol.org/vol14/iss1/art16.

Sutherland, W.J. (1998). Managing habitats and species. In *Conservation science and action.* (ed W.J. Sutherland), pp. 202-219. Blackwell Science, Oxford.

Sutherland, W.J., Pullin, A.S., Dolman, P.M., & Knight, T.M. (2004) The need for evidence-based conservation. *Trends in Ecology & Evolution*, **19**, 305-308.

Swart, J. & Lawes, M.J. (1996) The effect of habitat patch connectivity on samango monkey *(Cercopithecus mitis)* metapopulation persistence. *Ecological Modelling*, **93**, 57-74.

Sweanor, L.L., Logan, K.A., & Hornocker, M.G. (2000) Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology*, **14**, 798-808.

Tarara, E. (1986) Results of the Swara readers survey on black and white colobus. *Swara*, **10**, 23-24.

Taylor, P.D., Fahrig, L., Henein, K., & Merriam, G. (1993) Connectivity Is a vital element of landscape structure. *Oikos*, **68**, 571-573.

Telfer, S., Holt, A., Donaldson, R., & Lambin, X. (2001) Metapopulation processes and persistence in remnant water vole populations. *Oikos*, **95**, 31-42.

Thomas, C.D. (1994) Difficulties in deducing dynamics from static distributions. *Trends in Ecology & Evolution*, **9**, 300.

Thomas, C.D. & Kunin, W.E. (1999) The spatial structure of populations. *Journal of Animal Ecology*, **68**, 647-657.

Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R., & Goodger, B. (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268**, 1791-1796.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., & Pollard, J.H. (2002) Distance 4.0. In Research Unit for Wildlife Population Assessment. http:www.ruwpa.st-and.ac.uk/distance/, University of St. Andrews, UK.

Thomas, S.C. (1991) Population densities and patterns of habitat use among anthropoid primates of the Ituri forest, Zaire. *Biotropica*, **23**, 68-83.

Tilman, D., May, R.M., Lehman, C.L., & Nowak, M.S. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65-66.

Tischendorf, L., Bender, D.J., & Fahrig, L. (2003) Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology*, **18**, 41-50.

Tischendorf, L. & Fahrig, L. (2000) On the usage and measurement of landscape connectivity. *Oikos*, **90**, 7-19.

Tischendorf, L. & Fahrig, L. (2001) On the use of connectivity measures in spatial ecology. A reply. *Oikos*, **95**, 152-155.

Towns, D.R. & Williams, M. (1993) Single-Species Conservation in New-Zealand - Towards a Redefined Conceptual-Approach. *Journal of the Royal Society of New Zealand*, **23**, 61-78.

Turner, M.G. (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Evolutionary Systematics*, **20**, 171-197.

Turner, M.G., Arthaud, G.J., & Engstrom, R.T. (1995) Usefuleness of spatially explicit population models in land management. *Ecological Applications*, **5**, 12-16.

Tutin, C.E.G. (1999) Fragmented living: Behavioural ecology of primates in a forest fragment in the Lope Reserve, Gabon. *Primates*, **40**, 249-265.

Tutin, C.E.G., White, L.J.T., & Mackanga Missandzou, A. (1997) The use by rain forest mammals of natural forest fragments in an equatorial African savanna. *Conservation Biology*, **11**, 1190-1203.

Umapathy, G. & Kumar, A. (2000) The occurrence of arboreal mammals in the rain forest fragments in the Anamalai Hills, south India. *Biological Conservation*, **92**, 311-319.

UNEP (1982). Environmental problems of the East African region., Nairobi, Kenya.

Vandermeer, J. & Carvajal, R. (2001) Metapopulation dynamics and the quality of the matrix. *American Naturalist*, **158**, 211-220.

Vedder, A. & Fashing, P.J. (2002) Diet of a 300-member Angolan colobus monkey (*Colobus angolensis*) supergroup in the Nyungwe Forest, Rwanda. *American Journal of Physical Anthropology*, 159-160.

