Endemic forest birds of the Taita Hills: using a model species to understand the effects of habitat fragmentation on small populations

Mwangi Githiru
St. John's College

Submitted for the degree of Doctor of Philosophy
Edward Grey Institute of Field Ornithology
Department of Zoology
University of Oxford

Michaelmas Term, 2002

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It is in the rain forest
Where nature and its inhabitants inspire peace
Where one perceives the presence of God the creator
And where man appreciates the importance of the beings that surround him

Kjell von Sneidern, Ornithologist, 1995

Of the 10-20 million species of plants, animals and microbes estimated to be extant, perhaps half will become extinct in the next millennium. Most of these will disappear anonymously - unknown and undescribed by science. Others, with proper scientific names, will vanish quietly, their epitaphs simply stating, 'last collected in 1999.' A few charismatic species - primates, colourful birds, butterflies - will be kept from extinction by captive propagation, but most have no hope of ever returning to their long-since fragmented and degraded natural habitats. The survivors of this massive extinction event will be the ecological generalists, the weeds, the invaders.

Peter F. Brussard, 1999

ABSTRACT

Endemic forest birds of the Taita Hills: using a model species to understand the effects of habitat fragmentation on small populations

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Despite intense publicity, habitat loss still remains a serious threat to biodiversity. Forest destruction is its frontrunner, both in terms of physical habitat under threat and potential for biodiversity loss. In the fragmented landscape of the Taita Hills, SE Kenya, several bird species are facing the threat of extinction from forest loss. They are absent from many of the remnant forest patches and/or are showing negative effects with increasing disturbance. Using a relatively common forest-dependent bird species – the white-starred robin *Pogonocichla stellata* – as a model, the current status of this ecosystem was examined, and future patterns predicted in view of the unrelenting destruction. As expected, the robin population in the largest and most intact fragment (*c*135 ha) was the healthiest, suggesting that this was indeed the best quality habitat patch: it had the highest population density, highest productivity (low nest predation and high juvenile to adult ratio) and lowest turnover rates. Effects of forest deterioration were evident from the fact that the medium-sized patch (*c*95 ha), which is undergoing severe degradation, was a worse habitat for the robin than the tiny patches (*c*2-8 ha): it had the lowest population density, lowest productivity (highest nest predation rates and lowest juvenile to adult ratio), and highest turnover rates. The explanation for this is twofold. Besides the smallest patches facing lower levels of habitat loss recently, they also had high levels of dispersal between them. They occasionally operated as a fine-grained system with individuals moving between them in the space of a few days. In general, the robin metapopulation is demographically (rate of change, $\lambda = 0.996$) and genetically (at migration- and mutation-drift equilibrium) stable at present. The populations in the largest and smallest patches were potential sources providing emigrants that were possibly crucial in sustaining the population in the medium-sized patch (given its low productivity and high turnover rates). Overall, these findings underscore the importance of within-patch processes, both for ensuring persistence of subpopulations and providing dispersers, as well as between-patch processes (chiefly dispersal) for ensuring metapopulation persistence. Thus, by furnishing ample sample sizes that enabled work to be carried out in all fragments throughout this landscape, the model species approach was useful for identifying the need for a two-pronged conservation strategy. First, a need to focus within fragments to reduce habitat loss and degradation, and second, to address among fragment issues relating to land-use and maintaining a forested landscape, in order to enhance connectivity between patches. Finally, based on the mechanisms by which disturbance and fragmentation are affecting bird populations e.g. predator influxes from the surrounding matrix, conservation recommendations for the Taita Hills are offered.

ACKNOWLEDGEMENTS

As this long-drawn-out journey draws to a close, it would be neither prudent nor sincere to claim it has been all my doing. A host of people have contributed to this work, albeit in the most diverse of ways, but without which it would not have been anywhere near as close to what it is, if it would have been at all! I would like to thank them all and stress that they gave me the truth, the options, the alternatives – the choices I made were all entirely mine, and so were any errors stemming from them. Indebted feels insufficient [certainly too short!] to describe my feelings to everyone who contributed in one way or the other, though thankfulness-indebtedness do not feel like good justice either... I will attempt to acknowledge all the parties, in no real order, and hope not to leave anyone out.

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To my assistants, Bernard Amakobe and Max Chovu, who endured long – sometimes painful – stretches in the Hills with me throughout the fieldwork stints. Their hard work and dedication to this Cause, as though it were their very own, was fundamental to this ending. Many thanks for their friendship, company and most enjoyable time in the Hills.

