POPULATION STATUS AND GENETIC CHARACTERISTICS OF FOREST SPECIALIST AND GENERALIST BIRDS IN THE SAADANI-PANGANI ECOSYSTEM, TANZANIA

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A THESIS SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN WILDLIFE MANAGEMENT OF THE SOKOINE UNIVERSITY OF AGRICULTURE, MOROGORO, TANZANIA

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EXTENDED ABSTRACT

The Saadani-Pangani ecosystem form part of the east Africa coastal forests — and these forests, sitting along the coast of eastern Africa appears as small dotted patches but their biodiversity value is remarkably high. For example, they host about 4,050 species of vascular plants with 43% of them being endemic. The forests are either protected in forest reserves, or occurs in lands under private ownership. However, these forests have traditionally been impaired by suppression from human deleterious effects including forest clearing for subsistence agriculture and extensive livestock grazing. These disturbances cause habitat fragmentation which influence birds, including restricting dispersal of forest specialist species, for example. Therefore, this research was designed to assess the population status and genetic characteristics of forest dependant birds within fragmented forests in the Saadani-Pangani ecosystem, Tanzania. Two species, a forest specialist and a forest generalist were used as models. Specifically the research intended to: establish occurrence and population density; determine habitat preference; examine gene flow; and determine the effects of forest patch size and isolation on occurrence and abundance of the study species. Various techniques were used to collect data for achieving the objectives including line transects survey, mist netting, and laboratory analysis of molecular data to determine genetic makeup of individuals. Moreover, a number of methodologies were opted to analyse the data, including habitat modelling in Presence Program, density estimation using Distance Program, and forest patch size analysis using Quantum GIS software. Results showed that, the occurrence expressed as occupancy probability, and population density of the forest specialist species were higher in undisturbed habitat. On the other hand, the trend in occupancy probability, population density, and habitat preference of the forest generalist species opposed that of the forest specialist one. However, the genetic characteristics and gene flow of the forest specialist species did not differ among forest fragments. The findings under this research has provided useful information on statutes of forest specialist and generalist birds demonstrating their chance of persistence within fragmented habitat in the study system.

DECLARATION

I, Robert B. Modest, do here by declare to the Senate of the Sokoine University of Agriculture that this thesis is my own original work done within the period of registration and that it has neither been submitted nor being concurrently submitted in any other institution.

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DEDICATION

This thesis is dedicated to my wife Olivia and my son Eliud. Your encouragement and prayers have contributed to the success of this study.

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LIST OF ABBREVIATIONS

ABI	Applied Biosystems Inc
IUCN	International Union for Conservation of Nature
LOCPRIOR	Location Prior
MCMC	Markov chain Monte Carlo
QGIS	Quantum GIS (geographic information systems)
SMM	Stepwise Mutation Model
TANAPA	Tanzania National Parks
TPM	Two-phase Model
USGS	United States Geological Survey
WWF	World Wide Fund for Nature

CHAPTER ONE

Plate 1.1: View of the Saadani-Pangani Ecosystem

1.0 INTRODUCTION

1.1 Background Information

The Saadani-Pangani ecosystem form part of the east Africa coastal forests — and these forests which are recognized as World's biodiversity hotspot stand as dotted fragments stretching from southern Somalia up to the Limpopo River in Mozambique. They sit along the coast of eastern Africa and are found up to 1,030 meters above sea level (Clarke, 2000; WWF, 2014). The forests are either protected as forest reserves under forest protected area system or occur on lands under private ownership, and occasionally in sacred places (Conservation International, 2008). These forest patches are small in sizes, but their biodiversity value is remarkably high, for example, they host about 4,050 species of vascular plants with 43% of them being endemic (Conservation International, 2008). The forests also harbour more than 633 bird species of which 11 species are endemic (Azeria *et al.,* 2007; Conservation International, 2008).

On its wholly, the coastal forests in East Africa are believed to have had been connected to the Guineo-Congolian forests in west Africa before being separated by the upwelling of central Tanganyika plateau about 35 million years ago, but with some periods of reconnection until complete disjunction about 3 million years ago (Dicknson *et al.,* 1992). It is further claimed that, recurrent anthropogenic fires dating back as far as about 50 000 B.C. separated coastal forests from surrounding matrices restricting them to fire proof sites in moister areas including hill tops, riverine and ground water areas (Dicknson *et al.,* 1992). Moreover, on top of these historic pressures, the coastal forests in East Africa continued to face suppression from human deleterious effects including forest clearing for subsistence agriculture, human settlements and extensive livestock grazing (Burgess *et al.,* 1992; Dicknson *et al.,* 1992; Bloesch and Klötzli 2002; WWF, 2014). These practices on the one hand reduces forest sizes and damages matrices that otherwise would have acted as bridge habitat between forest fragments. The fragments on the other hand remain patched along the landscape, varying in size and degree of isolation, and their qualities depending on levels of degradation (Dicknson *et al.*, 1992; Clarke, 2000).

The quality of habitat however, is an important factor in determining how species such as birds use landscapes. Disturbed habitat such as fragmented forests variably influence birds including restricting dispersal of forest specialists, for instance (Cordeiro and Howe, 2003; Wittern and Berggren, 2007), thus hampering gene flow (Frankham, 1998; Gerlach and Musolf, 2000). The reason behind this phenomenon include psychological inhibition, whereby forest specialist birds for instance, fail to cross major forest gaps (Newmark, 1991). There are also effects on avifaunal composition, where for example forest visitors and generalists are positively favoured under disturbed habitat than forest specialist birds (Borghesio, 2008). Assessing population statuses and genetic characteristics of birds in fragmented habitat is thus fundamental in planning management options, particularly for those populations occurring in degraded and fragmented habitat.

Traditional methods for assessing population status of a species is by determining density and abundance (see for example Morrogh-Bernard *et al.*, 2003; Witmer, 2005), but most importantly by assessing threats and fitness (heath) of populations — since assigning priorities to mitigating those threats can save many local populations and rescue species in question from the risk of extinction (Rand *et al.*, 2012). Moreover, there is a number of considerations in assessing threats to species populations, one of them being biologists' judgments of the situation or decisions based on resources availability (Witmer, 2005). Indeed, the results of the assessment whether based on biologists' opinions, or logistically constrained are valuable and contribute on building knowledge of species conservation status applicable in quantifying species extinction risks (IUCN, 2003).

For example, analysis on habitat selection may provide valuable information on species fitness in their habitat and can help in identifying factors affecting species occurrence or abundance for predicting distribution and probable population status (Bibby *et al.*, 2000). This is because, apart from the general habitat provisions of food, water and shelter, birds have various specific needs when selecting suitable habitat, for instance when choosing nest sites, song posts, or perch sites (DeGraaf *et al.*, 1991), and these can in turn affect species reproductive process and survival (Patten *et al.*, 2004). For example, for some species such as North Island Robin *Petroica longipes* juveniles can hardly survive during postnatal dispersal unless they select suitable habitat that favours them during this delicate stage (Wittern and Berggren, 2007).

Furthermore, landscape characteristics such as size of forests are important in influencing bird populations in fragmented habitat. Effects of forest patch size and isolation on bird populations has been areas of research interest for most of bird ecologists and their reports present varied results (see for example Andren, 1994; Hanski, 1994; Connor *et al.*, 2000; Fahrig, 2003; Van Dorp and Opdam, 2005; Ferraz *et al.*, 2007; Jackson and Fahrig, 2012). Van Dorp and Opdam (2005) for example, reported habitat patch size as being the best predictor of species number and probability of occurrence of birds. Another interesting study was that reported by Uezu *et al.* (2005) on bird feeding guilds. This study reported patch size and isolation as affecting bird feeding guilds differently, whereby size was the main factor determining abundance of frugivorous species, while insectivorous were found being affected by the distance among patches.

1.2 Research Problem and Justification

1.2.1 Problem Statement

The Saadani-Pangani ecosystem contains a number of coastal forest patches that vary in habitat quality, degree of isolation, size, and content of endemism. Some of the forest patches in this ecosystem especially the bigger ones such as Zaraninge, Gendagenda and Msubugwe contain the majority of eastern African coastal forests bird endemics (Azeria *et al.*, 2007). But currently the forest patches in this ecosystem are shrinking in size and the quality of their habitat and that of surrounding matrices are deteriorating due to charcoal production, agriculture, wildfires and firewood collection (Dickinson *et al.*, 1992; WWF, 2014). This would affect the population status and genetic characteristics of birds especially forest specialists through restricting their movements for example — thus putting them at risk of extinction via inbreeding and lowered reproductive performance (Frankham, 1998; Gerlach and Musolf, 2000). Therefore, the persistence of several birds in this ecosystem particularly forest dependent species strictly endemic to coastal forests depend on the sustained quality of the forest patches as well as the quality of the matrices connecting them. However, prior to this study there was no evidence existing regarding the population status and genetic characteristics of forest birds residing the forest patches as well the matrices connecting the patches.

1.2.2 Research Justification

Previous ecological studies in the Saadani-Pangani ecosystem had concentrated on issues of savanna ecosystem dynamics and related plant-animal interactions (see for example, Tobler *et al.*, 2003; Treydte *et al.*, 2006; Cech *et al*., 2008). A few attempts to study birds in the area had limited to collection of data to produce checklists. Still, for forests like Kwamsisi not even a bird checklist was available. Hassan *et al.* (2013) studied birds in this ecosystem, but their main focus was on issues of response of bird communities on human induced disturbances. Therefore, understanding the population status and genetic characteristics of forest specialist and forest generalist birds with focus on occurrence and density, habitat preference, effect of patch size and isolation, and gene flow was an important aspiration of this study towards building up of information on bird ecology in this ecosystem. The findings will be useful in guiding the

Saadani National Park management, and other conservation agencies on forest bird conservation, as well as for sound decision making at different government levels on biodiversity conservation in general.

1.3 Objectives of the Study

1.3.1 General Objective

The overall objective of the study was to assess the population status and genetic characteristics of forest specialist and forest generalist birds in coastal forests of the Saadani-Pangani ecosystem using two model species, the Lowland Tiny Greenbul (*Phyllastrephus debilis*) as a forest specialist, and the Yellow-Bellied Greenbul (*Chlorocichla flaviventris*) as a forest generalist.

1.3.2 Specific Objectives

Specifically the study intended to:

a) Establish occurrence and population density of the study species inside selected forest patches and in vegetation matrices connecting the patches (Manuscript 1);
b) Determine habitat preference of the study species in selected forest patches and adjacent vegetation matrices (Manuscript 2);
c) Examine gene flow of the study species among selected forest patches (Manuscript 3); and
d) Determine the effect of patch size and isolation on occurrence and abundance of the study species (Manuscript 4).

1.4 Hypothesis

H_0: Habitat disturbance in the Saadani-Pangani ecosystem has no influence on subpopulations of forest specialist and forest generalist birds occupying the forest fragments.

H_1: Habitat disturbance in the Saadani-Pangani ecosystem influences subpopulations of forest specialist and forest generalist birds occupying the forest fragments.

1.5 Organization of the Theses

This theses contains three chapters, whereby chapter one presents information about the general settings of the study area, description of its biological values, and overall concepts of the research subject. Research problem and justification, objectives and hypothesis tested are also highlighted in this chapter. Chapter two present four manuscripts each covering one of the research objectives, while chapter three presents summary of the key findings, conclusion and recommendations of the study.

1.6 Methodology

1.6.1 Study System

The study was carried out in the Saadani-Pangani ecosystem in north-eastern coastal Tanzania. Data was however collected from four forest patches, namely Zaraninge (42.7 km^2), Kwamsisi (4.06 km^2), Gendagenda (10.97 km^2) and Msubugwe (22.32 km^2). Data was also collected in vegetation matrices connecting these forests (Fig. 1.1). Zaraninge and Kwamsisi forests are partly protected under SANAPA, whereby some of their segments fall under village authorities. Msubugwe and Gendagenda on the other hand have forest reserve statuses.

1.6.2 Criteria for Selection of Study Species

The two species, Lowland Tiny Greenbul (TG) and Yellow-bellied greenbul (YG) were selected as model birds according to three predetermined criteria: (1) one species is a forest specialist and the other one a forest generalist; (2) the species belong to the same family; and (3) possibility/chance of trapping them easily. The two bird species fulfilled all the stated criteria. TG is a forest specialist, and YG is a forest generalist that is widespread, typically in forest edge, but also in open scrubby habitat (Bennun, 1996; Fjeldsa *et al.*, 2007; Borghesio, 2008). By definition "forest specialists are species strictly dependent on interior of forests", so they are likely to disappear if the forest is modified, while "forest generalists are species that depend on undisturbed forest for some of their resources but which are able to live at the edges of forests or in modified, managed or secondary forests" (Bennun, 1996; Azeria *et al.*, 2007).

Since one of the objectives of the study involved capturing of birds for blood collection, trapability of the model birds was an important factor. To ascertain this, a one month trial capture was carried out in the study area before embarking on actual research to determine trapability of various bird species. The results of the trial capture showed that trapability of TG and YG was higher compared to other species, and this in addition to the other two criteria, was the basis of selecting TG and YG as model birds.

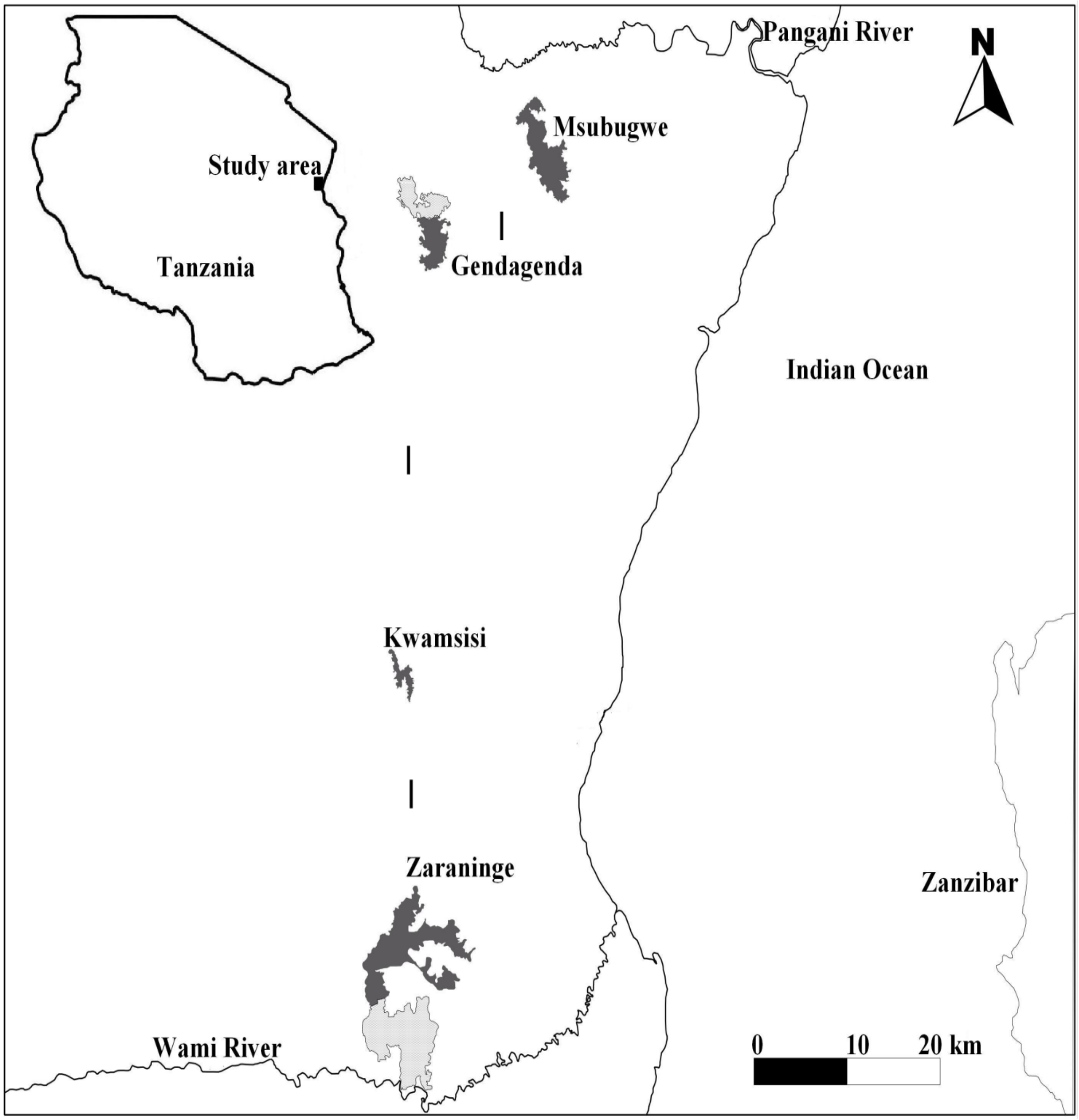

Figure 1.1: Map of the study area: Black shaded parts show study sites, thick lines show transects in matrices, while grey shows other mixed forests in continuum with study sites. The surface area for Zaraninge (darkened part) is about 42.7 km^2, Kwamsisi (4.06 km^2), Gendagenda (10.97 km^2), and Msubugwe (22.32 km^2). The distance from Zaraninge to Kwamsisi is about 16.6 km, and between Kwamsisi and Gendagenda is 34.6 km, while distance from Gendagenda to Msubugwe is about 10.2 km (Mapping: Robert B. Modest, Department of Wildlife Management, Sokoine University of Agriculture).

1.6.3 Study Design

The forest patches mentioned under section 1.6.1 were stratified into core and edge habitat. This was followed by establishing line transects in each of the stratum. Transects were also established in matrices connecting the forests. Transects orientation varied because some of the forests such as Kwamsisi and Gendagenda are not uniform in topography. Detailed description of study design are provided under each manuscript in chapter two.

1.6.4 Data Collection

1.6.4.1 Occurrence and Population Density

Recording occurrence of the study species along transects involved noting or coding the presence/absence of individuals during the survey (Nour *et al.,* 1999; Mackenzie *et al.,* 2006). On the other hand, Distance Sampling Techniques was employed in obtaining data for density estimation (Thomas *et al.,* 2010). This was achieved by recording number of individuals heard or sighted along transect, and by measuring perpendicular sighting distances of individuals (Bibby *et al.,* 2000; Thomas *et al.,* 2010).

1.6.4.2 Habitat Preference

In order to determine habitat preference of the two species, a number of vegetation variables were measured within 15 m radii circles at each bird sighting spot (Bibby *et al.,* 2000; Dallimer and King, 2007). The variables were; vegetation cover between 0 and 0.5 m high, vegetation cover between 0.5 and two meter high, and vegetation cover between two and six meter high. Others were; number of trees between six and 10 m high, number of climbers, number of trees >10 m high branching above half their height, and number of trees with dbh between 21 - 30 cm. Percentage canopy cover for trees >10 m high was also estimated.

1.6.4.3 Gene Flow and Genetic Characteristics

Gene flow and genetic characteristics was determined by analysing blood samples from birds captured in the study forests, whereby birds were trapped using mist nets, and a total of 59 blood samples were collected. All trapped birds were ringed and released at the same spots where they had been trapped. Upon collection, samples were temporarily handled in a mini-fridge before being deep frozen for longer storage. DNA was extracted using Invitrogen kit according to the manufacture’s protocol (lifetechnologies.com), and seven fluorescently labelled volatile Microsatellite Markers were used in individual genotyping.

1.6.4.4 Effect of Forest Patch Size and Isolation on Bird Abundance and Site Occupancy Probability

Patch isolation was evaluated based on distance between focal forests and other neighbouring patches within 500 m from the edge of focal forests (Moilanen and Nieminen, 2002; Prugh, 2009). The estimation of patch size was achieved by digitizing free satellite imagery acquired from LANDSAT TM 4 of USGS (Tucker *et al.*, 2004;

Prins and Clarke, 2006). All of the above GIS procedures were performed in Quantum GIS (QGIS) software (Quantum GIS Development Team, 2014).

1.6.5 Instruments Used

Data was gathered through surveying line transects and bird mist netting. Genetic work was done at the University of Antwerp using PCR and electrophoresis machines. Genotyping was done using ABI PRISM Applied Biosystems 3730XL DNA Analyser with GeneScan-500LIZ_3730 size standards. For GIS analysis, forest sizes were estimated in QGIS software using free satellite imagery acquired by LANDSAT TM 4.