Verbeylen, G., De Bruyn, L., Adriaensen, F., & Matthysen, E. (2003) Does matrix resistance influence Red squirrel (Sciurus vulgaris L. 1758) distribution in an urban landscape? *Landscape Ecology*, **18**, 791-805.

Verheyen, K., Vellend, M., Van Calster, H., Peterken, G., & Hermy, M. (2004) Metapopulation dynamics in changing landscapes: A new spatially realistic model for forest plants. *Ecology*, **85**, 3302-3312.

Viveiros de Castro, E.B. & Fernandez, F.A.S. (2004) Determinants of differential extinction vulnerabilities of small mammals in Atlantic forest fragments in Brazil. *Biological Conservation*, **119**, 73-80.

Wahlberg, N., Moilanen, A., & Hanski, I. (1996) Predicting the occurrence of endangered species in fragmented landscapes. *Science*, **273**, 1536-1538.

Walpole, M.J. & Leader-Williams, N. (2002) Tourism and flagship species in conservation. *Biodiversity and Conservation*, **11**, 543-547.

Walters, S. (2001) Landscape pattern and productivity effects on source-sink dynamics of deer populations. *Ecological Modelling*, **143**, 17-32.

Waltert, M., Lien, Faber, K., & Muhlenberg, M. (2002) Further declines of threatened primates in the Korup Project Area, south-west Cameroon. *Oryx*, **36**, 257-265.

Waser, P.M., Creel, S.R., & Lucas, J.R. (1994) Death and disappearance-estimating mortality risks associated with philopatry and dispersal. *Behavioural Ecology*, **5**, 135-141.

Wasserman, M.D. & Chapman, C.A. (2003) Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. *Journal of Animal Ecology*, **72**, 650-659.

WCMC (1992) *Global diversity : status of the earth's living resources.* Chapman & Hall, London.

Wethered, R. & Lawes, M.J. (2003) Matrix effects on bird assemblages in fragmented Afromontane forests in South Africa. *Biological Conservation*, **114**, 327-340.

White, F. (1976) The vegetation map of Africa: the history of a completed project. *Boissiera*, **24**, 659-666.

White, F. (1983) *Vegetation of Africa: a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa.* Unesco, Paris.

White, L. & Edwards, A. (2000). Methods for assessing the status of animal populations. In *Conservation research in the African rain forests* (eds L. White & A. Edwards), pp. 225-277. Multipress, Libreville, Gabon.

Whitesides, G.H., Oates, J.F., Green, S.M., & Kluberdanz, R.P. (1988) Estimating primate densities from transects in a West African rainforest - a comparison of techniques. *Journal of Animal Ecology*, **57**, 345-367.

Wieczkowski, J. (2004) Habitat structure of a non-forest corridor used by a group of Tana mangabeys (Cercopebus galeritus). *American Journal of Physical Anthropology*, **123**, 208.

Wiegand, T., Revilla, E., & Moloney, K.A. (2005) Effects of habitat loss and fragmentation on population dynamics. *Conservation Biology*, **19**, 108-121.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385-397.

Wiens, J.A. (1997). Metapopulation dynamics and landscape ecology. In *Metapopulation biology: ecology, genetics and evolution.* (eds I. Hanksi & M. Gilpin). Academic Press, San Diego.

Wiens, J.A., Stenseth, N.C., Vanhorne, B., & Ims, R.A. (1993a) Ecological mechanisms and landscape ecology. *Oikos*, **66**, 369-380.

Wiens, J.A., Stenseth, N.C., VanHorne, B., & Ims, R.A. (1993b) Ecological mechanisms and landscape ecology. *Oikos*, **66**, 369-380.

With, K.A. & Crist, T.O. (1995) Critical thresholds in species responses to landscape structure. *Ecology*, **76**, 2446-2459.

With, K.A., Gardner, R.H., & Turner, M.G. (1997) Landscape connectivity and population distributions in heterogeneous environments. *Oikos*, **78**, 151-169.