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Back home, my family – mum and dad, Wams, Mc, Kabs & Kana – have been pivotal, unwavering in their love and support, and ever so understanding. They still talk to me [seriously!] and I would like to dedicate this thesis to them for everything: **THANKS** guys. I cannot dare forget all the family and friends – the cuzos, grandis – who might have as well given up on me ages ago after I started playing-Tarzan and recluse, disappearing to the wilderness for days on end only to [suddenly] reappear, all shaggy and without proper town-orientation… Thanks for standing by me when it seemed I could care less [truth is that I always did!]. Also, in a way, thank too for all those jibes and quizzical looks – "*ati* what, [you study] birds?!?"

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...And thanks to God for constantly watching over me, keeping me safe, in the pink and full of beans...

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Introduction

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Introduction

CHAPTER 1

Human development around the cloud forest fragments of the Taita Hills, showing a typical wooded landscape

> Man's power to achieve good or to inflict evil surpasses the brightest hopes and the sharpest fears of all ages. We can turn rivers in their courses, level mountains to the plains. Oceans and land and sky are avenues for our colossal commerce. Disease diminishes and life lengthens. Yet the promise of this life is imperilled by the very genius that has made it possible. Nations amass wealth. Labour sweats to create, and turns out devices to level not only mountains but also cities. Science seems ready to confer upon us, as its final gift, the power to erase human life from this planet.
>
> **Dwight D. Eisenhower**

Adult white-starred robin
Pogonocichla stellata

Juvenile *P. stellata*

Chapter 1: General introduction

Summary

This chapter provides an overview of the entire thesis, giving the theoretical framework on which the study was based. In the first section, the broad issues forming the crux of the study are presented, viz. the process of forest loss and fragmentation, the consequences on organisms and the mechanisms by which they might occur, and finally an overview of specific approaches used to collect pertinent data that can be applied in conserving biodiversity in fragmented landscapes. The second section provides germane background information about the status quo of the study area and its biodiversity in general, as well as information about the study species that is not provided in individual result chapters. Also incorporated is an appraisal of the approach applied to study the general effects of forest destruction on birds. Finally, the overall aim of the thesis is presented, followed by the thesis structure and specific chapter hypotheses.

1.1 Fragmentation and tropical forests

1.1.1 The process

Destruction of natural and semi-natural habitats, especially tropical rain forests with their high species diversity, is proceeding at alarming rates in many parts of the world (Laurance and Bierregaard 1997; Holl and Kappelle 1999; Sih et al. 2000). In addition to loss of habitat and reduced patch size, forest loss and fragmentation also leads to increased distance between patches and an increase in new habitats (Andrén 1994); the proportion of edge exposed to other habitats is also bigger (Murcia 1995). Thus, fragmentation can be viewed as a two-sided process: first, distance-area effects (insularization and decreasing forest size) directly preventing successful dispersal and reducing population sizes, and second, landscape effects (reduced fragment-matrix and interior-edge ratios) increasing undesirable pressure from the surrounding matrix, such as predators and competitors (Rolstad 1991). In many cases, this results in remnant (indigenous) forest patches less than 100 ha (e.g., Kellman et al. 1996; Turner and Corlett 1996) and triggers a process leading to reduction in numbers (and finally extinction) of area- and edge-sensitive species (Saunders et al. 1991; Turner 1996; Flather and Bevers 2002). Still, the remnant patches can retain many species (Brokaw 1998), thereby adding an important dimension to the persistence of biodiversity in the entire landscape (Schelhas and Greenberg 1996). Indeed, they can act as last refugia for flora and fauna forming the basis for launching rescue attempts of threatened species (Turner and Corlett 1996), or as genetic reservoirs, or stepping-stones facilitating dispersal within the landscape (Stangel et al. 1992). For conservationists, the challenge is not only to limit the process of fragmentation and habitat loss, but also to understand how organisms respond to it so that the adverse effects can be avoided or reduced (Walters 1998; Harrison and Bruna 1999).