1.6.6 Data Analysis

1.6.6.1 Occurrence and Population Density

Estimation of bird density was achieved using the Conventional Distance Sampling (CDS) analysis engine in Program Distance (Thomas *et al.*, 2010). Bird occupancy probability estimation based on coding distance sampling data into presence/absence followed by modelling using single species–single seasons approach as descibed in Mackenzie *et al.* (2006).

1.6.6.2 Habitat Preference

Analysis of habitat preference was accomplished by modelling response of bird abundance on vegetation parameters using multiple regressions approach (Burnham and Anderson, 2002). Model selection based on second order Akaike Information Criterion

AIC_c whereby competing models were ranked in order to determine the best ones among candidate sets.

1.6.6.3 Gene Flow and Genetic Characteristics

Various analyses were performed to assess levels of population genetic differentiation and gene flow. Some of the analysis performed were; Hardy-Weinberg Equilibrium, Linkage Disequilibrium, and Mutation-drift Equilibrium tests. Population bottleneck and historic gene flow were also estimated.

1.6.6.4 Effect of Forest Patch Size and Isolation on Bird Abundance and Site Occupancy Probability

Forest patch metrics were measured from digitized satellite imagery using QGIS Program (Quantum GIS Development Team, 2014). Bird abundance estimation was achieved using the CDS analysis engine in Program Distance (Thomas *et al.*, 2010). Occupancy probabilities estimation was achieved by coding Distance Sampling data into presence/absence and thereafter modelling using Presence Program (Mackenzie *et al.*, 2006). Spearman's rank correlation test was used to examine whether landscape metrics covaried with bird abundances or mean occupancy probilities repectively (McDonald, 2009). All statistical analyses were perfomed in R program ver 2.15.1 (R core team, 2013).

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CHAPTER TWO

2.0 MANUSCRIPTS

This chapter contains a list of four manuscripts. Manuscript one present analysis of site occupancy probability and density of the study species, while manuscript two present investigations on habitat preference of the two study species within the study system. Manuscript three examines among fragments genetic diversity and gene flow in a forest dependant bird species. The fourth manuscript on the other hand present results on the influence of patch size and isolation on abundance and site occupancy probability of the two study species.

2.1 MANUSCRIPT ONE

Plate 2.1: Habitat disturbance in the study area. From top left: Timber sawing in Msubugwe, pineapple fields adjacent Zaraninge, tree felling in Msubugwe, snapshot of a healthy segment of the Zaraninge forest.

Site occupancy probability and density of two passerine birds differing in susceptibility to habitat degradation in Tanzanian coastal forests

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Abstract

A number of studies have demonstrated that site occupancy and density of wildlife are a function of habitat quality. This study was designed to investigate site occupancy probability and density of two passerine birds within a coastal landscape that is facing deleterious human pressure. The aim of the study was to find out whether site occupancy probability and density of forest specialist and generalist birds differ among habitat of varied degree of degradation. The study used two model birds namely, Tiny Greenbul which is a forest specialist, and Yellow-bellied Greenbul, a forest generalist species. To obtain data for density estimation, birds were surveyed using distance sampling protocol. Data for occupancy probability estimation was attained by coding distance data into presence/absence. Bird density was estimated using the CDS analysis engine in Program Distance, while occupancy probability was modelled using Presence Program. The density of the forest specialist was found to be higher in ideal non-disturbed habitat, and the opposite was true for the generalist species. Ideal non-disturbed habitat also influenced occupancy probability of the forest specialist than the generalist species. Since results of this work suggested that the worst habitat for the specialist species was the best refuge for the generalist one, it is hereby recommended that habitat should be maintained in their natural states while minimizing human induced pressure for species to delineate niches according to resource needs.

Key words: Birds, coastal forests, density, greenbuls, occupancy probability, Tanzania.

Introduction

The Tanzanian coastal forests are part of a network of forests that stretch along the coast of Eastern Africa to form the coastal forests of eastern Africa world's biodiversity hotspot (Burgess et al., 1998; Myers et al., 2000; Bloesch & Klötzli 2002; Azeria et al., 2007). These forests are globally re-known for being biodiversity rich and having high number of endemism in both flora and fauna (Burgess & Clarke, 2000; Pfeifer, 2012; BirdLife International, 2014). However, biodiversity within these forests is facing severe anthropogenic pressure emanating from activities such as pole collection, clearing for agriculture and tree felling for timber (Burgess & Clarke, 2000; Ahrends *et al*., 2010; WWF, 2014). Since these pressure are deleterious in nature, it is likely that enormous negative effects associate with them including reduction in density of wildlife to a lesser or non-viable populations (Otieno *et al*., 2011; Duraes *et al*., 2013; Otieno *et al*., 2014). As density is affected on the one hand, occupancy i.e. presence or absence of a species from a group of sampling sites (MacKenzie and Nichols, 2004; Reunanen et al., 2002) could be affected too. For example, habitat clearing for agriculture and selective tree removal might lessen specific resources crucial for a group of wildlife (for instance depletion of tree species that supply food to frugivores), which might then affect the wildlife visitation rate of the denuded area (Farwig *et al.*, 2009; Otieno et al., 2014). The effect of this can manifest through uneven distribution of animals (habitat specialist species in particular), with individuals congregating in resource rich spots for instance while avoiding unsuitable ones (Smith *et al.*, 2011; Scott, 2012; Mulwa, et al., 2013). As a consequence, there could be possibility of populations behaving as those within islands showing increased inbreeding (Frankham, 1998), increased disease incidences and body weakening, which in-turn can impact the general reproduction processes of the individuals (Frankham, 1998; Hone, 2007).

This study was therefore designed to uncover the abovementioned processes in the Saadani National Park and surrounding landscape. The landscape in the study area is dominated by coastal forests that show different levels of degradation due to fragmentation (Burgess & Muir, 1994; Burgess and Clarke, 2000). The forests are tiny and scattered, but they form majority of the remaining coastal forest fragments south of the Pangani River (Azeria, et al., 2007). Moreover, the vegetation show a varied level of succession following different land use systems the area have experienced. This is because before gazettement the SANAPA area was under different management regimes (i.e. a game reserve, a cattle ranch, sisal plantations, and private lands) — whereby hunting and tree cutting dominated (Bloesch & Klötzli, 2002; Tobler et al., 2003).

Indeed, establishing site occupancy probability (the proportion of sites that are occupied by a species), and density for species that have suffered habitat degradation such as the ones described above is essential for understanding change in species status over time. This study was therefore designed to investigate site occupancy probability and density of two passerine birds within the abovementioned landscape, an area that have suffered severe human deleterious pressure over its history. The two passerine birds used were the Lowland Tiny Greenbul which is a forest specialist mainly restricted to well-developed forested habitat and preferring forest interior (Fjeldsa et al., 2007; Borghesio, 2008), and Yellow-bellied Greenbul, a forest generalist preferring forest edge and disturbed woodlands and savannahs, but with equivalent capacity of utilizing forested habitat. The general habitat requirements of the two species is known (Bennun *et al.* 1996), but before the current study it was not known how the two sympatric birds respond to habitat degradation. The aim of the study was to find out whether site occupancy probability and density of the forest specialist (Lowland Tiny Greenbul) and the forest generalist (Yellow-bellied Greenbul) vary among habitat depicting different levels of degradation. The research hypothesis stated that, habitat degradation would result in a lower density and site occupancy for the forest specialist (Lowland Tiny Greenbul) and that the same conditions would have less effect on density and site occupancy of the forest generalist (Yellow-bellied Greenbul). The findings of the study are expected to provide useful information in decision making and on setting priorities for species management (Marcot, 2006).

Material and Methods

Study Area and Study Species

This study was carried out within the world's biodiversity hotspot in north-eastern Tanzania. The study site geographic coordinates are 6°16'42.94" and 6°16'57.65"S, and 38°32'08.35" and 38°51'17.37"E (Azeria et al., 2007). The data was however gathered from seven sites that encompassed four evergreen coastal forests, and three sites in matrices surrounding the forests (Fig. 2.1). The study species were Lowland Tiny

Greenbul (*Phyllastrephus debilis*) and Yellow-bellied Greenbul (*Chlorocichla flaviventris*). Further description of the study area and study species is given under Modest *et al.,* (2016).

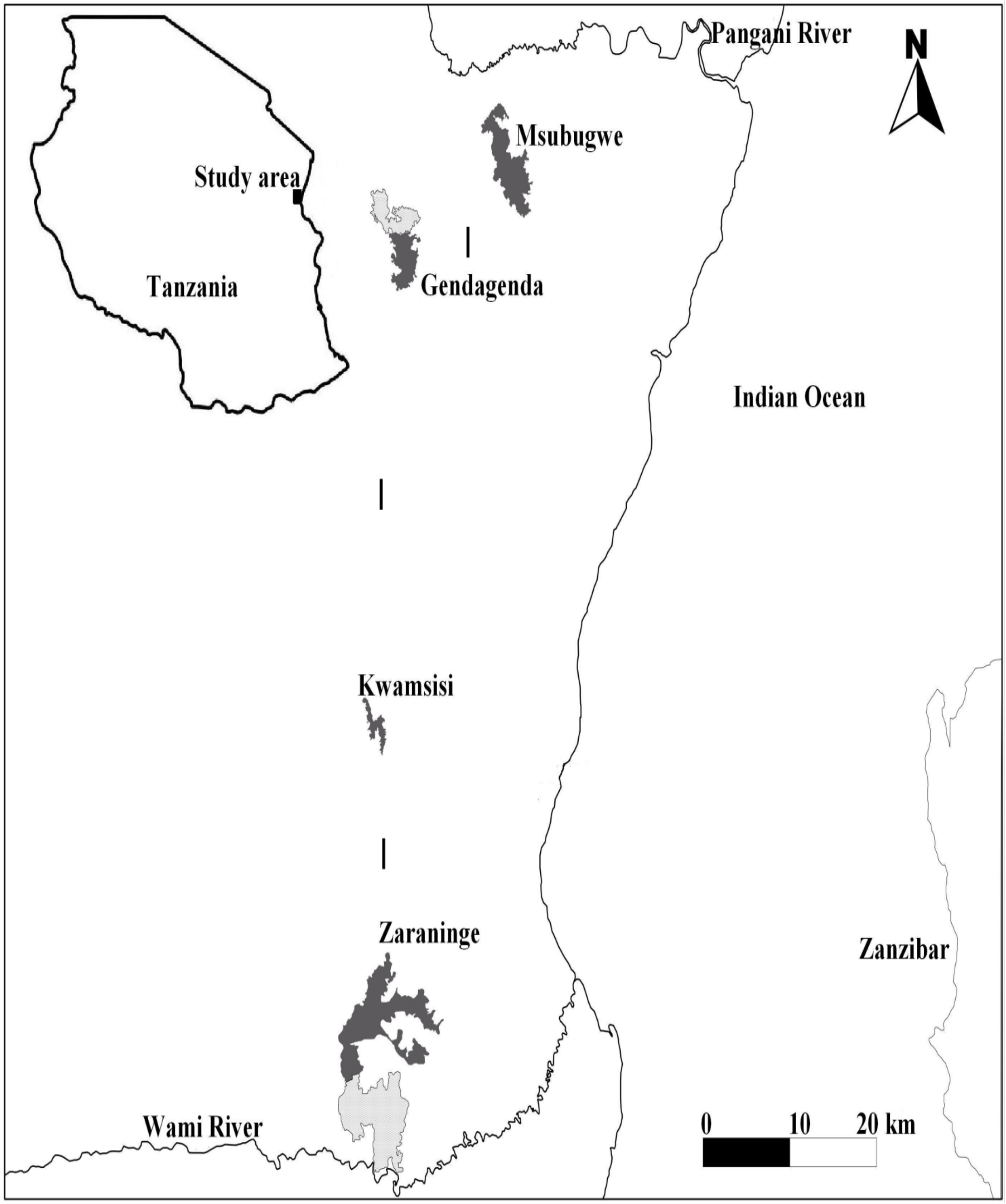

Figure 2.1: Map of the study area: Black shaded areas show dry evergreen coastal forests comprising study sites, thick lines show transects in matrices, while grey shows other mixed forests in continuum with study sites.

Sampling of Birds for Density Estimation

This study was carried out between October 2010 and June 2013. Birds were recorded along transects established within the forests and the matrices surrounding them (Fig.2.1). The study sites showed varied levels of habitat degradation and represented three categories of habitat types namely forests, savannahs and bushed acacia-woodland (Table 1.1). Within the forests data was collected from the interior habitat, and within 10 m from forest edges. Such distribution of transects in strata ensured that all representative habitat of both study species are sampled (Bibby et al., 2000). As the diameter for the Kwamsisi forest was at least one kilometre, the interior habitat for all study forests were regarded as areas about 500 m from edges. Judgement sampling procedure was followed in selecting locations for placement of first transects in each site (Morrison et al., 2001), after which random sampling was used in placing the remaining transects. The biggest forest (Zaraninge) was assigned nine transects (five in edge and four in core habitat), while Msubugwe which is the second biggest had six transects (three in edge and core respectively). Moreover, the Gendagenda forest had five transects (three in edge and two in core habitat), whereas the Kwamsisi had four transects (two in edge and core respectively). Transects were spaced at least ≥ 150 m so as to avoid double counting of birds, and the transect lengths ranged between 100 m and 500 m. On the other hand, a single transect measuring 4,000 m long was placed in matrices separating each of the two neighbouring forests. Afterwards the recorder visited each transect once per months (for a total of 24 visits) and recorded number of birds sighted or heard (Bibby et al., 2000; Thomas et al., 2010). The birds flying by were not recorded to reduce bias related to pseudo-replication (Bibby et al., 2000). In addition, perpendicular distances were measured from the transect line to the position where a bird was sighted or to the centre of cluster (Fewster et al., 2009; Thomas et al., 2010). Distances near transects were measured using a 100 m tape while those far away were estimated (Buckland et al., 1993; Bibby et al., 2000). Data collection commenced from 07.00 hours to 10.30 hours, followed by a break and then collection resumed from 15.30 hours to 18.30 hours.

Sampling of Birds for Occupancy Probability Estimation

The data for bird occupancy probability estimation was obtained by coding distance data (see above section) into presence/absence for modelling using Presence Program (Bibby et al., 2000; Mackenzie et al., 2003; Hines, 2006; Mackenzie *et al.,* 2006). Absence data was coded as zero (0) when no individual was recorded during distance sampling, and presence data was coded as one (1) when at least one individual was noted (Rogers et al., 2013; Hines, 2006). However, to account for uncertainty of not detecting the species when present (Mackenzie *et al.,* 2003; Mackenzie *et al.,* 2006), additional transects were surveyed on top of those used under distance sampling to equate eight transects (equally distributed between core and edge) in each of the forest patch except for Zaraninge which maintained nine transects. In the matrices however, three transects were maintained. Transects traversed different habitat types that depicted varied levels of disturbance which later on defined site-specific covariates (Table 1.1).

Table 1.1: Habitat types and site-specific covariates defined based on different levels of habitat disturbance for each study site.

Site	Habitat type	Level of disturbance	Covariate name	Covariate Abbreviation	Description
Zaraninge	Forest	Undisturbed	Undisturbed forest	NDF	Intact forest with less human influence.
Kwamsisi	Forest	Disturbed	Disturbed forest	DF	Obviously disturbed forest with moderate human influence resulting from small scale tree felling for timber.
Gendagenda	Forest	Lightly disturbed	Lightly disturbed forest	LDF	Less disturbed forest with mild human influence that results from collection of firewood and cutting of small poles for house construction.
Msubugwe	Forest	Highly disturbed	Highly disturbed forest	HDF	Severely disturbed forest facing large scale tree felling for timber using chainsaw.
Zaraninge/ Kwamsisi matrix	Savannah	Undisturbed	Undisturbed Savannah	UNS	Intact savannah vegetation without outside pressure from grazing livestock.
Kwamsisi/ Gendagenda matrix	Savannah	Lightly disturbed	Lightly disturbed savannah	LDS	Less disturbed savannah vegetation showing mild pressure from intruding grazing livestock.
Gendagenda/ Msubugwe matrix	Bushed-acacia woodland	Highly disturbed	Highly disturbed bushed acacia-woodland	HDW	Severely degraded savannah with subsequent conversion into acacia-woodlands following pressures from grazing livestock, settlements and clearing for agriculture.

Data Analysis

Bird density was estimated using the CDS analysis engine in Program Distance (Thomas et al., 2010). For each species four global models were run which Thomas et al. (2010) consider sufficient to give accurate estimates. The models were; uniform key with cosine adjustments, half-normal key with cosine adjustments, half-normal key with hermite polynomial adjustments, and hazard-rate key with simple polynomial adjustments. This was followed by post-stratification to obtain density estimate for each individual site shown in Fig. 2.1. However, estimates for matrices were pooled. Buckland et al. (1993) discourages truncating more that 5% of the data; thus, based on bin inspection, 0.25% of the data was truncated for Lowland Tiny Greenbul, and 0.15% for Yellow-bellied Greenbul to remove outlier observations. Data was then grouped into intervals while making sure that intervals were wider enough to accommodate diameter of the largest cluster observed in either species to allow for estimating density from individual encounters (Buckland et al., 1993; Thomas et al., 2010).

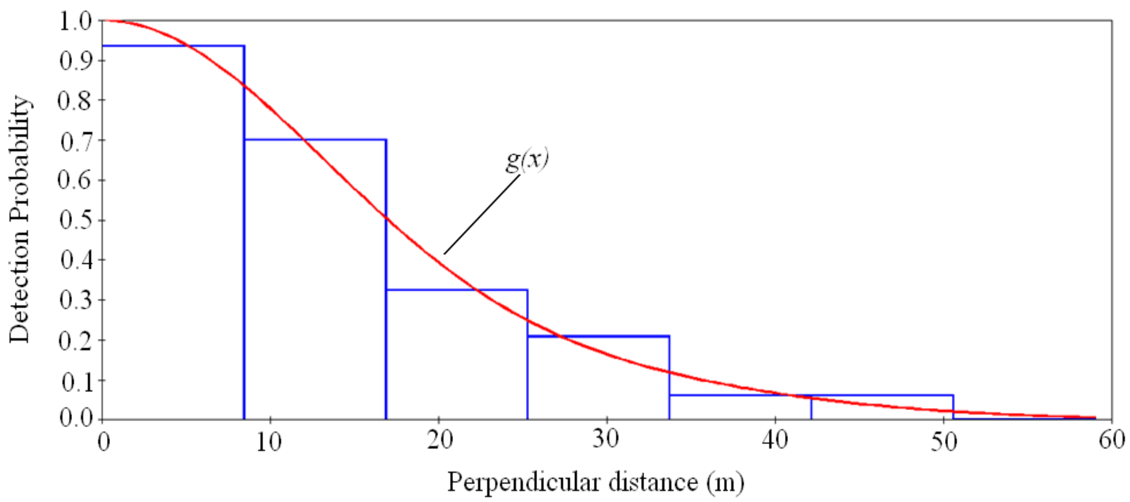

Figure 2.2: Detection curve for Lowland Tiny Greenbul's most global model

Best model selection to extract densities for individual sites based on three approaches; i) minimum Akaike, ii) minimum % CV (Table 1.2), and iii) the fit of the data based on observed distances (bars) and the fit of expected linear function *g(x)* on detection curve of the most global model (Buckland et al., 1993), Fig. 2.2 & 2.3.