Wolfheim, J.H. (1983) *Primates of the world: distribution, abundance and conservation.* Harwood, Seattle.

WWF-US (2003). Ecoregional reports: Northern Zanzibar-Inhambane coastal forest mosaic.
Schipper, J.
Burgess, N. D. (authors).

Young, T.P. (2000) Restoration ecology and conservation biology. *Biological Conservation*, **92**, 73-83.

APPENDIX I

Interview guide for historic interviews within the Kilifi and Mombasa District's

1. Kaya/Forest :
2. Location :

3. Name :
4. Age :
5. Standing/Occupation :

6. How long have you lived here? (life history, timescale)

7. Animals you used to get in the forest ?

8. Which ones are hunted and eaten ?

9. Which monkeys do you get in the forest ?

10. Do you know of any other monkey's you get at the coast, but are not found in your forest?
    (If colobus mentioned):
    describe what they look like, eat, behave, where the white is located on their body.

11. Do you ever remember colobus being here? (or told by father/grandfather/village elders?)
    YES/NO

    YES =
    Direct/Indirect report
    Details : e.g. (when, how often, how many, reason for disappearance)

    NO =
    Do you know of anyone who knows about the colobus

12. Any conflict between colobus and humans?

13. Were colobus ever hunted? Were there specialist hunters of colobus?

14. What were colobus used for?

a. Body parts *	(e.g. medicinal)
b. Meat *	(e.g. eaten, medicinal)
c. Skin *	(e.g. **ceremonial wear, dances**, rugs, hats etc.)

    What ceremonies? Which dances?
    Where did they wear the skin?
    Where did they get the skin? How much?
    Have you seen a skin?
    (draw where white was on the skin to differentiate btw. *C. angolensis* and *C. guereza* pelt)

15. Any local stories, superstitions about the colobus?
    * (any stories relating to the significance of using colobus?)

16. Any songs in your language about the colobus?

APPENDIX II

Guide for semi-structured interviews within Kwale District matrix

I. Settlement :

Date :	Size : m x m
Topographic map region :	Average no. huts:
Sample site ref :	Average population :
GPS Georef :	Distance to intercept vegetation transects :
Name/Description of location :	Name of nearest forest :

II. Participants background / exposure :

Name :	Occupation / standing :
Sex :	Born in area : YES / NO
Age category : (actual age :)	Time spent in settlement :
<16 16-25 25-40 40-60 >60	

1. How long do you spend outside observing &/or working in the sample area?
   Description : *(exact participant's words)*

Post classify :	Present time	Past
	days/wk *or* incidental	less/same/more
	hrs/day	*if less/more* > yr of change (child, married?)
	no. seasons	quantify days/wk; hrs/day; no.seasons

III. Colobus knowledge :

2. Can you list the monkey species at the coast?
   List in order (e.g. baboon, sykes, colobus = B/S/C)

3. What is the colobus (mbega) like?
   (Circle items mentioned) Appearance/Forest/Arboreal/Feeding/Behaviour/Infants/Othe

4. Can you pick out the coast colobus from these pictures?
   Prompting level : 0/1/2/3 *(for questions 2. to 4.)*

5. Have you seen colobus in the Kwale District? YES / NO
   If YES
   Where? *(list, and lead up to participant's matrix site)*
   If PARTICIPANT LIVES NEAR SIGHT OF COASTAL FOREST
   Do you see them at the forest edge? YES/NO, When? *(quantify time of day, frequency)*

6. Have you ever seen colobus out of forest?

7. Has anyone ever told you about seeing colobus out of forest?
   If NO (go to section **V**)
   If YES (go to section **IV**)

Continued ...

I. Colobus sighting outside forest :

1. How regularly do you see them? *(exact participant's words)*
   Actual no. sightings; weekly, monthly rarely; validate times in detail.
2. When did you last see them? *(exact participant's words)*
   Within last year, <5yrs, <10yrs; month?, season?
3. What did you see? *(exact participant's words)*

No. sightings in chronological order (most recent first) and give the following details for each :

Location

Sighting location : (direct/indirect)

Were they moving through your/this land, where?
verify/describe location (local/additional site)

What time of day?