Forest destruction normally results in habitats of different quality and thus potentially different demographic attributes for the populations within them. Generally, differences in habitat quality lead to good quality habitats producing more young (surplus) than poor quality ones (Dias 1996). This might result in a metapopulation structure or the creation of sources, sinks and pseudo-sinks (sensu Pulliam 1988; Pulliam and Danielson 1991; Hanski 1999). Metapopulations have been defined as explicitly involving colonization and extinction processes, with each population being at a risk of extinction (Moilanen and Hanski 1998). However, variation in both population traits (size and other demographic attributes) and patch features (size, quality and degree of isolation) implies that probabilities of survival will differ among subpopulations (Blondel and Lebreton 1996), sometimes resulting in mainland-island-like metapopulation scenarios (e.g., Harrison 1991; Newton 1998). Still, local populations are connected by among-population processes (e.g., dispersal, gene flow, colonization and extinction), which can affect and/or be affected by within-population processes (e.g., birth, death, competition). The metapopulation-approach therefore provides a conceptual tool for dealing with the interactions between within- and among-population aspects (Thrall et al. 2000). For instance, the optimum life history within a habitat patch might not only depend upon the conditions within the patch, but also on conditions in other patches and the structure of dispersal between them (Kawecki and Stearns 1993). This framework is useful for developing management strategies because it ensures a process-oriented and scale-appropriate approach to conservation, focussing on among-population processes which are critical for the persistence of many natural systems (Thrall et al. 2000). Primarily via dispersal, the metapopulation paradigm blends spatial structure of landscape elements with the dynamics of individual species i.e. 'scaling up' (Nunney and Campbell 1993; Desrochers et al. 1999).

1.1.2 The effects and mechanisms

How habitat loss and fragmentation affect bird species will obviously depend on the specific behaviour and requirements of the species. Changes in demographic attributes such as survival, reproductive success and recruitment, immigration and emigration rates may lead to fluctuations in population size, sometimes catastrophic, leading to species extinction (Perrins 1991; Roth and Johnson 1993). Forest-fragment size per se is perhaps the single best predictor of the probability of occurrence and the population densities of forest-interior or forest-dependent species (Rolstad 1991 and references therein). Related to habitat quality, increased mortality rates and impaired reproduction could also disrupt population dynamics and result in declining populations (Temple and Cary 1988; Lebreton et al. 1993; Donovan and Lamberson 2001). Furthermore, skewed sex ratios resulting from differential mortality might impair reproduction, as would increased nest predation or a scarcity of nesting sites in (small) highly-disturbed fragments (Small and Hunter 1988; Latta et al. 1995). Dispersal or species mobility also plays an important part in the persistence of metapopulations in fragmented landscapes (Reed 1998). The model of Urban and Shugart (1986) demonstrated a relationship between reproduction and dispersal, where impaired reproduction led to fewer surplus individuals, allowing restricted dispersal to play a more important role in determining species distribution. In reverse, an available pool of surplus non-breeders can help ameliorate the effects of diminished dispersal. However, reduced dispersal can result in a loss of genetic diversity through drift and inbreeding effects, which can independently increase the extinction risk (e.g., Daniels et al. 2000).

Studies of individual behaviour can clearly further our understanding of how populations fare in fragmented habitats (Dale et al. 1994; Caro 1999). For instance, we know little about what birds know at the ecological landscape scale and how they use that to influence their decisions on both dispersal and habitat selection (Blondel and Lebreton 1996; Lima and Zollner 1996; Grubb and Doherty 1999). For the most part, dispersal distances and the influence of the landscape on individual movement remain unclear (Caro 1999). Other behaviours linked with population declines include those that are associated with negative population growth rates, such as Allee effects (Allee et al. 1949), which may reduce per capita growth rates at low population densities (Stephens and Sutherland 1999). Including behaviour in population extinction models helps improve their predictive abilities (Reed 1998); indeed, a dearth of behavioural information may limit the development of explicit individual-based population models (Lima and Zollner 1996; Daniels et al. 2000). Although the fusion of demography, genetics and behaviour is vital for resolving the mechanisms by which fragmentation (and resulting environmental heterogeneity) affects bird species (Blondel and Lebreton 1996; Walters 1998; Lindenmayer and Peakall 2000), few studies have looked at the effects of spatial structure on demographic and genetic processes in the context of conservation (Clarke and Young 2000).