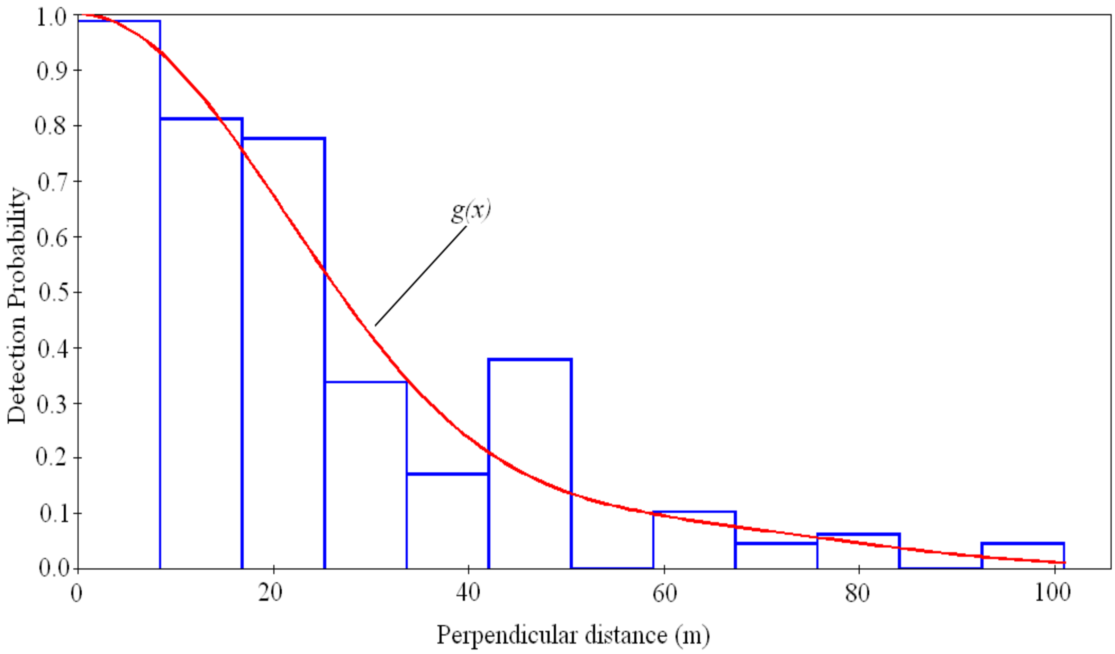

Figure 2.3: Detection curve for Yellow-bellied Greenbul's most global model

Bird occupancy probability estimation based on coding data obtained during distance sampling as detailed in previous sections. In order to meet the closure assumptions for modelling in Program Presence, data was sorted by seasons, and only the data collected within two consecutive months of each season was analysed (Mackenzie et al., 2003; Mackenzie et al., 2006). Four seasons were classified — November to December (short rainy season), April to May (long rainy season), February to early March (short dry season), and July to August (long dry season). Afterwards, the *a* *priori* model was established to accommodate site-specific covariates described in Table 1.1, and survey specific covariates representing survey seasons (Appendix 1.1). For each species and season three model were evaluated; 1) a constant model, where both occupancy and detection probabilities were held constant; 2) a model in which occupancy was a function of site-specific covariates while detection probability was a function of survey-specific covariates; and 3) a model where both occupancy and detection probabilities were functions of site-specific covariates (Appendix 1.1). Site-specific covariates were defined by combining habitat types with levels of habitat disturbance in each sampling location (Marques & Buckland, 1993; Mackenzie et al., 2003; Mackenzie *et al.*, 2006), and this resulted to seven categories of covariates described under Table 1.1. Survey-specific covariates on the other hand were classified based on respective seasons covered during bird survey. Classification of sites to obtain different categories of site-specific covariates was achieved following the researcher's experience with the study area, and through reviewing of literature (see for example, Burgess & Clarke, 2000; Hassan *et al.*, 2013).

When defining *a priori* models, only those covariates that were believed could potentially explain occupancy probability and detection probabilities of the two study species were incorporated (Mackenzie et al., 2003; Mackenzie et al., 2006; Newmark et al., 2011; Rogers et al., 2013). Then Program Presence ver. 6.1 was used to build models for each season separately using single-season single-species approach to estimate site occupancy probability, and detection probability, through application of likelihood theory (MacKenzie et al., 2003; Mackenzie et al., 2006; Rogers et al., 2013). The influence of site covariates on occupancy probability was determined using the logit link function.

Model selection based on AIC to evaluate model support of the data and to assess the strength of each site and survey specific covariates on influencing each of the two species. Following this procedure, models with delta Akaike of ≤ 2 were considered to have support in the data and were treated further on averaging (Burnham & Anderson 2002). Averaging of competing set of candidate models was achieved using the following formula:

$$\hat{\theta}_A = \sum_{j=1}^{m} w_j \hat{\theta}_j$$

Where w_j = Akaike weight for model j, θ_j = overall detectability or occupancy for model j, θ_A = overall detectability or occupancy for the averaged model (Burnham & Anderson 2002).

Results

Bird Density

The best global models for each of the study species were half-normal/cosine. The mean density across all sites for Lowland Tiny Greenbul was 0.43 birds/ha and that of Yellow-bellied Greenbul was 0.23 birds/ha. Although for Lowland Tiny Greenbul the Akaike value of the Half-normal/Cosine was greater than that of Hazard-rate/Simple polynomial, it was the fit of the line near transects that was most important (see Buckland et al., 1993). In addition, DCV for the Half-normal/Cosine model was lower than that of Hazard-rate/Simple polynomial for the Lowland Tiny Greenbul (Table 1.2).

Table 1.2: Models built in CDS engine of Program Distance to estimate density for the two study species: Global density was estimated as mean of strata estimates weighed by total effort in each stratum. The candidate models selected for extracting density estimates are in bold. *Abbreviations:* AIC = Akaike information criterion, D = Density estimate (mean individuals per ha), LCL = Lower Confidence interval, UCL = Upper Confidence interval, DCV = Density Coefficient of Variation.

Species and Model Name	AIC	D	D LCL	D UCL	D CV
Tiny Greenbul					
Uniform/Cosine	2212.9330	0.3480	0.2322	0.5215	0.1953
Hazard-rate/Simple polynomial	2124.2250	0.4783	0.2046	1.1180	0.4494
Half-normal/Cosine	**2132.7880**	**0.4309**	**0.2904**	**0.6393**	**0.1905**
Half-normal/Hermit polynomial	2141.7550	0.4000	0.2721	0.5880	0.1854
Yellow-bellied Greenbul					
Uniform/Cosine	2550.9020	0.2302	0.1933	0.2743	0.0852
Hazard-rate/Simple polynomial	2544.6700	0.2191	0.1818	0.2641	0.0919
Half-normal/Hermit polynomial	2573.3110	0.2009	0.1684	0.2398	0.0856
Half-normal/Cosine	**2542.4720**	**0.2340**	**0.1945**	**0.2816**	**0.0905**

Site specific density extracted from estimates of global model for each of the two species including their respective confidence intervals are presented in Table 1.3. For Lowland Tiny Greenbul, the highest density was 1.36 birds/ha in Zaraninge, while its lowest density was 0.04 birds/ha in matrix. On the other hand, the highest density for the Yellow-bellied Greenbul was 0.52 birds/ha in Msubugwe, whereas its lowest density was 0.12 birds/ha in matrix.

Table 1.3: **Density (birds/ha) for each site as extracted from estimates of best model for each of the study species: Estimate = density estimate, %CV = percentage coefficient of variance for density estimate, LCI = lower confidence interval, UCI = upper confidence interval.**

Species and Stratum	Estimate	%CV	LCI	UCI
Tiny Greenbul				
Gendagenda	0.4951	44.8300	0.1547	1.5844
Kwamsisi	0.4387	62.9500	0.0746	2.5786
Matrix	0.0381	75.3200	0.0026	0.5678
Msubugwe	0.6983	52.7800	0.2005	2.4320
Zaraninge	1.3648	24.3500	0.7879	2.3640
Yellow-bellied Greenbul				
Gendagenda	0.4925	23.2200	0.2816	0.8614
Kwamsisi	0.1803	44.3000	0.0505	0.6436
Matrix	0.1157	15.1700	0.0786	0.1703
Msubugwe	0.5223	15.1700	0.3686	0.7402
Zaraninge	0.2383	20.8600	0.1515	0.3746

Site occupancy and detection probabilities

With respect to data collected during short rainy season, four models were supported by the data within delta AIC of ≤ 2 for the Lowland Tiny Greenbul. Non disturbed forest (NDF) and season effect expressed as *p*(survey) were the most influential parameters for this species accounting for the highest Akaike weight of 0.31 compared to the rest of the models. For the Yellow-bellied Greenbul however, only the constant model (a model without any covariate) was supported (Table 1.4). The overall averaged estimates for models having Akaike value of ≤ 2 during the short rainy season were; Lowland Tiny Greenbul $\overline{\hat{\psi}}$ = 0.60, $\overline{\hat{p}}$ = 0.42; and Yellow-bellied Greenbul $\overline{\hat{\psi}}$ = 0.27, $\overline{\hat{p}}$= 0.17.

Table 1.4: **Occupancy models for the two species over the short rainy season: Parameters in parenthesis indicate covariates used in fitting the model. Delta AIC = difference between maximum and minimum Akaike values of competing models; ωi = Akaike weight; No. Par = Number of parameters; $\hat{\psi}$ = estimated overall occupancy probability; $\hat{p}$ = estimated overall detection probability; *SE* = the standard error. For description of abbreviated parameters see Table 1.1 in the methodology section.**

Model /Species	Delta AIC	ωi	No.Par	$\hat{\psi}$	SE($\hat{\psi}$)	$\hat{p}$	$SE(\hat{p})$
Lowland Tiny Greenbul							
ψ(NDF),p(survey)	0.00	0.31	4	0.69	0.11	0.56	0.12
ψ(NDF),p(NDF)	1.13	0.17	5	0.79	0.23	0.47	0.18
ψ(HDF),p(HDF)	1.13	0.17	5	0.79	0.23	0.47	0.18
ψ(LDF),*p(Survey)*	1.35	0.16	4	0.72	0.19	0.52	0.15
Yellow-bellied Greenbul							
ψ (.),p(.)	0.00	0.27	2	0.99	0.12	0.61	0.09

Seven models were supported by the data for the Lowland Tiny Greenbul with respect to long dry season. Non disturbed habitat (NDF) and season effects were the most influencing parameters for this species by having Akaike weight of 0.19. Five models were supported, but again the constant model was the most influencing for the Yellow-bellied Greenbul by having Akaike weight of 0.17 (Table 1.5). The overall averaged estimates for models having Akaike values of ≤ 2 during the long dry season were; Lowland Tiny Greenbul $\bar{\hat{\psi}}$ = 0.38, $\bar{\hat{p}}$ = 0.39; Yellow-bellied Greenbul $\bar{\hat{\psi}}$ = 0.49, $\bar{\hat{p}}$ = 0.30.

Table 1.5: Occupancy models for the two species over the long dry season: Abbreviations as in Table 1.4 above.

Model/Species	Delta AIC	ωi	No.Par.	$\hat{\psi}$	SE($\hat{\psi}$)	$\hat{p}$	$SE(\hat{p})$
Tiny Greenbul							
ψ(NDF),p(Survey)	0.00	0.19	4	0.41	0.20	0.44	0.20
ψ(NDF),p(NDF)	0.18	0.17	5	0.48	0.08	0.49	0.17
ψ(DF),p(Survey)	0.99	0.12	4	0.41	0.20	0.44	0.20
ψ(LDF),p(Survey)	0.99	0.12	4	0.41	0.20	0.44	0.20
ψ(HDF),p(Survey)	0.99	0.12	4	0.41	0.20	0.44	0.20
ψ(LDF),p(LDF)	1.78	0.08	5	0.47	0.30	0.43	0.25
ψ(HDF),p(HDF)	1.78	0.08	5	0.47	0.30	0.43	0.25
Yellow-bellied Greenbul							
ψ(.),p(.)	0.00	0.17	2	0.75	0.17	0.49	0.12
ψ(DF),p(Survey)	0.02	0.17	4	0.75	0.17	0.49	0.14
ψ(DF),p(DF)	0.62	0.13	5	0.86	0.13	0.44	0.13
ψ(NDF),p(NDF)	1.55	0.08	5	0.84	0.12	0.45	0.13
ψ(NDF),p(Survey)	1.57	0.08	4	0.75	0.20	0.49	0.14

During the long rainy season three models were supported by the data for both species with constant model being the best models. The rest of the models included either site-specific and/or survey-specific covariates, but with lower weights (Table 1.6). The overall averaged estimates for models having Akaike value of ≤ 2 during the long rainy season were: Lowland Tiny Greenbul $\overline{\hat{\psi}}$ = 0.53 $\overline{\hat{p}}$ = 0.34; and Yellow-bellied Greenbul $\overline{\hat{\psi}}$= 0.45, $\overline{\hat{p}}$ = 0.27.

Table 1.6: Occupancy models for the two species over the long rainy season: Abbreviations as in Table 1.4.

Model/Species	Delta AIC	ωi	No.Par	$\hat{\psi}$	SE($\hat{\psi}$)	$\hat{p}$	$SE(\hat{p})$
Tiny Greenbul							
ψ(.),p(.)	0.00	0.31	2	0.85	0.15	0.53	0.11
ψ(NDF),p(survey)	1.03	0.18	4	0.79	0.10	0.58	0.11
ψ(NDF),p(NDF)	1.58	0.14	5	0.88	0.10	0.50	0.16
Yellow-bellied Greenbul							
ψ(.),p(.)	0.00	0.20	2	0.83	0.16	0.52	0.11
ψ(DF),p(DF)	0.26	0.17	5	0.90	0.11	0.49	0.12
ψ(DF),p(survey)	0.39	0.16	4	0.83	0.18	0.52	0.13

Only the constant models were supported by the data during the short dry season for both species (Table 1.7). It was during this season where the overall averaged estimates particularly the occupancy probability for the two species were more or less similar. The overall averaged estimates for models having Akaike value of ≤ 2 during the short dry season were; Lowland Tiny Greenbul $\overline{\hat{\psi}}$ = 0.35, $\overline{\hat{p}}$ = 0.13; and Yellow-bellied Greenbul $\overline{\hat{\psi}}$ = 0.34, $\overline{\hat{p}}$ = 0.18.

Table 1.7: **Occupancy models for the two species over the short dry season: Abbreviations as in Table 1.4.**

Model/Species	DeltaAIC	ωi	No.Par.	$\hat{\psi}$	$SE(\hat{\psi})$	$\hat{p}$	$SE(\hat{p})$
Tiny Greenbul							
ψ (.),p(.)	0	0.42	2	0.84	0.42	0.31	0.16
Yellow-bellied Greenbul							
ψ(.),p(.)	0	0.34	2	0.99	0.10	0.53	0.06

Discussion

Bird Density

The highest density for the forest specialist Lowland Tiny Greenbul i.e. 1.365 birds/ha was recorded in Zaraninge, a forest that was categorized as undisturbed. On contrast, the density of this species in Msubugwe, a highly disturbed forest was 0.698 birds/ha, about half of the density recorded in Zaraninge. But this density (i.e. for Msubugwe) was higher compared to the densities recorded in either Gendagenda or Kwamsisi. Thus, the fact that Msubugwe forest is larger than Kwamsisi or Gendagenda, this suggest that patch size also matters in influencing the species (Connor et al., 2000; Fahrig, 2001).

Indeed, the observed decrease in density of the Lowland Tiny Greenbul, (a forest specialist species) following increase in level of habitat disturbance (refer Zaraninge vs Msubugwe in Table 1.1) signify that this species is sensitive to habitat degradation (Maclean et al., 2003; Cleary & Mooers, 2006; Dunn & Romdal, 2006; Gillies & St. Clair, 2009). This trend has as well been observed in other forest specialist species elsewhere. For example, a study on Turner's Eremomela, a forest specialist and globally endangered species reported the same tendency whereby a higher density i.e. 1.11 birds/ha of this species was recorded from intact habitat in South Nandi Forest (Kenya) compared to 0.43 birds/ha reported from the degraded Kakamega forest (Otieno et al. 2011; Otieno et al. 2014).

On the other hand, despite the fact that Zaraninge is the largest among the forests covered by this study, and the fact that this forest received the highest sampling intensity compared to others, the density of the Yellow-bellied Greenbul i.e. 0.238 birds/ha in this undisturbed forest was extremely low. The density of this species however was the highest in Msubugwe, a forest described as highly disturbed. Therefore, this suggest that, for the Yellow-bellied Greenbul (a forest generalist), ideal non-disturbed habitat are not important for its survival (Bennun et al., 1996; Gillies & St. Clair, 2009). However, an important observation for the Yellow-bellied Greenbul is its lowest density in the matrix habitat. The lower density of this species in the matrix when viewed together with its higher density in Msubugwe forest suggest that, this species (being a forest generalist) partially remain tied to forested habitat for some of its activities. This clearly support the view that for forest generalist species, despite their capabilities in utilizing a wide range of habitat, they usually depend on forests for some of their requirements such as sites for laying eggs (Bennun et al., 1996).

Site occupancy and detection probability

With exception of constant models, the parameter NDF (undisturbed forest) was the only site-specific covariate that was incorporated in best models of the forest specialist species, Lowland Tiny Greenbul, whereby this covariate appeared twice in best models of this species across the four seasons modelled. In addition, all other models that incorporated NDF always ranked higher compared to models incorporating other site-specific covariates. Moreover, as revealed above in the density section, this observation also indicate that ideal non-disturbed forests form important habitat for the species. This is in proof of the previous findings such as that reported by Bennun et al., (1996) as well as Otieno et al., (2014) on response of forest specialist species under disturbed habitat. On the other hand, for the Yellow-bellied Greenbul, a generalist species, no site-specific covariates appeared in its best model indicating that site-specific covariates are not as important as for the forest specialist species. Thus, the higher weights given the constant models for the Yellow-bellied Greenbul suggest that this species is not biased towards any habitat type, despite its dependence on forests for some of its requirements as described above (Bennun et al., 1996).

Moreover, the occupancy probabilities of both species seemed to be influenced by seasonality. For example, the Lowland Tiny Greenbul had the highest overall averaged occupancy probability of 0.60 during the short rainy season compared to the lowest occupancy probability of 0.35 for the short dry season. The higher occupancy probability during the short rainy season probably corresponds with the beginning of the breeding season of the species that is reported to commence in October (Fishpool & Tobias, 2005). During this season birds are probably active with nest construction, and are presumably displaying for finding mates where it is easy to detect (Martine et al., 2000). In addition to this fact, the trend of site occupancy by the species might suggest that the Lowland Tiny Greenbul is not a sedentary species as previously thought since its site occupancy probabilities varied across seasons. Therefore, it is presumed that, this species is able to swap habitat between matrices and forests though majority of individuals remain within forests. On the other hand, the higher occupancy probability for the Yellow-bellied Greenbul during long dry season probably coincide with ripening of fruits that possibly attracts the species to those favourably feeding sites (Cordeiro & Howe, 2003; Cordeiro et al. 2004; R. B. Modest, unpublished). Yellow-bellied Greenbul is highly attracted to fruits (Hockey et al., 2005), and in the current work it was noted that the species was more active during the period when shrubs and climbers are bearing ripe berries. Thus, it is possibly that these seasonal food resources are responsible for making the species more noticeable during the long dry season compared to other seasons (Scott, 2012).

In conclusion, both density and site occupancy probability analyses suggest a contrasting susceptibility of the model birds on habitat degradation, whereby ideal non-disturbed habitat positively influence the forest specialist species, and the opposite is true for the forest generalist. The results thus provide a challenge regarding habitat management for these species in the study area. This is because there is a possibility that the worst habitat for one of the species forms the best refuge for the other. Thus, it is strongly recommended that efforts to maintain habitat in their natural states be committed much as possible since in absence of human pressures the species will obviously delineate their niches according to their requirements. It is further recommended that; 1) habitat destruction within the study area should be stopped immediately through enforcing existing laws and regulations, 2) a long term monitoring study to explore persistence and density trend of the forests specialist species in the forest fragments should be undertaken, and that 3) a telemetry study on Lowland Tiny Greenbul should be carry out to determine its seasonal movements to confirm whether it is sedentary within forests or it swaps between forests and matrices.

Acknowledgments

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Appendix 1.1*: a priori* models for determining occupancy (ψ), and detection probabilities (p) of the two species: See Table 1.1 on description of abbreviations.