Date ref: (month/year)

Season:

Vegetation

List vegetation type:

Height:

Bare ground cover (%):

Colobus food trees: (present/absent), list spp:

Similarity to intercept vegetation sample site?
YES/NO, If NO : other ref/description:

Is the land always like this all year round?
YES/NO, If NO (give details, does it effect colobus movement?)

Colobus movement

How many colobus did you see?

What were they climbing on?

Height of travel:

How did they move ? *(exact participant's words)*

Post classify : Feeding / Resting
Slow
Fast

What do you think made them cross through your land? *(exact participant's words)*

Post classify :

Travel *(heading from-to, draw map to illustrate)*
Feeding *(on what/show interviewer?)*
Chased *(details)*

I. Final questions :

1. Do the colobus ever cause you trouble on your land?
2. Do you know of anyone else who might spend a lot of time (or more time than you) outside and could me with answering these questions?
3. Notes : *(post interview comments on reliability of participant)*

II. Additional discussion with elderly participants :

4. Was the land always like this?
5. Were colobus ever seen here in the past?
6. Did your fathers/elders ever talk of seeing them here?
7. Did you ever see colobus travelling between forest or within forest at this site?
8. Did you ever know of a forest patch that used to have colobus in it, but now has none? (why?)
9. Did you ever know of a forest patch that had no colobus in it and the colobus moved in? (where do you think they came from?)

APPENDIX III

Primate photo cards used during matrix, semi-structured interviews

Papio hamadryas cynocephalus

Colobus guereza

Chlorocebus aethiops

Cercopithecus mitus albogularis

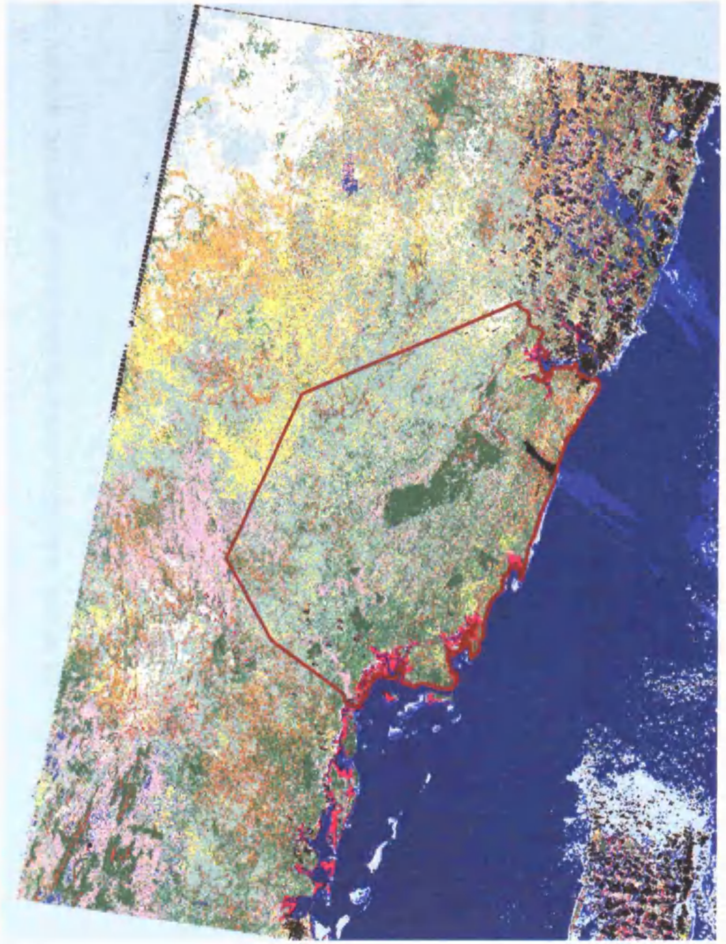
☑ *Colobus angolensis palliatus*

(A)