Model/Species	No.par.	Description
Yellow-bellied Greenbul		
ψ (.),p(.)	2	Both occupancy and detection probability are constant
ψ (NDF),*p(Survey)*	4	Occupancy influenced by non-disturbed forest, detection probability influenced by survey season
ψ (LDF),*p(Survey)*	4	Occupancy influenced by lightly disturbed forest, detection probability influenced by survey season
ψ (DF),*p(Survey)*	4	Occupancy influenced by disturbed forest, detection probability influenced by survey season
ψ (HDF),*p(Survey)*	4	Occupancy influenced by heavily disturbed forest, detection probability influenced by survey season
ψ (NDF),*p*(NDF)	5	Both occupancy & detection influenced by non-disturbed forest
ψ (LDF),*p*(LDF)	5	Both occupancy & detection influenced by lightly disturbed forest
ψ (DF),*p*(DF)	5	Both occupancy & detection influenced by disturbed forest
ψ (HDF),*p*(HDF)	5	Both occupancy & detection influenced by heavily disturbed forest
ψ (UNS),*p(Survey)*	4	Occupancy influenced by undisturbed savannah, detection probability influenced by survey season
ψ (LDS),*p(Survey)*	4	Occupancy influenced by lightly disturbed savannah, detection probability influenced by survey season
ψ (HDW),*p(Survey)*	4	Occupancy influenced by heavily disturbed savannah, detection probability influenced by survey season
ψ (UNS),*p*(UNS)	5	Both occupancy & detection influenced by undisturbed savannah
ψ (LDS),*p*(LDS)	5	Both occupancy & detection influenced by lightly disturbed savannah
ψ (HDW),*p*(HDW)	5	Both occupancy & detection influenced by heavily disturbed savannah
Tiny Greenbul		
ψ (.),p(.)	2	Both occupancy and detection probability are constant
ψ (NDF),*p(Survey)*	4	Occupancy influenced by non-disturbed forest, detection probability influenced by survey season
ψ (LDF),*p(Survey)*	4	Occupancy influenced by lightly disturbed forest, detection probability influenced by survey season
ψ (DF),*p(Survey)*	4	Occupancy influenced by disturbed forest, detection probability influenced by survey season
ψ (HDF),*p(Survey)*	4	Occupancy influenced by heavily disturbed forest, detection probability influenced by survey season
ψ (NDF),*p*(NDF)	5	Both occupancy & detection influenced by non-disturbed forest
ψ (LDF),*p*(LDF)	5	Both occupancy & detection influenced by lightly disturbed forest
ψ (DF),*p*(DF)	5	Both occupancy & detection influenced by disturbed forest
ψ (HDF),*p*(HDF)	5	Both occupancy & detection influenced by heavily disturbed forest

2.2 MANUSCRIPT TWO

Plate 2.2: The view of Gendagenda forest

Contrasting preference of vegetation structures in two sympatric greenbul birds differing in distributional range within the East Africa coastal forests

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ABSTRACT

Structure of vegetation hold significant implications in birds' welfare particularly in forest specialist species. For species occupying fragmented forests, investigation in their relation with vegetation of varied structural formation is worth undertaking. Here vegetation features separating habitat requirements of two sympatric bird species (generalist and specialist) were modelled using multiple regression analysis. The results showed that the two species portrayed strong contrast in their preference of vegetation parameters modelled, whereby most of parameters determined decrease in abundance of the forest generalist species while the opposite was true for the forest specialist species. Three vegetation parameters namely, trees >10 m high branching above half their heights, trees between 6 & 10 m high, and canopy cover were the most important parameters in influencing the two species though differently. Thus, practices that tend to modify vegetation structure in the study area by reducing canopy cover for instance, negatively affect the forest specialist with parallel positive or no effect on the forest generalist species. It is thus insisted that ongoing habitat alteration in the study area including tree cutting is placing forest specialist birds on risk of population instability with possibility of driving them to local extinction. Therefore, it is recommended that efforts be directed towards safeguarding vegetation in their natural states for the welfare of forest specialist birds and the biodiversity in general.

Key words: Akaike Information Criterion, forest birds, forest specialist and generalist birds, habitat disturbance, vegetation cover.

INTRODUCTION

A range of environmental factors such as topography, climatic condition, and vegetation formation play a fundamental role in influencing distribution, densities and dynamics of wildlife, including birds (Reese *et al.* 2005). For forest birds, structure of vegetation such as canopy cover, heights and stem number per unit area are key drivers in influencing their habitat preference and determining their abundance and foraging behaviour (cf. Watson *et al.* 2004). The effect can either be direct, for example, when structures of vegetation influence their choice on foraging grounds, such as in canopy feeder species, or indirect through shaping cover and other resources such as abundance of insects that form their diet (Ferger *et al.* 2014). On the other hand, some birds lack a 'bird's-eye view' of the landscape that is important in guiding movements in many bird species, and instead they mainly rely on vegetation structures when assessing movement routes, for instance on crossing forest gaps (Gillies & St. Clair 2008; Betts et al. 2014). In this regard, the structure of vegetation hold significant implications in birds' wellbeing, particularly in forest specialist species (Owino *et al.* 2008, Rakotoarisoa & Capparella 2013). For sustained support therefore, qualities of vegetation in providing the abovementioned services is crucial (Mortelliti 2010).

The East Africa coastal forests are among the world's biodiversity hotspot and globally recognized for their importance in supporting large numbers of species (Burgess & Clarke 2000; BirdLife International 2014). For example, while most of the forests in this hotspot are typically patchy and scattered, they host about 633 bird species of which at least 11 are endemic (Azeria *et al.* 2007; Conservation

International 2008). However, these forests have historically been subject of modification following deleterious human pressure including tree cutting and clearing for agriculture (Burgess & Clarke 2000, Ahrends *et al.* 2010, WWF 2014). As a consequence, there has been shrinkage and decrease in quality of forest patches and landscapes surrounding these patches with utmost change in vegetation structure (Azeria *et al.* 2007). The changes, for example, reduction in canopy cover and tree density is probably impacting birds negatively and there is a possibility of driving some to local extinction (Burgess & Clarke 2000, Sekercioglu 2002, Otieno et al. 2011, BirdLife International, 2014).

Because of their habitat specialization some greenbuls in East Africa coastal forests occur in patchy distributions and are sensitive to habitat disturbance (Fanshawe & Bennun 1991, Cordeiro & Githiru 2000). For some species such as Lowland Tiny Greenbul, habitat specialization make them fall victims of nature and state of their host habitat as their wellbeing largely depend on status of habitat and local conditions (Ewers & Didham 2006, Devictor et al. 2008). Moreover, their strict association with severely degraded habitat such as in East Africa coastal forests increase their chance of facing challenges in resource partitioning particularly at microhabitat level (cf. Gordon 2000, Herrera et al. 2003), and probably this affects their fitness and persistence (see for example Gordon 2000). Based on this background, habitat use of two closely related and sympatric bird species was modelled using a set of structural vegetation parameters to elucidate differences in their fine scale habitat requirements within a human influenced landscape in East Africa coastal forests. One of the species was Lowland Tiny Greenbul which is a forest specialist, with patchy distribution and mainly restricted to well developed and forested habitat. The other species was Yellow-bellied Greenbul, which is capable of utilizing forested habitat, but largely preferring forest edge and disturbed woodlands (del Hoyo *et al.* 2005, Borghesio 2008). The main aim was to answer this question; "at what level of vegetation features do microhabitat requirements of the two sympatric greenbuls differs?" The fact that the two species can coexist particularly within forest edges and within well-developed savannahs and woodlands, investigation in vegetation structure separating their habitat requirements within fragmented forests is worth undertaking. This can help in setting priority in management and conservation of these two closely related sympatric birds. The hypothesis tested stated that, while the vertical vegetation structures showing primary undisturbed conditions would positively influence the Lowland Tiny Greenbul, the Yellow-bellied Greenbul would be influenced negatively.

MATERIAL AND METHODS

Study area and study species

The study area was the Saadani National Park (SANAPA) and neighbouring landscapes (Fig. 2.4). The geographic location of the study area is 6°16'42.94" and 6°16'57.65"S, and 38°32'08.35" and 38°51'17.37"E (Azeria et al. 2007). There are four vegetation complexes in the area; "(i) A heterogeneous forest-savannah-grassland mosaic, (ii) the coastal forests, (iii) a shoreline with salt flats, coastal fringe forests, herbaceous dune vegetation and mangrove forests and, (iv) a maritime ecosystem" (Blösch & Klötzli 2002). The data was however collected from four forests namely; Zaraninge (covering only the plateau segment of the forest), Kwamsisi, Gendagenda, and Msubugwe. In addition, data was collected from the matrices connecting these forests. The coastal forests in this area on the other hand comprises unique vegetation formation with only a few common tree species such as *Adansonia digitata*, *Afzelia quanzensis*, *Pteleopsis myrtifolia*, and *Synaptolepis kirkii* shared with adjourning woodlands and savannahs (Bloesch & Klötzli 2002). Moreover, the forests-savannah/woodland mosaic is largely interspersed along with human modified habitat including settlements, agricultural fields and pastureland (Burgess and Clarke, 2000). The bird species involved under the study were Lowland Tiny Greenbul and Yellow-bellied Greenbul. Further description of the study species as well as information regarding rainfall and biodiversity of the area is given under Modest et al., (2016).

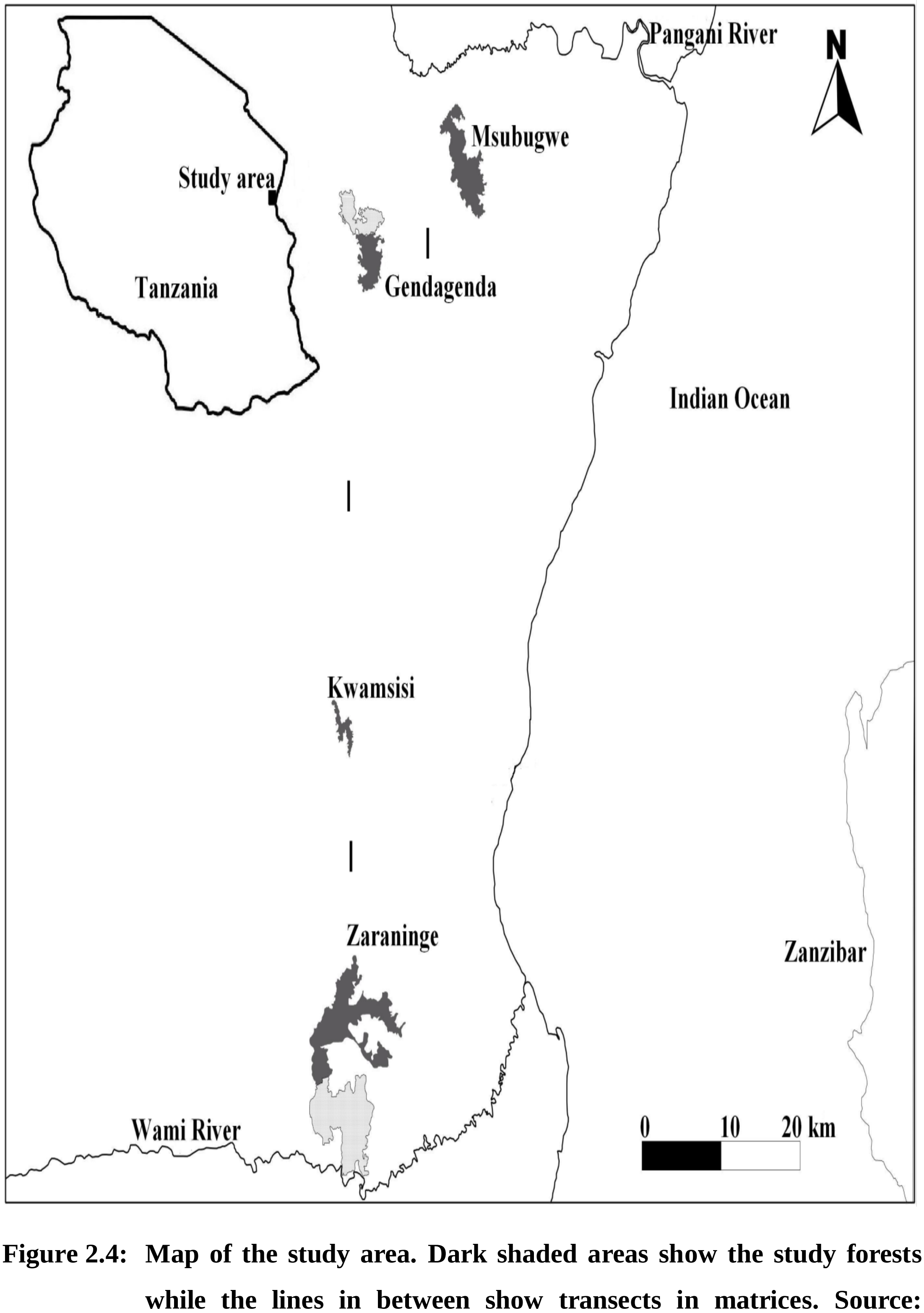

Figure 2.4: Map of the study area. Dark shaded areas show the study forests while the lines in between show transects in matrices. Source: Modest, R.B. (Unpublished PhD thesis, Sokoine University of Agriculture).

Field procedures

Data was collected on a monthly basis from October 2010 to June 2013, and each sampling site was visited 24 times. Bird were recorded along transects using distance sampling protocol as detailed by Modest et al., (2016), whereby a recorder walked along transects and noted birds seen or heard. In addition, GPS coordinates were recorded and a flag was fixed at each bird sighting spot to facilitate identification of the spot when re-visited.

During the second visit of the bird sighting spots, the researcher measured vegetation parameters within 15 m radii circles centred at each spot (Bibby *et al.* 2000, Dallimer & King 2007). To take advantage of early morning and late evening hours when bird activities are high, the vegetation data was either collected on the way back or on the second day after bird survey (Bibby *et al.* 2000). Since studies on species-habitat relationship requires recording parameters based on presence/absence, the spots where the Lowland Tiny Greenbul was encountered alone were considered as spots where Yellow-bellied Greenbul was absent and vice versa (Bibby *et al.* 2000). The parameters described below were recorded from three layers of the vegetation at each bird sighting spots. At the ground layer the following were recorded; percentage vegetation cover between 0 and 0.5 m high, percentage vegetation cover between 0.5 and 2 m high, and percentage vegetation cover between 2 and 6 m high. These parameters were visually estimated (Jennings et al. 1999), and the estimation was achieved within 3 m radii circles (which were then averaged) positioned inside the bigger circles mentioned above. Moreover, in the mid-storey layer, number of trees between 6 and 10 m high as well as number of climbers were counted. Finally, from the upper-storey layer, number of trees >10 m high branching above half their height, and number of trees with dbh between 21 - 30 cm were counted. In the same layer, percentage canopy cover for trees >10 m high was also estimated.

To estimate canopy cover, two lines each 30 m long were established across the centre of the 15 m radii circles mentioned above, and 10 random points were sampled at inter-distances of three (3) m on each line. Quantification of canopy cover was achieved using a crosswire sighting tube constructed from a 1.5 inch PVC (Jennings *et al.* 1999), and the final percent canopy cover was calculated as $C = N_c/N_t$, where, N_c is the number of canopy hit at crosswire, and N_t is the total number of points sampled i.e. 20 points (Jennings *et al.* 1999, Shahabuddin & Kumar 2007). Tree heights on the other hand were recorded using Suunto hypsometer (Božić et al. 2005, Andersen et al. 2006, West 2009), whereas dbh were obtained after converting circumferences measured at breast height (about 1.3 m high) using the formula, i.e. diameter = circumference/π (Thampanya *et al.* 2006, Shahabuddin & Kumar 2007).

Analysis

The data collected during distance sampling as described in the field procedure was coded into presence/absence for regressing against vegetation parameters. Preliminary analysis indicated that parameters were not correlated at Pearson $r \geq 0.7$ (StatSoft, Inc. 2014). Then multiple regression analysis was performed using package glmulti in R (Calcagno 2012) to build candidate sets of models. Regression was on bird indices of abundance (presence/absence), referred to as "bird abundance" in this paper against vegetation parameters. Secondly, the second order Akaike

Information Criterion AIC_c was used to rank and determine competing models based on their Akaike values and weights. Upon ranking, a model having smallest AIC value, but with bigger Akaike weight was selected as the best one (Burnham & Anderson 2002). Then package visreg: visualization of regression models (Breheny & Burchett 2012) was used to plot graphs for the parameters displayed in best models for visualizing trend on response of bird abundance against vegetation parameters. Since information theoretical approach yields a set of competing models, all candidate models having Akaike values of ≤ 2 were averaged and inferenced using package MuMIn: (Multi-model inference) of *R* program version 2.15.1 (Barton 2012, R Core Team 2012). Model averaging yielded averaged coefficients and importance values explaining probability influence of each individual parameters on bird abundance (Burnham & Anderson 2002). On the other hand, to account for the uncertainty associated with parameter estimate as well as to evaluate statistical significance of each parameter, 95 % confidence intervals were also calculated (Burnham & Anderson 2002). Finally, descriptive statistics was carried out for characterizing parameters displayed in best models and to deduce differences in bird counts among study sites (StatSoft, Inc. 2014).

RESULTS

A total of 1,088 individual birds were recorded during the entire study period including 642 Lowland Tiny Greenbul and 446 Yellow-bellied Greenbul. For the Akaike Information Criterion analysis, Yellow-bellied Greenbul had six models supported by the data within delta Akaike of ≤ 2 (Table 2.1). The best model for this species explained 29.7% influence on bird abundance, whereby the second best model explained 18.4% followed by gradual fall for the rest of the models. Akaike values suggested that the best model was 1.61 times likely to support abundance of the species than the second best model. However, the amount of variation shown among candidate models was low (r^2 from 0.172 – 0.181) signifying that the models cannot solely influence the species abundance (Table 2.1). On the other hand, only three models were supported by the data within delta Akaike of ≤ 2 for the Lowland Tiny Greenbul (Table 2.1). The best model for this species explained 49.9 % influence on abundance whereas the second best model had a 30.6% influence. Based on Akaike values, the best model was 1.63 times likely to support the species abundance than the second best model. As for the Yellow-bellied Greenbul, the amount of variation explained by the competing models was low (r^2 from 0.362 – 0.368), also implying that the models cannot solely explain abundance of this species (Table 2.1).

Table 2.1: Multi-model inference based of vegetation parameters against bird abundance: Models are arranged based on Akaike weights with best models at the top of the list for each species. df = degree of freedom, logLik = log likelihood, AICc = Akaike's Information Criterion, delta = difference between maximum and minimum Akaike values of competing models, ωi = Akaike weight, r^2 = r square.

Species / Model	r^2	df	logLik	AICc	delta	ωi
Yellow-bellied Greenbul						
No. of climbers + Percent canopy cover + No. of trees >10 m high branching above half their height + No. of trees between 6 & 10 m high	0.1795	6	-593.64	1199.5	0.00	0.297
No. of climbers + No. of trees with dbh between 21 & 30 cm + Percent canopy cover + No. of trees >10 m high branching above half their height + No. of trees between 6 & 10 m high	0.1819	7	-593.08	1200.5	0.95	0.184
No. of climbers + Percent canopy cover + No. of trees >10 m high branching above half their height	0.1725	5	-595.27	1200.7	1.20	0.163
No. of climbers + No. of trees with dbh between 21 & 30 cm + Percent canopy cover + No. of trees between 6 & 10 m high	0.1758	6	-594.49	1201.2	1.70	0.127
No. of climbers + Percent canopy cover + Percentage vegetation cover between 2 & 6 m high + No. trees >10 m high branching above half their heights + No. of trees between 6 & 10 m high	0.1800	7	-593.52	1201.3	1.84	0.118
No. of climbers + No. of trees with dbh between 21 and 30 cm + Percent canopy cover + No. of trees >10 m high branching above half their heights	0.1752	6	-594.63	1201.5	1.98	0.111
Tiny Greenbul						
No. of trees with dbh between 21 & 30 cm + Percent canopy cover + Percentage vegetation cover between 2 & 6 m high + No. of trees >10 m high branching above half their heights + No. of trees between 6 & 10 m high	0.3672	7	-798.92	1612.1	0.00	0.499
No. of trees with dbh between 21 & 30 cm + Percent canopy cover + Percentage vegetation cover between 2 & 6 m high + No. of trees >10 m high branching above half their heights	0.3622	6	-800.45	1613.1	0.98	0.306
No. of climbers + No. of trees with dbh between 21 & 30 cm + Percent canopy cover + Percentage vegetation cover between 2 & 6 m high + No. of trees >10 m high branching above half their height + No. of trees between 6 & 10 m high	0.3676	8	-798.82	1614	1.89	0.194

Table 2.2 shows averaged coefficients for the vegetation parameters regressed. Percentage canopy cover was the most important parameter in explaining decline in Yellow-bellied Greenbul abundance, whereby this parameter had an important value of one (1). On the other hand, trees >10 m high branching above half their heights, together with trees with dbh between 21 & 30 cm were, in addition to percent canopy cover the most important parameters in explaining increase in abundance of Lowland Tiny Greenbul, each having an important value of one (1).