2003 LANDSAT-TM IMAGE OF THE STUDY SITE (166/063, 30-01-03)

(B)

FULL LANDSAT TM CLASSIFICATION SHOWING LOCATION OF MATRIX WITHIN 5KM OF COASTAL FOREST



Appendix V

Adult female: immature ratio for *C. a. palliatus* groups

As a crude measure of asynchronous population dynamics between subpopulations of *C. a. palliatus*, the following index of population growth was used:

1. A subset of 55 occupied habitat patches were selected for comparison. Although many habitat patches had complete data on total group counts, group demographics were not always fully explicit for all patches (i.e. quality 3 counts, see Chapter 2 for more details). Therefore, only the habitat patches where complete group demographics were known, were selected.

2. Only those habitat patches where four or more complete group demographics were known were selected.

3. This resulted in a comparison of eight habitat patches.

4. The average ratios of immatures (i.e. juveniles and infants) to adult females, for each habitat patch were tested for significant variation using a one-way analysis of variance (ANOVA).

5. A significant difference was found between the immature to adult female ratio's between habitat patches (F = 2.48; df = 7, p = 0.02)

Appendix VI

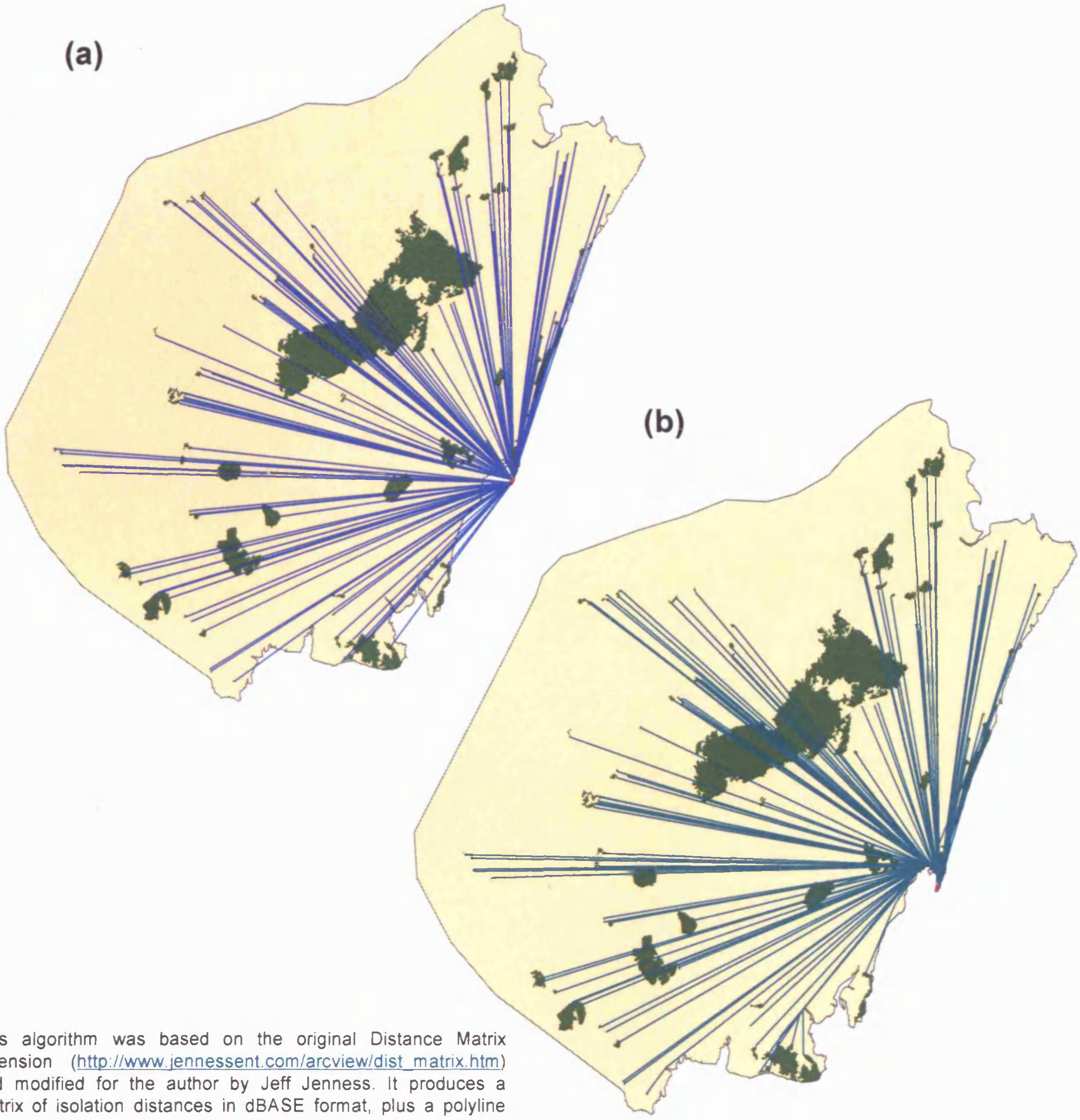
Symbols used in Chapters 5 and 6

Symbol	Explanation
E_i	Probability of patch extinction when occupied
C_i	Probability of patch colonization when empty
S_i	Connectivity of a patch
S_i^{MQ}	Connectivity of a patch including the effects of matrix quality
p_i	Observed occupancy of a patch *i*
p_i^*	Probability of occupancy of patch *I* *(expressed as the proportion of 1000 model simulation replicates where J_i = 1)*
J_i	Predicted occupancy of patch *i* (expressed as 1 or 0)
A_i	Area of patch *i*
A_o	Maximum patch area for which annual extinction probability equals unity
lA_i	Area of patch *i* following 10-50% forest loss from patch edge.
d_{ij}	Distance between patches *i* and *j*