Table 2.2: Multi model-averaged coefficients explaining association between various vegetation parameters and abundance of the study species: Estim. = coefficients estimates, St.Er = standard error, Adj.SE = adjusted standard error, p = p-value, LCI = lower confidence interval, UCI = upper confidence interval, IV = Importance Value.

Species/Parameter	Estim.	St. Er.	Ad.SE	p	LCI	UCI	IV
Yellow Bellied Greenbul							
(Intercept)	1.818	0.151	0.151	0.000	1.521	2.115	
Percent canopy cover	-0.012	0.002	0.002	0.000	-0.017	-0.006	1.00
No. of climbers	-0.033	0.013	0.013	0.013	-0.060	-0.007	0.93
No. of trees >10 m high branching above half their heights	-0.061	0.032	0.032	0.061	-0.124	0.003	0.69
No. of trees between 6 & 10 m high	0.026	0.014	0.014	0.076	-0.003	0.054	0.65
No. of trees with dbh between 21 & 30 cm	-0.054	0.043	0.043	0.210	-0.139	0.031	0.45
Percentage vegetation cover between 2 & 6 m high	0.001	0.003	0.003	0.681	-0.005	0.008	0.26
Percentage vegetation cover between 0.5 & 2 m	-0.001	0.003	0.003	0.826	-0.006	0.005	0.25
Tiny Greenbul							
(Intercept)	-0.275	0.325	0.325	0.397	-0.913	0.362	
No. of trees with dbh between 21 & 30 cm	0.233	0.073	0.073	0.001	0.089	0.377	1.00
Percent canopy cover	0.026	0.004	0.004	0.000	0.018	0.034	1.00
No. of trees >10 m high branching above half their heights	0.222	0.056	0.056	0.000	0.112	0.331	1.00
Percentage vegetation cover between 2 & 6 m high	0.012	0.005	0.005	0.031	0.001	0.022	0.82
No. of trees between 6 & 10 m high	-0.043	0.025	0.025	0.079	-0.092	0.005	0.64
Percentage vegetation cover between 0.5 & 2 m high	0.002	0.006	0.005	0.759	-0.009	0.012	0.28
No. of climbers	0.011	0.024	0.024	0.634	-0.035	0.058	0.26

Figure 2.5 presents pattern of association between bird abundance and each of the three parameters that were shared among best models of the two species. Though in opposite trend, the association between bird abundance and vegetation parameters looked stronger for Lowland Tiny Greenbul compared to Yellow-belied Greenbul.

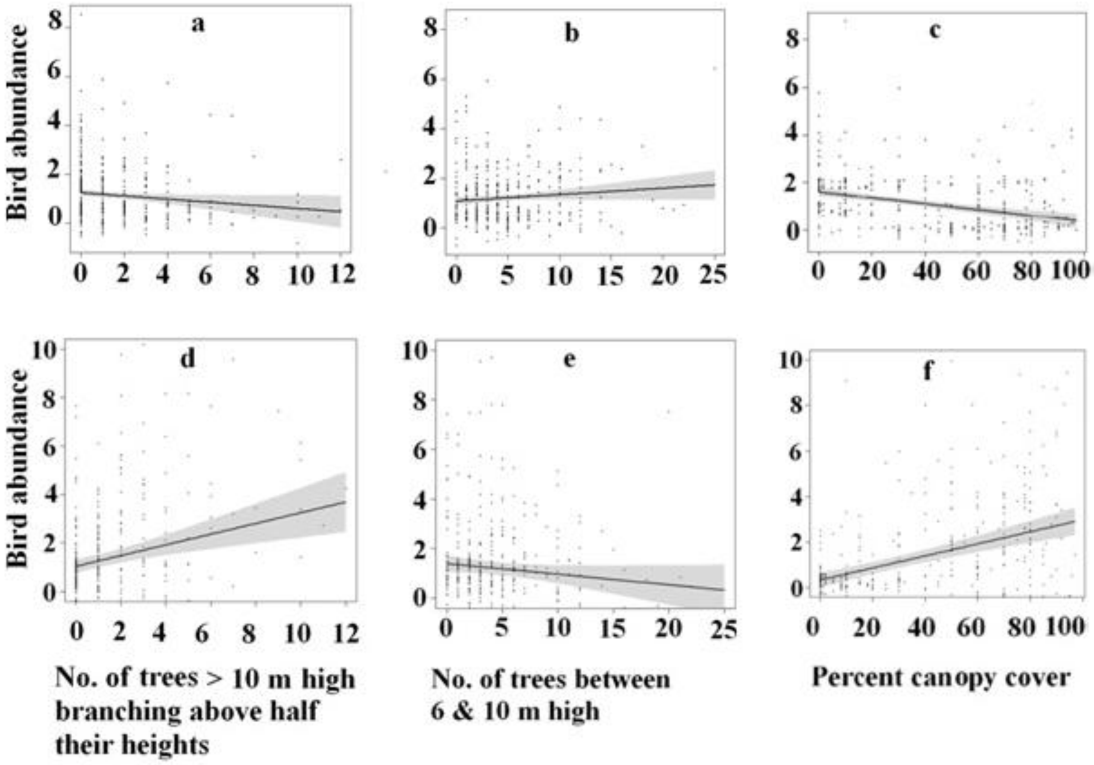

Figure 2.5: Response of bird abundance in relation to vegetation parameters shared in best models of the study species: Yellow-bellied Greenbul (a - c), and Lowland Tiny Greenbul (d – f).

Since vegetation parameters were measured at spots where either of the species was present or absent respectively, results showed that mean values of parameters displayed in best model was higher at spots where Lowland Tiny Greenbul was present but Yellow-bellied Greenbul absent, $p < 0.05$, except for the parameter "trees between 6 and 10 m high" which did not differ significantly for both species $p > 0.05$ (Table 2.3).

Table 2.3: Descriptive statistics and two sample t-test for comparing between means of vegetation parameters displayed in best models at present/absent locations in each species. *Abbreviations*: t = values of t in a two sample t-test, df = degree of freedom.

Species/Parameter	Species present			Species absent			Significance of Mean Differences		
	Min	**Max**	**Mean**	**Min**	**Max**	**Mean**	**t**	**df**	**p-value**
Yellow Bellied Greenbul									
Percent canopy cover	0	95	23.8	0	97	61.3	13.45	381	<0.001
No. of trees >10 m high branching above half their heights	0	12	0.8	0	12	2.5	7.10	380	<0.001
No. of climbers	0	10	4.9	0	10	6.4	3.26	381	0.0012
No. of trees between 6 &10 m high	0	25	4.5	0	20	4.3	-0.47	381	0.638
Tiny Greenbul									
No. of trees with dbh between 21 & 30 cm	0	09	2.0	0	07	0.6	-8.63	381	<0.001
Percent canopy cover	0	97	60.1	0	95	21.6	-14.35	381	<0.001
Percentage cover of vegetation between 2 & 6 m high	0	85	49.1	0	95	40.1	-4.42	381	<0.001
No. of trees >10 m high branching above half their heights	0	12	2.4	0	12	0.7	-8.32	380	<0.001
No. of trees between 6 &10 m high	0	20	4.3	0	25	4.4	0.26	381	0.793

DISCUSSION

The total number of individuals recorded for the Lowland Tiny Greenbul i.e. 642 birds was relatively higher compared to that of Yellow-bellied Greenbul i.e. 446 individuals. The observed higher number of Lowland Tiny Greenbul over that of Yellow-bellied Greenbul could be due to the fact that Yellow-bellied Greenbul mainly occurs as singles or pairs while Lowland Tiny Greenbul tends to occur in groups and therefore easy to spot. In addition, Lowland Tiny Greenbul tends to occur in mixed-species flocks, which facilitates spotting especially while flocking with noisy species such as Dark-backed Weaver or Square-tailed Drongo (Stevenson & Fanshawe 2002).

The statistical analyses and modelling results showed that the two species portray strong contrast in their preference of vegetation parameters modelled, with most of parameters determining decrease in abundance of the forest generalist species, Yellow-bellied Greenbul while the opposite being true for the forest specialist species, Lowland Tiny Greenbul. It is important to note that, for the parameters shared in best models of the two species (Fig. 2.5), the positive response of Lowland Tiny Greenbul, at the same time the negative response of Yellow-Bellied Greenbul with trees > 10 m high branching above half their heights could be revealing differences in capabilities of the two species in utilizing habitat of varied qualities. Presence of trees branching above half their own height in forested habitat is indicator that such forests or at least that particular sampled spot is in its primary state (Bibby *et al.* 2000, Cleary & Mooers 2006, Gillies & St. Clair 2009). Thus, despite the fact that habitat in the study area have been degraded to unprecedented state, the observed positive association between Lowland Tiny Greenbul’s abundance with trees > 10 m high branching above half their heights reveals that this species being a forest specialist is biased in the way it selects habitat, mainly preferring sites that maintain their original primary conditions (Bennun & Pomeroy 1996, Gillies & St. Clair 2009). On the other hand, for the Yellow-bellied Greenbul, the negative association with trees > 10 m high branching above half their heights, again the negative association with closed canopy cover, in addition to its positive association with midsized trees "trees between six & 10 m high" is an indication that this species selects edge and open habitat in matrices. This is because in natural and closed canopy forests trees with intermediate heights are fewer following competition for light were most of trees tend to grow taller for reaching up solar radiation (Bibby 2000, Sheil *et al.* 2006, Coomes & Allen 2007). The opposite trend however applies to Lowland Tiny Greenbul with respect to its reaction on edge and open habitat.

Indeed, given the current state of forest degradation in the coastal forests of north-eastern Tanzania (Hassan *et al.* 2013, Birdlife International 2014), the present findings shed light on uncertainties regarding the future of the forest specialist species Lowland Tiny Greenbul in the study area. It is hereby presumed that continued degradation of the environment leading to accelerated loss of primary habitat in the study area based on practices such as tree cutting and clearing for agriculture could deliver the species to difficulty situations including possible local extinction in the near future. Similar consequences have been reported elsewhere in Vikindu forest in the neighbourhood south of Zaraninge forest, whereby selective logging led to local extinction of Sokoke pipit (BirdLife International 2014). The Sokoke pipit which in its general habitat needs is comparable to Lowland Tiny Greenbul (Musila *et al.* 2001, del Hoyo *et al.* 2005) is an endemic and forest specialist bird preferring open understory habitat with deep litters, and it is restricted within East Africa coastal forests (Musila *et al.* 2001, Owino *et al.* 2008, Otieno *et al.* 2013). For the Yellow-bellied Greenbul however, habitat destruction seems not to be a serious problem as the species has even been documented to raise its young from a potted plant under the house terrace (Geyser 2013).

In conclusion, the analysis suggests a high contrast on preference of vertical vegetation structures between the two greenbuls. Accordingly, practices that tend to reduce canopy cover including tree cutting or clearing for agriculture negatively affects Lowland Tiny Greenbul (a forest specialist), with parallel positive or no effects on a forest generalist Yellow-bellied Greenbul (Neuschulz *et al.* 2011). Moreover, it is imperative to emphasize the importance of maintaining quantity of available habitat for the forest specialist. This is because the analysis showed that, parameters recorded from sites where Lowland Tiny Greenbul (a forest specialist) was present but Yellow-bellied Greenbul (a forests generalist) missing always carried higher mean values (Table 2.3). The field experience also supports this as Lowland Tiny Greenbul was not recorded in the matrix connecting Gendagenda and Msubugwe forests, an area that have been heavily degraded by grazing livestock. The reason for missing the species in this matrix could be due to vegetation alteration, as this matrix which was once savannah is currently facing intensive grazing by livestock with major transformation of its vegetation into acacia woodlands. Therefore, this give implication that management options towards improving habitat for forest specialist birds in the study system should aim at improving both quality and quantity of available habitat especially when considering vegetation rehabilitation (Hobbs and Hanley 1990, Walters *et al.* 2002). Moreover, the management option employing necessary efforts at ceasing canopy cover reduction from the study area (especially within forests) by controlling such deleterious human pressure including tree cutting is recommended as this would positively support Lowland Tiny Greenbul though with negative implication for the Yellow-bellied Greenbul populations. However, this option would likely restore un-replaceable habitat for the forest specialist species while a forest generalist would have a chance to expand its habitat range e.g. by moving to edges or more open habitat in matrices (Duraes et al. 2013, Estavillo et al. 2013).

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2.3 MANUSCRIPT THREE

Genetic diversity and gene flow in a forest dependant bird species in fragmented lowland coastal forests, north eastern Tanzania

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Abstract

Genetic diversity is lost faster in isolated and small populations compared to populations in contiguous habitat. For example, reducing forest size and increasing among fragment distances negatively impend natural processes and genetic makeup of individuals through reducing within fragments population size or restricting gene flow. However, in flying organisms such as birds the gene flow is believed to restrict differentiation among isolated but closer subpopulations so that prolonged isolation or odd migration barriers become prerequisite for population differentiation to effect. This study therefore investigated gene flow and genetic diversity in a forest specialist bird species to determine effect of fragmentation on subdivided populations. DNA was extracted using Invitrogen kit, and a total of seven Microsatellite Markers were applied during PCR amplification. The PCR products fragment sizing was carried out on an ABI PRISM DNA Analyser. Results showed that, there was weak among population genetic differentiation with most of differences accounted for within individuals. Moreover, despite being a forest specialist, the study species seemed to tolerate habitat alteration as it appeared that it is able to disperse amongst fragmented populations following the maintenance of gene flow. Cutting trees within gullies is discouraged so as to maintain primary condition of these environments since they act as dispersal corridors for forest specialist birds.

Key words: AMOVA . forest specialist and generalist . genetic structure . population differentiation. Saadani.

Introduction

Fragmentation of wildlife habitat can either be innate, where patches of similar types are naturally implanted in matrices of other habitat types (Watson 2002; Wilson *et al.* 2009), or human induced, where anthropogenic deleterious pressures reduces size and increases isolation of patches (Fahrig 2001; Fahrig 2003; Watson *et al.* 2004). Certainly, both types of fragmentation have equal chance of exposing wildlife populations to disastrous environmental processes such as climate change, thereby increasing likelihood of driving them to risks of extinction (Frankham 2005). This is because as population size is reduced and patch isolation is increased for example, there is a risk of within population increased inbreeding and genetic drift leading to loss of gene diversity which reduces individual fitness (Frankham *et al.* 2002). Since genetic diversity is lost faster in isolated and small populations compared to populations in contiguous habitat, for the specialist species with limited capability in penetrating non-natural habitat for dispersal, fragmentation affects them the most (Davies *et al.* 2004). Investigating genetic structure of forest dependent birds whose populations are affected by habitat fragmentation such as those in the coastal forests of east Africa is thus crucial in order to plan for necessary management options.

On its wholly, the coastal forests landscape in East Africa is believed to have had been separated from the Guineo-Congolian forests in west Africa by the upwelling of central Tanganyika plateau about 35 million years ago (Dicknson *et al.* 1992). Moreover, there were some periods of reconnection until complete disjunction about 3 million years ago. It is further said that recurrent anthropogenic fires dating back as far as about 50,000 B.C. separated evergreen coastal forest patches from surrounding matrices restricting them to fire proof sites in moister areas including on hill tops, riverines and ground water areas (Dicknson *et al.* 1992). Indeed, after all these historical pressures, the coastal forests in east Africa continued to face suppression from human deleterious effects including forest clearing for subsistence agriculture, human settlements and extensive livestock grazing, resulting in reducing their sizes and increasing among fragments distances (Burgess, *et al.* 1992, Bloesch and Klötzli 2002; WWF 2014).

Reducing forest size and increasing among fragment distances as pointed out earlier, can negatively impend natural processes and genetic makeup of individuals due to increased inbreeding (Andersen and Damgaard 2004; Fahrig 2003), gene erosion and/or reduced resistance to stochastic events (Allentoft and O'Brien 2010). However, other hypotheses exist on explaining genetic processes in wildlife populations within fragmented habitat. For example, it is proclaimed that, species with small patched populations but occurring in naturally fragmented landscape upon suffering additional fragmentation can portray a delay in loss of their genetic diversity compared to those species originating from contiguous large habitat (Richmond, 2009). Furthermore, it is said that populations in larger unbroken landscapes depicting genetic equilibrium are expected to comply with isolation by distance theory such that as distance among subpopulations increases there occurs some population differentiation as well (Slatkin 1993). These hypotheses however are invalidated when populations face severe habitat fragmentation such that gene flow is severed even at shorter distances (Gerlach and Musolf, 2000). However, in airborne organisms such as birds the gene flow is believed to restrict differentiation among isolated but closer subpopulations so that prolonged isolation or odd migration barriers become prerequisite for population differentiation to effect (Price, 2010). Therefore this study was designed to investigate whether populations of a forest dependant bird species that have suffered from both natural and human induced fragmentation do maintain gene flow and genetic diversity among fragments. The model bird used under the current study was Lowland Tiny Greenbul, a forest dependant bird mainly restricted to well developed and forested habitat and believed to be sedentary (del Hoyo *et al.* 2005; Fishpool and Tobias, 2005). Sedentary organisms or those species with shorter migratory expanse are believed to differentiate at shorter geographic scale unlike those species capable of roaming longer distances (Kisel and Barraclough 2010). Therefore, the Lowland Tiny Greenbul, a small, common species, and non-efficient disperser was a good candidate for this study. In addition, its presence within the lowland East Africa coastal forests, where habitat fragmentations has caused isolation of many forests into tiny patches, makes it a good candidate to answer the study question. The aim was to identify patterns of gene diversity and genetic differentiation among subpopulations of the species in question. The research hypothesis stated that, gene diversity and gene flow of the study species would be higher in larger and closer than in smaller and distant forest patches. The results are expected to save as a guiding tool in planning necessary management options, such as setting priority in protection of highly-threatened species.

Materials and Methods

Study Site and Study Species

The study was carried out in the coastal forests of north eastern Tanzania. The area is dominated mainly by woodlands and savannas. However, Bloesch and Klötzli (2004) defined six types of coastal forests in the ecosystem namely: small hilltop forests; Gully forests; Thicket clumps; Gallery forests; Groundwater forests; and large hilltop forests. The forest patches within this landscape are of varied sizes, and their qualities together with that of matrices vary in level of habitat degradation (Hassan et al. 2013; R. B. Modest, unpublished data), Table 3.1. However, under this study, the data was gathered from four dry evergreen coastal forests namely Zaraninge, Kwamsisi, Gendagenda and Msubugwe (Fig. 3.1). Further description of the study area including rainfall and biodiversity data is given in Modest *et al.,* 2016. The same study also provide description of the study species.

Table 3.1: Description of habitat types sampled: No sampling was done in the matrices but they are described here due to their importance in connecting the study forests. Classification of habitat types based on literature review and the researcher's experience with the study area.

Site	Habitat type	Area	Status
Zaraninge (Plateau only)	Large hilltop forest	42.7 km^2	Intact forest with less human influence.
Kwamsisi	Hilltop forest	4.06 km^2	Obviously disturbed forest with moderate human influence resulting from small scale tree felling for timber.
Gendagenda	Hilltop forest	10.97 km^2	Less disturbed forest with mild human influence that result from collection of firewood and cutting of small poles for house construction.
Msubugwe	Groundwater forest	22.32 km^2	Severely disturbed forest facing large scale tree felling for timber using chainsaw.
Zaraninge/ Kwamsisi matrix	Savannah	NA	Intact savannah vegetation without outside pressure from grazing livestock.
Kwamsisi/ Gendagenda matrix	Savannah	NA	Less disturbed savannah vegetation with mild pressure from intruding grazing livestock.
Gendagenda/ Msubugwe matrix	Bushed-acacia woodland	NA	Severely degraded savannah with subsequent conversion into acacia-woodlands following pressures from grazing livestock, settlements and clearing for agriculture.

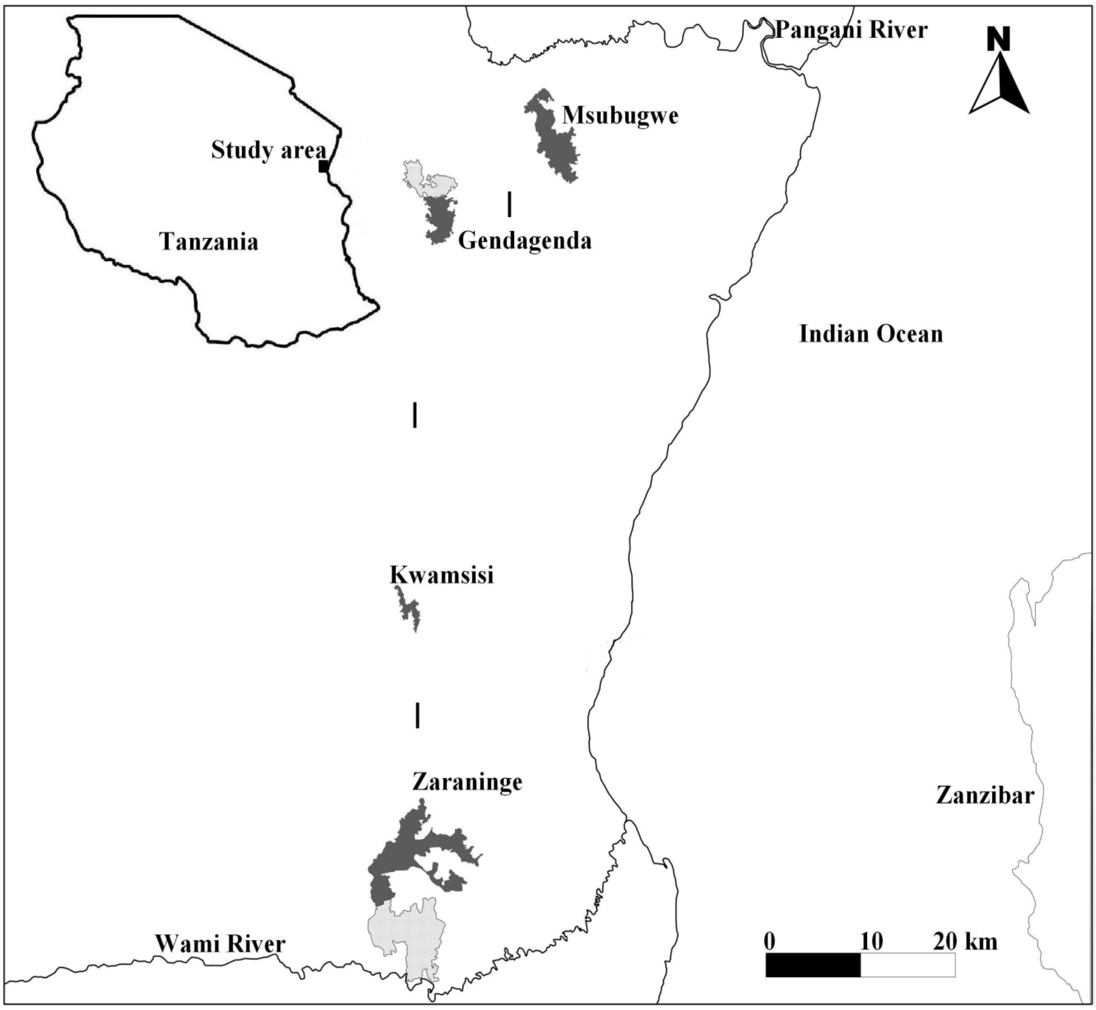

Figure 3.1: Map of the study area: Dark areas indicate study forests. Source: Modest, R.B. (Unpublished PhD thesis, Sokoine University of Agriculture).

Field Sampling Procedure, DNA Extraction and Genotyping

Between October 2010 and June 2013 birds were trapped using mist nets for collecting blood samples. Despite rigorous efforts employed in trapping birds, with trapping activities spanning over 70 weeks, only 59 birds were trapped from four forest fragments namely; Zaraninge (26), Gendagenda (14), Msubugwe (12), and Kwamsisi (7). There was difficulties in bird capture within Gendagenda, Msubugwe and Kwamsisi forests, and this is attributed to habitat disturbances (Hassan et al. 2013; R. B. Modest, unpublished). Blood was collected from brachial vein using a fine needle syringe and preserved in a 1.5 mL tubes containing 95% ethanol (Galbusera *et al.* 2004). All trapped birds were ringed and released at the same trapping spot. Upon collection, samples were temporary handled in a fridge before being transferred to minus 18°C for longer storage. DNA was extracted using Invitrogen kit according to the manufacture's protocol (lifetechnologies.com). Purity and quality of the extracted DNA was analysed by running on 0.8% agarose gel. PCR amplifications were conducted under the following conditions; 5 min at 95°C followed by 30 cycles for 30 sec at 94°C, 90 sec at 57°C, 90 sec at 72°C, and a final extension step for 20 min at 72°C. PCR amplification was attained in a 12.5 µl reaction volume containing 5ųl Accupower PCR Premix (*BIONEER*, *DAEJEON*, *KOREA*), 1 ųl template DNA (10ng), 3 ųl of RNA free water, and 0.5 ųl of 10ųM (forward and reverse) of seven fluorescently labelled highly volatile Microsatellite Markers. Markers and products range are shown in appendix 3.1. PCR product fragment analysis was carried out on an ABI PRISM Applied Biosystems 3730XL DNA Analyser with GeneScan-500LIZ_3730 size standards. Genotyping was achieved using GENEMAPPER ver. 4.0 and Peak Scanner ver. 2.0 software (Applied Biosystems).

Population Characteristics and Gene Diversity

Presence of genotyping errors due to null alleles, allele dropout, scoring and typographic errors was checked using MICRO CHECKER software (Glaubitz 2004). Loci across the four populations were tested to check whether they were under Hardy-Weinberg Equilibrium by comparing observed and expected levels of heterozygosity using exact test in ARLEQUIN software ver. 3.0. The Markov chain was set at 1000000 and number of dememorization steps set at 100000 (Excoffier and Lischer 2010). Since testing for Hardy-Weinberg Equilibrium was done on seven loci, the Bonferroni correction approach was used for testing multiple hypotheses. Allelic richness and inbreeding coefficient were estimated using FSTAT software ver. 2.9.3.2 (Goudet 2001). The linkage disequilibrium was tested in ARLEQUIN software ver. 3.0 (Excoffier and Lischer 2010).

Testing for Departure from Mutation Drift - Equilibrium, Genetic Differentiation and Gene Flow

Structure Program ver 2.3.4 was used to detect if there are any genetic structures in the data by inferring possible number of clusters into which individuals can be referred to their population of origin (Pritchard et al. 2000). STRUCTURE probabilistically assigns individuals into genetic clusters (k) depending on their multi-locus genotypes that minimize within clusters deviation from Hardy–Weinberg equilibrium and linkage disequilibrium. The burn in was set at 500000, while the

MCMC was set at 2500000 under correlated allele frequency model. Moreover, k (number of clusters) was set as being from 2 - 7 and performed 20 iterations. Determining the maximum k was achieved by adding the number of sampling locations (i.e. four locations) plus three (3) — which is a constant number (Pritchard et al. 2000). LOCPRIOR = 1 was used so that the program uses the sampling information as priori (Pritchard et al. 2000). Then an ad hoc quantity Delta K calculated based on the second order rate of change of the likelihood Delta K was used (Evano et al. 2005) to identify the true value of k (number of clusters) in Structure Harvester (Earl et al. 2012).

Upon confirming existence of genetic structure within the data, hierarchical AMOVA was used, with the number of permutations set at 85,000 to explore genetic differences among the four populations in the study area (Cardoni et al. 2013; Zhang et al. 2013). Two approaches were used, first by treating all populations as a single group (Table 3.3) and, second by considering minimum distance between forests to form groups. The latter resulted into three other groups with the following combination: Msubugwe/Gendagenda, Gendagenda/Kwamsisi and Kwamsisi/Zaraninge (Table 3.4). As a measure of current gene flow, assignment method in GENECLASS ver. 2.0 was used (Paetkau et al. 2004; Piry et al. 2004) to identify first generation migrants within each population under the L_home / L_max Likelihood ratio with Paetkau et al. (1995) criterion, and Paetkau et al. (2004) simulation algorithm. To assess whether populations have departed from genetic equilibrium due to recent reduction in gene flow, the software BOTTLENECK ver. 5.1.26 was used (Cornuet and Luikart 1996) to check whether the number of loci with heterozygote excess is higher than expected by chance under mutation-drift equilibrium. Since mutation drift underlying the study populations was uncertain, two methods were used namely, the Stepwise Mutation Model (SMM) and the Two-phase Model (TPM) (Cornuet and Luikart 1996). As suggested by author 95% of SMM was assumed in TPM and 100000 iterations were performed (Cornuet and Luikart, 1996). Moreover, historic gene flow was calculated from all loci using POPEGENE ver 3.2 (Yeh et al. 1999). Though the sample size and number of loci to test for microsatellite data is species specific and sometimes ad hoc (Hoban *et al.* 2013), generally the sample size and number of loci scored under the current study were low, therefore, gene flow was estimated based on F_{ST} (Gaggiotti et al. 1999). Finally, in order to visualize population resemblances, a Nei's genetic distance matrix was constructed using POPGENE ver. 3.2 (Yeh et al. 1999).

Results

Population Characteristics and Gene Diversity

All loci were polymorphic, and all populations showed similar level of intrapopulation polymorphism with mean allelic richness (A_R) corrected for sample size ranging from 3.18 to 3.54. Inbreeding coefficient F_{IS} did not deviate much from zero indicating that the populations were under random mating with no excess homozygosity or excess heterozygosity (Table 3.2), although two loci deviated from Hardy-Weinberg Equilibrium after Bonferroni correction. No linkage disequilibrium was detected between any pair of loci (all $p > 0.007$ after Bonferroni correction).

Table 3.2: Microsatellite diversity for the four populations sampled: A_R = allelic richness corrected for sample size, F_{IS} = inbreeding coefficient, H_O = observed heterozygosity, H_E = expected heterozygosity, and p = p value after Bonferroni correction.

	Msubugwe n =14					Gendagenda n=12				
Locus	**A_R**	**F_{IS}**	**H_O**	**H_E**	**p**	**A_R**	**F_{IS}**	**H_O**	**H_E**	**p**
Ls1	3.313	-0.138	0.769	0.665	0.112	3.301	-0.165	0.750	0.663	0.063
Mcyų4	3.896	0.100	0.615	0.828	0.038	5.083	0.264	0.700	0.774	0.011
Ls2	1.978	-0.294	0.077	0.212	0.017	1.785	0.647	0.500	0.391	0.076
Pca4	3.464	0.149	0.364	0.571	0.013	3.361	0.375	0.556	0.647	0.053
Pdo40	3.359	0.281	0.692	0.606	0.143	3.909	-0.149	0.455	0.623	0.019
Ase18	4.216	0.273	0.667	0.754	0.043	4.028	0.120	0.545	0.740	0.044
Indigo41	2.000	-0.149	0.462	0.551	0.110	2.384	0.168	0.600	0.526	0.143
Average	**3.180**	**0.063**	**0.520**	**0.600**	**0.070**	**3.410**	**0.134**	**0.590**	**0.620**	**0.060**
	Zaraninge n = 26					**Kwamsisi n = 7**				
Ls1	4.108	-0.125	0.826	0.736	0.053	2.000	-0.500	0.714	0.495	0.063
Mcyų4	4.292	0.168	0.640	0.767	0.001	4.362	0.063	0.714	0.758	0.051
Ls2	1.673	-0.087	0.192	0.177	0.143	2.000	0.143	0.429	0.495	0.143
Pca4	3.011	-0.236	0.652	0.530	0.112	3.363	0.442	0.286	0.495	0.023
Pdo40	3.507	0.177	0.480	0.581	0.003	2.713	-0.364	0.714	0.538	0.143
Ase18	4.811	-0.021	0.800	0.784	0.080	5.000	0.500	0.400	0.756	0.007
Indigo41	3.362	-0.109	0.720	0.651	0.117	4.000	0.515	0.400	0.778	0.026
Average	**3.540**	**-0.021**	**0.620**	**0.600**	**0.070**	**3.350**	**0.169**	**0.520**	**0.620**	**0.070**

Mutation Drift- Equilibrium, Genetic Differentiation and Gene Flow

Among population genetic differentiation was weak when the four populations were combined into a single group, $F_{ST} < 0.05$. However, most of the differentiations were accounted for within individuals (96.37%), while within population differences expressed only 2.8% (Table 3.3).

Table 3.3: AMOVA genetic variance components and hierarchical F statistics for the Lowland Tiny Greenbul (all four populations combined in one group)

Source of variation	Sum of squares	Variance components	Percentage of variation	F statistics
Among populations	1.533	0.00342	0.83	0.00831_{FST}
Among individuals within populations	22.657	0.01151	2.8	0.02820_{FIS}
Within individuals	23	0.39655	96.37	0.03628_{FIT}

When every two adjacent populations were combined to form groups, still there was weak, but noticeable among populations genetic differentiation for the Gendagenda/Kwamsisi and Kwamsisi/Zaraninge groups respectively, all $F_{ST} < 0.05$. As for the single group reported above, most of variations were expressed by within individual differentiations. However, for the Msubugwe/Gendagenda group, the F_{ST} values was negative indicating that among populations differentiation between these two localities was very minimal (Table 3.4).

Table 3.4: AMOVA genetic variance component and hierarchical F statistics for the Lowland Tiny Greenbul (groups were formed based on minimum geographic distance between them).

Group	Source of variation	Sum of squares	Variance components	Percentage variation	F statistics
Msubugwe & Gendagenda	Among populations	1.374	-0.04437	-2.10993	-0.02110_{FST}
	Among individuals within populations	49.729	0.21923	10.42532	0.10210_{FIS}
	Within individuals	45	1.92797	91.68461	0.08315_{FIT}
Gendagenda & Kwamsisi	Among populations	3.066	0.03956	1.83013	0.01830_{FST}
	Among individuals within populations	40.407	0.28893	13.36705	0.13616_{FIS}
	Within individuals	35	1.83301	84.80281	0.1519_{FIT}
Kwamsisi & Zaraninge	Among populations	2.921	0.03678	1.70796	0.01708_{FST}
	Among individuals within populations	61.651	0.01858	0.86274	0.00878_{FIS}
	Within individuals	64.5	2.0983	97.4293	0.02571_{FIT}

Table 3.5 shows Nei's Unbiased Measure of genetic distance. The lowest value was obtained between Gendagenda and Msubugwe implying closer resemblance of these two populations separated by a distance of about 10 km, and this might indicate that these two populations might have a recent common ancestor. On the other hand, the highest Nei’s value was observed between Zaraninge and Msubugwe — the forests which are about 64 km apart. Note: Kwamsisi data was not included in the genetic distance analysis due to small sample size in order to minimize possibility of biased estimates.

Table 3.5: Nei's Unbiased Measure of genetic distance among subpopulations

Population	Msubugwe	Gendagenda	Zaraninge
Msubugwe	-		
Gendagenda	0.01	-	
Zaraninge	0.03	0.02	-

Historic gene flow among subpopulations estimated from all loci was high. The number of migrant per generation between Gendagenda and Zaraninge was 15.52, and that between Zaraninge and Msubugwe was 14.40. Gene flow between Gendagenda and Msubugwe was not calculated because these populations were not genetically different based on F_{ST} values. Note: Kwamsisi data was not included in the analysis of gene flow due to small sample size to minimize possibility of biased estimates.

As a measure of current gene flow, GENECLASS2 identified eight individuals as first generation migrants between subpopulations (Table 3.6). However, GENECLASS2 did not identify any first generation migrant in Zaraninge. It is probably that the power to infer all possible first generation migrants was weak due to small sample size and a few markers used. The current gene flow however was generally lower relative to historic gene flow presented in the above paragraph.

Table 3. 6: Current gene flow estimates of first generation migrants (F_0) among the four populations

Population	No. of first generation migrants	Probable population of origin
Gendagenda	4	Zaraninge (2*), Msubugwe (2*)
Kwamsisi	3	Zaraninge (1*), Msubugwe (1*), Gendagenda (1*)
Msubugwe	1	Gendagenda (1*)
Zaraninge	0	-
Total	**8**	

Number of individuals contributed from each respective population*

Structure Harvester identified three possible genetic clusters modelled under Program Structure algorithm runs. The numbers of genetic clusters from the Structure algorithm runs were identified based on the highest delta k returned by the Structure Harvester software. Optimal clustering for the study populations was obtained at K = 3 (delta k = 0.8), Table 3.7.

Table 3.7: Number of genetic clusters based on Program Structure algorithm runs

K	Reps	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	Delta K
2	20	-989.795	1.1523	-	-	-
3	**20**	**-995.285**	**4.2**	**-5.49**	**3.365**	**0.801184**
4	20	-997.41	5.0232	-2.125	0.455	0.09058
5	20	-999.99	5.2295	-2.58	4.16	0.795493
6	20	-998.41	3.1609	1.58	0.955	0.302126
7	20	-997.785	3.1245	0.625	-	-

There was no evidence of population bottleneck in all subpopulations under mutation drift-equilibrium with Bottleneck analysis, all $p > 0.007$ after Bonferroni correction. In addition, the data fitted equally the two models under SMM and TPM (Table 3.8).

Table 3.8: Levels of excess of heterozygosity in the four sampled populations: Wilcoxon levels of significance for the two mutation models are presented.

Locality	SMM	TPM
Msubugwe	0.46875	0.40625
Gendagenda	0.76563	0.76563
Kwamsisi	0.65625	0.65625
Zaraninge	0.99609	0.99609

Discussion

In spite of differences in habitat quality among forests and different level of deterioration of matrices separating them, the results as revealed by AMOVA $F_{ST,}$ showed low level of population genetic differentiation. Nevertheless, the three clusters identified in Structure Harvester indicate that the populations contain genetic structures as the LOCPRIOR = 1 model used in the analysis does not tend to find population genetic clusters if none exist (Hubisz et al. 2009). Since the matrices separating the forest fragments were under varied levels of habitat deterioration, for example with the Gendagenda/Msubugwe matrix being heavily degraded by grazing livestock (R. B. Modest unpublished data), it was generally expected that these matrices would act as barriers to gene flow (Frankham 1998; Gerlach and Musolf 2000). As this was not the case, the maintained similarities among populations can base on three plausible reasons (citing the Msubugwe/Gendagenda matrix because of its importance due to severity of degradation) as explained below:

First, it is presumed that the subpopulations of this species are continuous within different habitat across the landscape in the sense that fragmentation has not affected migration pattern of the species (Measey et al. 2007). Nevertheless, this is not free of doubts as bird survey under parallel study (R. B. Modest unpublished) missed to record any individual Lowland Tiny Greenbul in matrix separating Gendagenda and Msubugwe forests, a matrix which is heavily degraded by grazing livestock. The same survey however, recorded this species though in a few occasions in the Zaraninge-Kwamsisi and Kwamsisi-Gendagenda matrices — these two matrices are experiencing none to mild intrusion of grazing livestock respectively. These scenario suggest that, the Lowland Tiny Greenbul, despite being a forest specialist species can tolerate habitat alteration while strategically using severely degraded habitat as probably the case of Gendagenda-Msubugwe matrix. Thus, there is a possibility of this species crossing highly degraded habitat by using the so called ‘greenways’ i.e. remnants of original habitat within deteriorated landscape (Bennett 2003). For example, for the Gendagenda-Msubugwe matrix, there is narrow strip of unblocked habitat that run along a gully of a seasonal spring that sprawl from the northern part of Msubugwe joining the other spring from Gendagenda in the course before empting in the Pangani river. It is this narrow corridor (Newmark 1993; Bennett 2003; Sekercioglu 2009) that is probably maintaining gene flow between Gendagenda and Msubugwe subpopulations. Although the matrix in the northern part of Msubugwe was outside the scope of this study, ability of this species to use strips of vegetation emerging along narrow valleys is confirmed with the Zaraninge-Kwamsisi matrix, where a parallel study occasionally sighted this species in vegetation along a gully, five kilometres north of Zaraninge. In connection to this, some previous studies have reported gully habitat as important corridors or stepping stones in linking fragmented habitat (Bennett 2003; Seaman and Schulze 2010). This is because gully habitat are deemed to be floristically similar to bigger forests where they connect, and there is favourable microclimate associated with them (Bloesch and Klötzli 2004; Smith et al. 2011). Therefore, it is these two features (explained above) that probably permit sensitive species such as Lowland Tiny Greenbul to traverse hostile environments such as the Gendagenda-Msubugwe matrix.