d_{ij}^*	Modified isolation distance (i.e. after loss of forest to the edges of habitat patches)
m_{ij}	Average matrix quality between habitat patches *i* and *j*
m_{max}	Maximum matrix quality = 3
b	IF model parameter : scales population size with patch area
α	IF model parameter : $1/\alpha$ is the average dispersal distances for the species
x	IF model parameter : scales extinction risk to patch area
e	IF model parameter : average extinction risk
y	IF model parameter : scales efficiency of colonization to connectivity
w	IF model parameter : scales matrix permeability to matrix quality
M_{pop}	Metapopulation size = total number of occupied patches (i.e. total number of populations)
M_{ind}	Metapopulation size = total number of individuals
M^{1}_{ind}	Metapopulation size = total number of individuals, when patch *i* has been removed
U_i	Contribution of patch *i* to metapopulation size = $M_{ind} - M_{ind}^{-i}$

Appendix VII

Patch isolation distances using ArcView 3.2 distance matrix extension.

n.b. this appendix illustrates the isolation matrix for one coastal forest patch only.



This algorithm was based on the original Distance Matrix extension (http://www.jennessent.com/arcview/dist_matrix.htm) and modified for the author by Jeff Jenness. It produces a matrix of isolation distances in dBASE format, plus a polyline shapefile of connecting lines for all pairs of features in a polygon feature theme. This extension uses the exact vector-based straight-line distance between polygon edges whenever possible. If any of the connecting lines intersect the mainland boundary however (Fig A), the algorithm discards that line and resorts to cost-distance-based methods (Fig B). Grids for cost-distance paths are a minimum of 100,000 cells, and a maximum cell size of 25 meters. The analysis extent is based on the combined extent of the two polygons in question, expanded in increments of 50% until a patch exists that connects them. Restricting the analysis extent in this way lets us generate a finer-resolution grid and speeds-up processing time.