Second, in addition to abilities of the species on dispersing through human modified habitat (which facilitate contemporary gene flow), the observed similarities among subpopulations could also be depicting historic range wide distribution of the species (Busch, et al. 2000). It can be presumed that individuals were in greater numbers in the recent past, and could have enjoyed freedom of movements among forest fragments through the then permeable matrices until when human induced habitat destruction begun. The genetic structure data and gene flow analysis also support this as individuals expressed similar level of allelic richness, high historic gene flow, yet reduced rate of current gene flow. Richmond et al. (2009) pointed out that some species experience delayed genetic differentiation after population separation depending on genetic makeup of individuals, "the hypothesis which can be tested with simulation methods that incorporate effect of population size, longevity, and mating pattern to predict the expected time lag in genetic erosion under different scenario of population connectivity". While it is already known that local abundances of the Lowland Tiny Greenbul in northeast Tanzanian coastal forests has not been reduced drastically to affect random mating among fragments (R. B. Modest, unpublished), longevity and mating pattern remain open questions to allow for predicting time lag for the among fragments genetic differentiation of the species.

Third, it is believed that species that live in naturally patched environments are usually slower in responding to environmental changes than those species that originate from large continuous habitat (Richmond et al. 2009). Probably this could be another reason on why the forest specialist species under study is maintaining population genetic similarities among fragmented habitats. Thus, it can be presumed that the study species persisted longer within these fragmented habitat, and despite being forest dependant, the species has developed skills of copying with challenging environments such as capability of penetrating difficult corridors as stated above.

Indeed due to low level of population differentiation, absence of population bottleneck, and the high gene flow observed, it is hereby concluded that, the species subpopulations within different forest fragments still maintain high levels of genetic similarities despite of the current state of within and among forests habitat degradation. It is further concluded that despite being a forest specialist, individuals of the species are capable of utilizing trivial remnants of original habitat that remain amid degraded matrices for dispersal. Since this study was constrained by small sample size, and the fact that a few makers were used, a follow up study is recommended to collect adequate samples and apply sufficient markers to compare with the results in the current study. It is further recommended that, translocation of pastoralists from the Msubugwe-Gendagenda matrix be given priority for the habitat to restore to allow the species to disperse freely among forest fragments. Moreover, strict control measures to stop tree cutting within forests and in matrices is recommended for the benefit the study species and the entire ecosystem. Finally, the importance of gully forests in maintaining gene flow among fragments is overemphasized — thus, cutting trees within gullies is discouraged so as to preserve primary condition of these environments for the benefit of the species.

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Appendix 3.1: Microsatellite Markers specifications and products range for the Lowland Tiny Greenbul in the Saadani-Pangani Ecosystem Tanzania.

Locus	**Species***	**Reference**	**Product size (bp)**
Ls1	*Lanius ludovicianus*	Mundy & Woodruff 1996	190–214
Mcyμ4	*Malurus cyaneus*	Double *et al.* 1997	132–152
Ase18	*Acrocephalus sechellensis*	Richardson *et al.* 2000	236–353
Indigo41	*Vidua chalybeata*	Sefc *et al.* 2001	276–312
Ls2	*Lanius ludovicianus*	Mundy & Woodruff 1996	191–200
Pca4	*Parus caeruleus*	Dowson *et al.*, 2000	152-164
Pdo40	*Passer domesticus*	Dowson *et al.*, 2012	301-335

*Species which the marker was originally developed for

2.4 MANUSCRIPT FOUR

Plate 3.1: Vegetation patches of the study area: Green areas depict coastal forests.

Spatial metrics effect of forest fragmentation on forest bird abundance and site occupancy probability: the influence of patch size and isolation

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Abstract

Forest patch size and isolation play key roles in influencing species persistence in fragmented forests. The persistence of taxa within fragments however, is dependent on source-sink meta-population process. Unveiling species - patch area/isolation relationships therefore may help in providing guidance for setting landscape management options especially for habitat specialist species. Therefore this study was designed to investigate relationship between forest patch size and isolation with abundance on the one hand, and occupancy probability on the other hand in forest dependant birds within fragmented forests in north east Tanzania. Birds were surveyed following distance sampling protocol and spatial metrics were estimated from orthorectified cloud free satellite imagery. Results showed that size of focal forests and distance between patches were the most influencial metrics in explaining both abundance and occupancy probabilities of the study species. Much importantly, the analyses provided evidence of existence of patch size/isolation-occupancy relationship that is characterized by higher occupancy rate of large patches, and distance dependent dispersal decrease with increasing gap among patches. Any deleterious use that lead to minimizing the size of the forest patches and/or increasing distance among patches is discouraged for the benefit of the forest specialists and the ecosystem functioning in general.

Key words: Biogeography, East Africa coastal forests, habitat fragmentation, hotspot

Introduction

Forest patch size and isolation play key roles in influencing species persistence in fragmented habitat, in particular if the patches themselves represent the once connected forest remnants (Laurence et al. 2002). Isolation and size of forest remnants in a landscape on the other hand can be a resultant of two causes; One, if fragmentation is an intrinsic process whereby patches of similar types are naturally implanted in a matrix of other habitat types (Watson 2002; Wilson et al. 2009), and two, if fragmentation is resulting from human causes (Fahrig 2001; Fahrig 2003; Watson et al. 2004). Historically, forest patches in many African savannah landscapes are a result of natural fragmentation (Bond 2008), and such naturally occurring forest fragments, for some regions such as the East Africa Coastal forests are associated with high number of biodiversity and endemism (Dicknson et al. 1992; Azeria 2007). This is because during their historic fragmentation, the fragments inherited some taxa that lack alternative habitat in matrices except within fragments themselves (Dicknson et al. 1992; Watson 2002; Fahrig 2003). However, the persistence of taxa within these fragments is dependent on source-sink meta-population process (Hanski 1998; Watson 2002) that is in line with theories of island biogeography (MacArthur and Wilson 1967). Thus, which species is to go or stay as a reaction to fragmentation is a crucial issue in landscape management (Watson 2002; Suk et al. 2014).

Unfortunately, in many instances, fragmentation in naturally occurring forest patches has been escalated by human induced environmental alteration including clearance for agriculture, livestock grazing and manmade fires, as for example the case of coastal landscape in north east Tanzania (Dicknson et al. 1992; Bloesch and Kloetzl

2002). These practices consequently reduce forest patch size and increase patch isolation with possibility of causing local extinction especially in those species with less ability in crossing non-natural habitat for dispersal (Brooks et al. 1999; Laurance et al. 2002). However, local populations face possible extinction risks when alteration of habitat hosting them reaches certain minimum thresholds in size and extent of isolation (Lande 1987; With and King 1995; Fahrig 2001; Ance et al. 2003; Suarez-Rubio et al. 2013). Thus, unveiling species-patch area/isolation relationships may help in providing guidance for setting options for landscape management particularly in protecting habitat specialist species (Hanski and Ovaskainen 2000; Fahrig 2003; Samaniego and Marquet 2013). This study therefore was designed to investigate relationship between forest patch size and isolation with abundance on the one hand, and occupancy probability on the other hand in forest dependant birds in one of the landscape that have experienced both historic and human induced fragmentation. The study focused on North East Tanzania within a coastal forests landscape that is currently under threat following practices such as subsistence agriculture, forest clearing for human settlements and extensive livestock grazing (Burgess et al. 1992, Dicknson et al. 1992; Fjeldså and Lovett 1997; Bloesch and Kloetzl 2002; WWF 2014).

The forest dependant birds used as models were the Lowland Tiny Greenbul *Phyllastrephus debilis* which is a forest specialist mainly restricted to well-developed forested habitat and preferring forest interior, and Yellow-bellied Greenbul *Chlorocichla flaviventris*, a forest generalist preferring forest edge and disturbed woodlands and savannahs, but with equivalent capacity of utilizing forested habitat

(Fishpool and Tobias 2005; Fjeldsa et al. 2007; Borghesio 2008). Differentiation between the forest specialist and the forest generalist birds was important because forest specialists are more vulnerable to fragmentation relative to generalist species (Connor et al. 2000; Laurance et al. 2002; Ewers and Didham 2006). The aim of the study was to assess the influence of forest spatial metrics specifically fragment area and inter-patch distance on abundance and occupancy probabilities of the two species with emphasis on their long term conservation plan. The hypothesis stated that, the negative effect of smaller forest fragments and larger inter-patch distances would be more evident in the forest specialist species than the forest generalist one.

Methodology

Study System and Study Species

This study was carried out within the lowland coastal landscape in north-eastern Tanzania covering Saadani National Park and surrounding areas. The area is located between 6°16′42.94″and 6°16′57.65″S, and between 38°32′08.35″ and 38°51′17.37″E (Azeria et al. 2007). However, four evergreen coastal forests namely Zaraninge, Kwamsisi, Gendagenda and Msubugwe were considered under study (Fig. 4.1). The study system experiences two rainy seasons with short rains commencing in October through December, and long rains from March to May (Bloesch and Klötzli 2002). The area is rich in biodiversity in both flora and fauna (Clarke 2000; Azeria et al. 2007), where for example, all the East Africa coastal forests endemic birds are represented within this coastal landscape (Burgess and Muir 1994; Azeria et al. 2007). These include the Sokoke pipit *Anthus sokokensis,* Little Yellow Flycatcher *Erythrocercus holochlorus,* Fischer’s Greenbul *Phyllastrephus fischeri,* Kretschmer's Longbill *Macrosphenus kretschmeri,* and Plain-backed Sunbird *Anthreptes reichenowi* (Azeria et al. 2007).

The study species, Lowland Tiny Greenbul and Yellow-bellied Greenbul are sympatric passerine bird species in the family of bulbuls Pycnonotidae (Sibley and Monroe 1990), though with contrasting lifestyles (del Hoyo et al. 2005; BirdLife International 2014). The Lowland Tiny Greenbul mainly preferring forested habitat is categorized as a forest specialist, while Yellow-bellied Greenbul, which prefer areas that are more open but capable of utilizing forested habitat to a lesser degree is referred to as a forest generalist (Fjeldsa et al. 2007; Borghesio 2008). The Lowland Tiny Greenbul *Phyllastrephus debilis* is distributed within moist lowland forests, but also may occur in dense bushes around forest edges (Fishpool and Tobias 2005). The species is mainly tied to forest interior in East Africa (Keith et al. 1992) and mostly forages on butterflies, bees, wasps, locusts and ants (Fishpool and Tobias 2005). On the contrary, Yellow-bellied Greenbul exhibits a wider range, which encompasses East, Central and Southern Africa (del Hoyo et al. 2005; Fjeldsa et al. 2007; Borghesio 2008; BirdLife International 2014). The species prefers forest edges, and/or open areas within thickets or wooded savannas (Fishpool and Tobias 2005), and its diet is comprised of fruits, seeds, flowers and insects (Keith et al. 1992; Hockey et al. 2005).

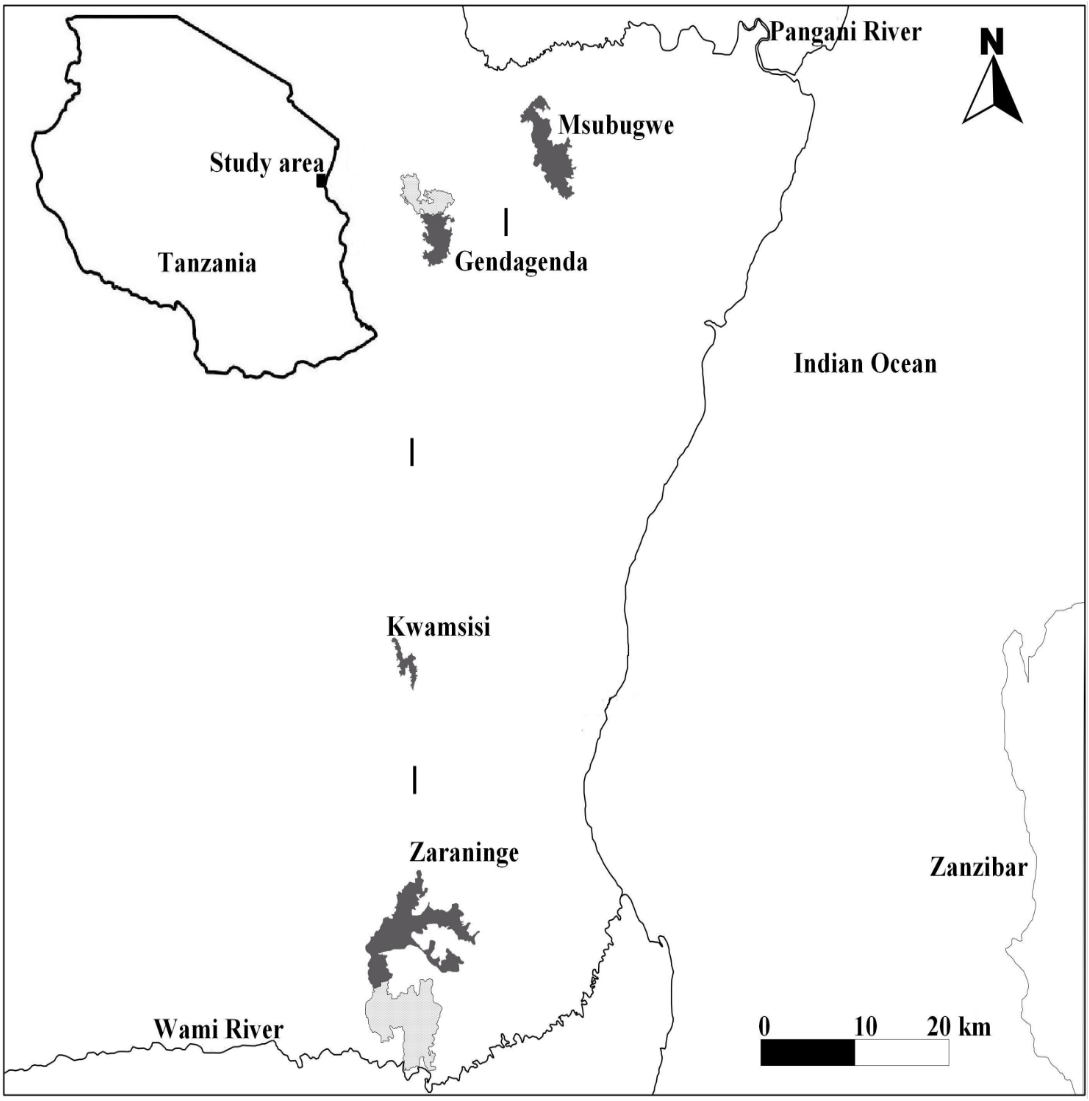

Figure 4.1: Map of the study area: Black shaded areas show dry evergreen coastal forests comprising study sites, thick lines show transects in matrices, while grey shows other mixed forests in continuum with study sites. The surface area for Zaraninge (darkened part) is about 42.7 km^2, Kwamsisi (4.06 km^2), Gendagenda (10.97 km^2), and Msubugwe (22.32 km^2). The distance from Zaraninge to Kwamsisi is about 16.6 km, and between Kwamsisi and Gendagenda is 34.6 km, while distance from Gendagenda to Msubugwe is about 10.2 km. Source: Modest, R.B. (Unpublished PhD thesis, Sokoine University of Agriculture).

Bird Sampling

Fieldwork began from October 2010 and ended in June 2013. However, for logistical reasons, data was not collected between February and June 2011, and October 2012 through January 2013. A minimum of 24 monthly visits were paid per study site during the entire fieldwork. A single observer walked transects once monthly and noted number of birds sighted or heard (Bibby et al. 2000; Thomas et al. 2010). Sampling occurred either in the morning from 07.00 to 10.30 hours or later in the day from 15.30 to 18.30 hours. Data was collected along transects established in interior habitat (500 m from forest edges), and within 10 m of forest edge inwards. Such distribution of transects in strata ensured that all representative habitat of both species are sampled (Bibby et al. 2000). Establishment of first transect in each stratum followed judgment sampling procedure, which involve subjective selection of sampling site that are representative of the study area (Morrison et al. 2001). However, after establishing the first transect, placement of subsequent transects was random while ensuring that the distances between them was $\geq$150 m to avoid double counting of birds (Bibby et al. 2000). Moreover, varying number of transects were assigned in individual forests depending on their size. Zaraninge forest had nine transects of which three were in the segment of the forest that is managed by the Saadani village (two in core and one in edge habitat), while the other six were in the remainder portion of the forest (three in core and edge habitat respectively). Msubugwe had six transects (three in core and edge habitat respectively), and there were five transects in Gendagenda (three in core and two in edge habitat). Kwamsisi received four transects with two in core and edge respectively. For the Zaraninge forest, the segment that falls under Saadani Village management was alienated from the bigger segment that falls under Saadani NP in order to realize the effect of forest disturbance on abundance and occupancy probability of the study species. This is because in Zaraninge forest, the segment that is managed by the Saadani village is usually frequented by Mbebwe residents for firewood collection and for scaring vermin such as baboon that raid their crops.

On the other hand, the data for modelling species site occupancy probabilities was obtained by coding Distance sampling data into presence/absence (Bibby et al. 2000; Mackenzie et al. 2003). However, in order to account for uncertainty of not detecting the species when present (Mackenzie et al. 2003; Mackenzie et al. 2006), additional transects (on top of those used under distance sampling) were surveyed for presence/absence data collection, and this equated to eight transects (distributed equally between core and edge habitat) in each of the forest patch. In Zaraninge forest however, the nine transects were maintained (five in edge and four in core habitat), and the transect lengths ranged between 100 m to 500 m.

Satellite imagery analysis

Orthorectified cloud free satellite imagery acquired by LANDSAT TM 4 in February 2014 was digitized to determine forest patch size and distance among the patches (Tucker et al. 2004; Prins and Clarke 2006). Wherever part of imagery was covered by cloud or where it was difficult to alienate forest patches from surrounding vegetation, another clouds free imagery was overlaid based on known features of the landscape to increase resolution (Kirui et al. 2013). The focal patch areas were measured first, afterwards, distance from edge of focal patch to edge of nearest patches (patches > 50 ha in size) were measured within 500 m of focal patch (radial distance). These two were taken as key landscape metrics that are considered important in influencing species persistence in fragmented forests (Andren 1994; Hanski 1999). Moreover, other metrics on forest patches that were > 50 ha in size and whose edges fell within 500 m of each focal forest were measured. These were; number of forest patches, and nearest concentric distance between patches. Others were; mean surface area of all forest patches — surface area of focal forest included (local patch area), and mean surface area of forest patches surrounding focal forest — surface area of focal patch excluded (buffer area). Selection of these landscape metrics based on reviewing literature on landscape features that are deemed important in influencing bird abundance and occupancy probability (see for example Prugh 2009; Moilanen and Nieminen 2002). Identification of most of forest patches on imagery was achieved using GPS coordinates collected during field work, and where GPS coordinates were not available, visual inspection of imagery was opted. All GIS procedures were performed in Quantum GIS (QGIS) software (Quantum GIS Development Team, 2014).

Bird abundance and occupancy probability estimation

Bird abundance was estimated using the Conventional Distance Sampling (CDS) analysis engine in Program Distance (Thomas *et al.* 2010). For each species four models which Thomas *et al.* (2010) consider sufficient to give accurate estimates were run. These models were; uniform key with cosine adjustments, half-normal key with cosine adjustments, half-normal key with hermite polynomial adjustments, and hazard-rate key with simple polynomial adjustments. Selection of best global model based on Akaike Information Criterion and individual site densities were obtained by post-stratification.

Data for occupancy probability modelling was classified in four seasons namely: November to December ─ short rainy season; April to May ─ long rainy season; February to early March ─ short dry season; and July to August ─ long dry season. Only two models per season for each species were run i.e. a constant model *psi*(.),*p*(.) where both occupancy and detection probabilities were assumed constant, and the second model which kept occupancy probability constant while allowing detection probability to vary per season — *psi*(.)*p*(survey). The Program Presence version 6.1 was used to build models for each season separately using single-season, single-species approach (Mackenzie et al. 2003; Mackenzie et al. 2006; Rogers et al. 2013). The Akaike Information Criterion was applied in model selection, and for competing models averaging was accomplished as detailed in Burnham and Anderson (2002).

Finally, for each forest, paired dependent variables (abundance and mean occupancy probability respectively) were screened against independent variables (landscape metrics) using scatter plots. Afterwards the variables that were non-monotomically related were discarded (McDonald 2009). This resulted in two landscape metrics namely number of forest patches > 50 ha, and concentric distance among patches being droped from further analysis. Then the Spearman's rank correlation test was used to determine whether the retained landscape metrics covaried with bird abundance and mean occupancy probability repectively (Keyser et al. 1998; McDonald 2009; Suk et al. 2014). For visual interpretation, bird occupancy probability and log transformed bird abundance were plotted against log forests sizes (Lee 2002). All statistical analyses were perfomed in R program version 2.15.1 (R core team 2013).

Results

The association between bird abundance and occupancy probability with focal forest sizes is shown in Fig.4.2 for the Lowland Tiny Greenbul, and Fig.4.3 for the Yellow-bellied Greenbul. For the Lowland Tiny Greenbul, both abundance and occupancy probability remained constant with small sized patches, but abundance increased gradually with mid sized towards larger patches. The occupancy probability however showed an abrupt increase begining with mid sized towards larger patches.

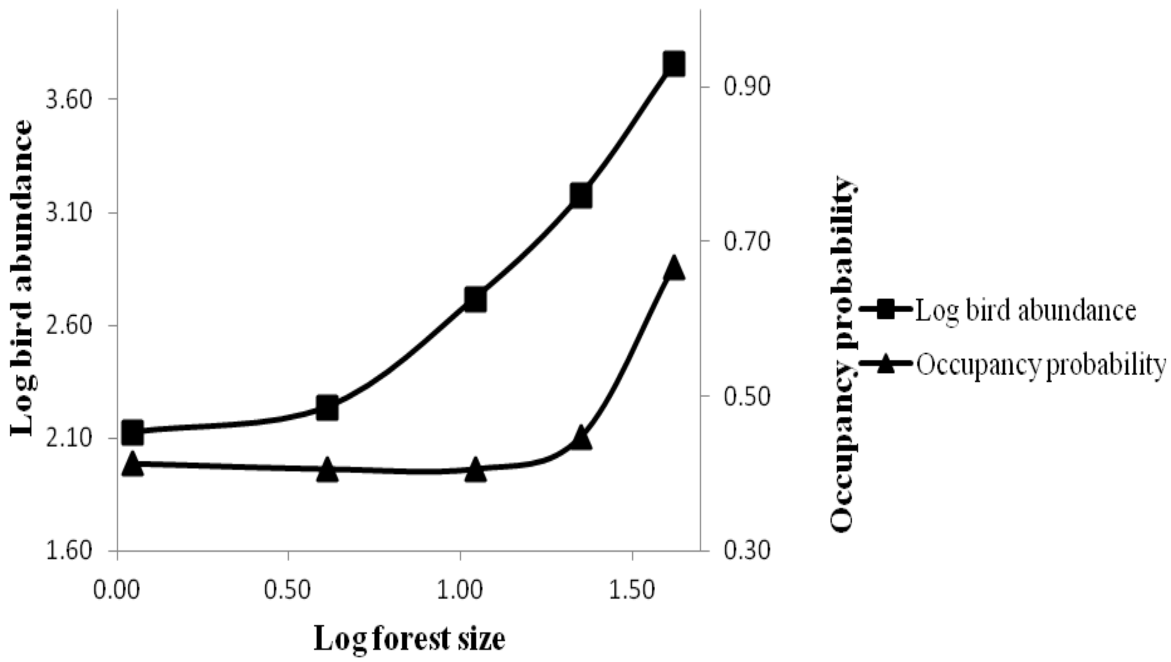

Figure 4.2: Forest size versus bird abundance and bird occupancy probability for Lowland Tiny Greenbul

For the Yellow-bellied Greenbul, there was an initial increase in association between increase in abundance and increase in forest size. The increase was however halted and followed by a fall upon reaching the biggest forest patch. The occupancy probability on the other hand showed similar trend as abundance, but with an abrupt fall with the biggest patch.

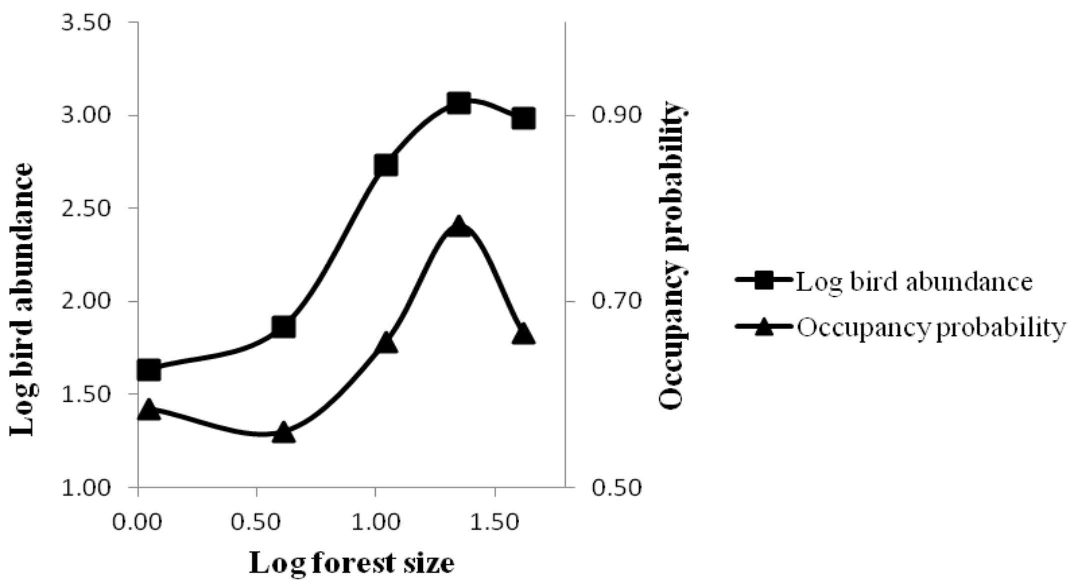

Figure 4.3: Forest size versus bird abundance and bird occupancy probability for Yellow-bellied Greenbul.

Table 4.1 shows Spearman's rank correlation coefficients for the association between indices of patch isolation and bird abundance. Radial distance (distance between edge of focal forest and edge of adjacent forest patches) was the most important landacape metrics that influenced the two species abundance. The Spearman's rank correlation coefficients for the forest specialist Lowland Tiny Greebul was stronger indicating that as distance betweeen focal forests and adjacent patches increase the abundance of this species decrease. The same trend was exhibited by the generalist species, but with a lesser effect. The other metrics showed no association to weak negative and positive associations.

Table 4.1: Spearman's rank correlation coefficients showing association between bird abundance estimate and indices of patch isolation: Buffer area = mean area of forest patches surrounding focal forest within 500 m (area of focal forest excluded); radial distance = mean edge to edge distance between focal forest and surrounding patches; local patch area = surface area of forest patches surrounding focal forests (surface area of focal forest included); r = Spearman's rank correllation coefficients; df = degree of freedom; p = value.

Estimate	**Species/ indices of patch isolation**	**Correlation Coefficient**		
Abundance		r	df	p
	Lowland Tiny Greenbul			
	buffer area	0.00	3	1.00
	radial distance	-0.90	3	0.04
	local patch area	0.20	3	0.74
	Yellow-bellied Greenbul			
	buffer area	-0.10	3	0.87
	radial distance	-0.70	3	0.19
	local patch area	0.05	3	0.93

As for abundance, radial distance demonstrated negative association with occupancy probability for the two species though with intermediate effects (Table 4.2). The other two metrics however showed positive effects, with association being intermediate for the Lowland Tiny Greenbul, but weak for the Yellow-bellied Greenbul.

Table 4.2: Spearman's rank correllation coefficients showing association between bird occupancy probability estimates and indices of patch isolation: Abbreviations as in Table 4.1 above.

Estimate	**Species/ indices of patch isolation**	**Correlation Coefficient**		
		r	df	p
Occupancy probability	***Lowland Tiny Greenbul***			
	buffer Area	0.67	3	0.22
	radial distance	-0.41	3	0.49
	local patch area	0.79	3	0.11
	Yellow-bellied Greenbul			
	buffer Area	0.30	3	0.62
	radial distance	-0.60	3	0.28
	local patch area	0.41	3	0.49

Discussion

The analyses under this study indicated that, focal patch area was an important landscape metrics in influencing both abundance and occupancy probability of the forest specialist species, and these findings conform to previous related studies (see for example Hanski 1994; Ferraz et al. 2007; Prugh et al. 2008). Moreover, the influence of patch area on abundance and occupancy probability of the Yellow-bellied Greenbul was positive, but seemed to reach a threshold beyond which both abundance and occupancy probability dropped as patch area increased, suggesting that larger patches within fragmented landscapes are not important for generalist species (Wilson et al. 2007). On the other hand, the association between patch size with both abundance and occupancy probability of the forest specialist species clearly indicated that, with small sized patches abundance and occupancy probability were non-increasing but showed a shoot up as forest patch increased from a certain size. This implies that for the forest specialist species there exist minimum patch sizes below which individuals may not tolerate (Fahrig 2001; Ance et al. 2003;

Suarez-Rubio et al. 2013). Hence, although a minimal threshold of forest patches was not set during analysis, for the sound management of the species, it is important to observe minimum patch size in the study area. This is because some studies have indicated that negative effects of forest size on specialist species became evident when at least 20-30% of original habitat disappears from the broader landscape (see for example Fahrig 2003; Vergara and Armesto 2008).

Moreover, radial distance seemed to be an important landscape metrics that negatively influenced both species abundance and occupancy probability. Radial distance is the most widely used measure to express forest patch isolation (Moilanen and Nieminen 2002; Prugh 2009), and many studies have expressed its implication on species abundance and site occupancy probability within fragmented habitat (e.g. Uezu et al. 2005). The effect of radial distance on forest specialist under this study was stronger than that for the forest generalist species probably due to differences existing between these species in utilizing landscapes. Lowland Tiny Greenbul is a small bodied species compared to Yellow-bellied Greenbul which is bigger bodied (Fishpool and Tobias 2005), and larger bodied species are reported to efficiently use gaps in fragmented habitat than small bodied ones (Jackson and Fahrig 2012). Therefore, this morphological disparity could probably be responsible for differences observed on the influence of radial distance on abundance and occupancy probability of the two species (Thornton and Fletcher 2013). Therefore, following the analysis in the current study, maintenance of minimum distance among fragments which probably aid in dispersal for the forest specialist species is hereby overemphasised (Uezu et al. 2005). This is because, there is a tendency that was observed throughout the study system where vegetation surrounding larger protected forests were being cleared for creating agricultural lands. These practices are likely hampering the forest specialist in utilizing forest patches that surrounds focal forests since the source-sink meta-population process of the species is probably interrupted (MacArthur and Wilson 1967; Hanski 1998).

On the other hand, with respect to the remainder of the metrics analysed, buffer area and local patch area also showed positive relationships with site occupancy probability for the forest specialist. The probable explanations could lie in the habitat need of forest specialists where cover is most important (Trzcinski et al. 1999). Although these landscape metrics could not explain influence on abundance of the forest specialist species, the positive relationship with occupancy probability is worth explaining in the same concepts of source-sink and meta-population dynamics. For the generalist species however, buffer area and local patch area which can be explained in terms of amount of cover surrounding focal occupied forests seemed unimportant. Nevertheless, this is not exceptional as this species is known for its ability to utilize even non-forested habitat (Geyser 2013).

In conclusion, the analyses provide evidences of existence of patch size/isolation - occupancy relationship within fragmented forests in north east Tanzania for both specialist and generalist species — the evidence being stronger in the specialist one. Although the analyses did not include sensitivity analysis (Henle et al. 2004), it can be generalized that the patch occupancy pattern especially of the forest specialist followed the meta-population processes as the occupancy pattern was characterized by higher occupancy rate of large patches and distance dependent dispersal that decreased with increasing gap among patches. Therefore, the importance of maintaining habitat in natural states through discouraging any deleterious use that otherwise would lead to minimizing the sizes of the forest patches and increasing gaps among patches is overemphasized for the benefit of the forest specialists and the ecosystem functioning in general.

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CHAPTER THREE

3.0 SUMMARY OF THE MAJOR FINDINGS, CONCLUSIONS AND RECOMMENDATIONS

3.1 Summary of the Major Findings

3.1.1 Occurrence and Population Density of Study Species

3.1.1.1 Bird Density

The study recorded higher density 1.365 birds/ha for the forest specialist Lowland Tiny Greenbul in Zaraninge forest, a forest that was categorized as comprising ideal non-disturbed habitat. On contrast, the density of this species in Msubugwe, which is a highly disturbed forest was 0.698 birds/ha about half of that recorded in Zaraninge — suggesting the importance of ideal non-disturbed habitat for the species. However, the density of this species in Msubugwe forest (i.e. 0.698 birds/ha) was higher compared to the densities recorded in Gendagenda and Kwamsisi respectively. On the other hand, the highest density of the forest generalists was recorded in Msubugwe, a forest that was categorized as highly disturbed. Indeed, despite the fact that Zaraninge is the largest forest in the study area with about 42.7 km^2, and the fact that it received more sampling efforts compared to other forests, the density estimate of Yellow-bellied Greenbul of 0.238 birds/ha in this forest was extremely low. This implies that for Yellow-bellied Greenbul, being a forest generalist species, ideal non disturbed habitat are not important.

3.1.1.2 Site Occupancy Probability

The Lowland Tiny Greenbul which is a forest specialist species occupied mostly ideal non disturbed habitat, while Yellow-bellied Greenbul being a forest generalist was not biased towards any habitat type. The occupancy probability of the two species however seemed to be influenced with seasonality. For example, the Lowland Tiny Greenbul had the highest overall averaged occupancy probability of 0.60 during the short rainy season, which probably corresponded with the beginning of breeding season that commence from October. During this season, birds are probably active with nest construction, and presumably are as well displaying for finding mates where it is easy to detect. The occupancy probability of the Yellow-bellied Greenbul in contrary was higher during long dry season. It was presumed that this was due to coincidence with ripening of fruits within coastal forests — as the species is highly attracted to fruit foods, and this probably facilitated its spotting.

3.1.2 Habitat Preference of the Study Species

Statistical analyses and modelling results showed that the two study species portray strong contrast in their preference of vegetation parameters modelled. This is because most of parameters determined decrease in abundance of the forest generalist species while the opposite was true for the forest specialist one. For example, while the Lowland Tiny Greenbul responded positively to a parameter that is an indicator of good quality forests i.e. "trees > 10 m high branching above half their heights", the generalist species responded negatively to this parameter.

3.1.3 Gene Flow among Forest Patches and Population Characteristics

Analysis of genetic data showed low level of population differentiation among forest fragments. The maintained similarities among subpopulations of the study species was attributed to three plausible reasons: One, it was assumed that the subpopulations of the study species are continuous within different habitat across the landscape in the sense that fragmentation has not affected individuals migration patterns. Two, it was also presumed that the observed similarities among subpopulations of the study species could be depicting its historic range wide distribution. Thus, the subpopulations were assumed to have had higher densities in the recent past and were able to interact and exchange genetic materials in absence of barriers to gene flow as opposed to the current situation. Three, it was assumed that the study species has persisted longer within fragmented habitat and despite being forest dependant, the species has developed strategies to overcome challenges in crossing degraded habitat among forest fragments.

3.1.4 Effects of Forest Patch Size and Isolation on Occurrence and Abundance of Study Species

Forest patch size was the most important landscape metrics in influencing both abundance and occupancy probability of the forest specialist species. The results clearly showed that with small sized patches, abundance and occupancy of the species were non-increasing, but showed a shoot up as forest patch increased from a certain size. This implies that for the forest specialist, there exist minimum patch size thresholds below which individuals may not tolerate. Moreover, the influence of patch size on abundance and occupancy probability of the forest generalist species was also positive, however, there was a threshold beyond which both abundance and occupancy probability dropped as patch area increased. This suggested that larger patches within fragmented landscapes are not important for this generalist bird. The radial distance on the other hand, negatively influenced both species abundance and occupancy probabilities. The effect of radial distance on forest specialist however was stronger than that of the forest generalist species probably due to differences existing in abilities of these species on utilizing open landscapes. Nevertheless, this discrepancy was attributed to morphological differences rather than habitat specialization, as the Lowland Tiny Greenbul is small bodied species compared to Yellow-bellied Greenbul, and larger bodied species are reported to efficiently use gaps in fragmented habitat than small bodied ones.

3.2 Conclusions

This study has provided invaluable information on population status and genetic characteristics of forest specialist and generalist birds in the Saadani-Pangani ecosystem Tanzania. The information on pattern of habitat selection, density and patch occupancy probabilities, genetic characteristics, and species-patch size/isolation relationship will cater as useful guides in management and conservation of forest birds in the Saadani National Park, and elsewhere. On the other hand, this study has found a number of contrasting phenomena between the two model birds which could bring challenges to managers when setting priorities on conserving the species in question. For example, with habitat selection pattern, the study have reported high divergence in habitat preference by the two species, for instance, with the worst habitat for one species forming the best refuge for the other.

The study however, has provided a piece of advice to managers especially in ensuring maintenance of habitat in their natural states much as possible since in absence of human intrusion that damage the environment, the species will obviously delineate their niches according to their requirements. Therefore, in a nutshell, this theses draws the following conclusions:

1. In the Saadani-Pangani ecosystem, the forest specialist species Lowland Tiny Greenbul is influenced by ideal non-disturbed habitat. The forest generalist species Yellow-Bellied Greenbul however, is not biased towards any habitat types, though regardless of habitat quality, it is inclined towards forested habitat.

2. There is low level of genetic differentiation among subpopulations of the forest specialist species. Thus, it is established that, following the observed similarities among subpopulations, the forest specialist species, Lowland Tiny Greenbul that was previously thought to be sedentary (i.e. confined only to larger forests) is capable of utilizing trivial remnants of original habitat in matrices — and this aid its dispersal.

3. There are exit patch size/isolation-occupancy relationship especially for the forest specialist species. This relationship follows the meta-population processes as occupancy rate of the species was high in large patches compared to smaller ones, and there was distance dependent dispersal that decreased with increasing gap among patches.

Thus, based on analyses of density, habitat preference, and populations genetic characteristics, this study generally concludes that, the populations of both specialist and generalist birds within East Africa coastal forests in the Saadani-Pangani ecosystem are viable, such that bird abundance is high (cf. IUCN criteria), there is maintained gene flow among subpopulations, and there is resource partitioning between generalist and specialist species that minimize competition.

3.3 Recommendations

To maintain health populations of both specialists and generalist birds in east Africa coastal forests in the Saadani-Pangani ecosystem, this study recommend the following:

- There should be application of strict control measures to stop the ongoing habitat destruction within the study area, especially in the matrix between Msubugwe and Gendagenda. This is because the Msubugwe-Gendagenda matrix is facing severe habitat degradation following intensive livestock grazing, the practice which interferes dispersal of the forests specialist species.
- Management practices that will safeguard forests and ensure representations of varied vertical structuring in canopy layers are recommended for welfare of forest specialist birds and other wildlife.
- There should be a follow up study to gather adequate samples and apply sufficient markers to compare with the genetic analyses of the current study.

This is because the current study was constrained with a small sample size, and only a few markers were used.

- Pastoralists in the Msubugwe-Gendagenda matrix should be evicted to allow for vegetation rehabilitation as intensive livestock grazing in the matrix is seriously destroying the habitat.

- Tree cutting within gullies should be discouraged as gully forests are important in maintaining among fragments gene flow of the forest specialist.

- Finally, this study discourage any deleterious use along forests edges in order to maintain original sizes of forest patches, and minimize distance among patches as these two factors (size and distance among patches) were found to be fundamental in influencing study species abundance and occurrence.