1.1.3 Research strategies

Predicting the effects of habitat disturbance on flora and fauna (and hence effectiveness of different conservation measures) is complex because of the many interactions involved, as well as the dynamic and variable nature of the system (Sutherland 2000). Therefore, in order to elucidate some of the mechanisms behind the problems associated with fragmentation on birds, there is a need to examine a wide range of ecological correlates of sensitivity, such as nesting and foraging habits, population size and social structure (Walters 1998). Different species differ in their sensitivity, and hence responses, to habitat fragmentation (Warburton 1997); for instance, common and rare species may not respond similarly to habitat disturbance (Perrins 1991; Caughley 1994; Maina and Howe 2000). Various indicator species – species thought to be ecologically representative of particular environments and/or of other wildlife species also associated with those environments – have been proposed for study (as models) in order to understand the general effects of fragmentation on organisms in a habitat (e.g., Noss 1990; Lambeck 1997; Hutto 1998). Though such indicator species have been used for driving management plans (Landres et al. 1988; Morrison et al. 1998), the among-species variation in sensitivity renders their suitability as exact indicators of other species or taxa debatable (e.g., Lawton et al. 1998; Lindenmayer et al. 2002). Thus, before projecting findings from one species (or population) to entire avifaunas, we need to distinguish between correlative patterns and causal mechanisms, as only the latter can explicitly demonstrate validity of such prognosis (Green and Hirons 1991; Perrins 1991; Marzluff and Sallabanks 1998). Better still, rather than thinking of ecological indicator species as representatives of other species (e.g., to directly infer population viability of another species), they are likely to be more useful for monitoring general ecosystem conditions (Morrison et al. 1998). This bridges the gap between use of species-to-species indicators and structure-based indicators, where (in the latter) spatial features at the landscape-level are used to develop a solution for conserving elements within the mosaic (Forman and Collinge 1996; Lindenmayer et al. 2000). Working at the ecosystem level is imperative because the solutions to fragmentation problems need to be placed on a broader framework of land use and its impacts on entire ecosystems and landscapes (Wiens 1994; Noss 1996; Opdam and Wiens 2002).

Conservation biology aims at investigating and describing the biodiversity of the world, understanding the effects of human activities, and developing practical interdisciplinary approaches to protecting and restoring ecological diversity (Primack 2000). Yet, there remains an urgent need for actual data to strengthen the scientific basis for conservation (Diamond et al. 1987; Green and Hirons 1991). Conservation strategies for small (and fragmented) populations can vary depending on the relative importance of loss of genetic variation and demographic/environmental effects on the perceived threat (Lande 1988b; Saunders et al. 1991; Westemeier et al. 1998). Some schools of thought contend that environmental and demographic consequences of human disturbance present a greater threat to wild populations because they occur at a swifter rate than any genetic problems that might arise from these processes (e.g., Lande 1988b; Caro and Laurenson 1994). Others stress the importance of genetic aspects (e.g., Avise 1989; Vucetich and Waite 1999). While demography is of primary importance in managing populations for conservation, genetic as well as behavioural processes are also important because they can directly affect demography (e.g., Dietz et al. 2000), or provide further insights into the demography of a population, e.g., by revealing past geographic structure and distribution (Lacy 1988; Milligan et al. 1994). Moreover, when detrimental demographic and genetic effects of fragmentation are combined, they sometimes have a synergistic effect on population viability (e.g., Daniels et al. 2000; Oostermeijer 2000).

Ultimately, however, even with a complete understanding of the population processes that are a consequence of fragmentation, conservation biologists must also become active teachers, politicians, organizers, motivators, managers and practitioners (Primack 2000; Whitten et al. 2001). While research is important in providing a better grasp of the problem, socio-economic (Holl and Kappelle 1999) and education issues such as training and raising the awareness of local resource stakeholders (Bennun 2002) ultimately govern the usefulness of research findings for conservation. Translating research into conservation remains tricky, especially because of the conflicts between conservation-demands on the one hand, and political and socio-economic interests on the other (Grajal and Stenquist 1998). The positive correlation between human population density and bird species richness in Africa (Balmford et al. 2001) implies that conservation conflicts are inevitable. Short-term economic sacrifices need to be made, especially by incumbent governments, for long-term environmental gains (James et al. 1999).

1.2 The Taita Hills system

1.2.1 The background

1.2.1.1 Study area: geographic information and conservation status

The Taita Hills lie in south-eastern Kenya at 03°20′S, 38°15′E, about 150 km inland from the coast, and cover an area of about 250 km^2 (Brooks et al. 1998a). Geologically, they are the northernmost part of the Eastern Arc mountains (Lovett 1986; Lovett and Wasser 1993), a global biodiversity hot-spot (Myers 1990; Mittermeier et al. 1998) and part of the Tanzania-Malawi Mountains Endemic Bird Area (Stattersfield et al. 1998) (Fig. 1.1a). The combined effects of long isolation—they were separated from the main Guineo-Congolian forests of west and central Africa by the Miocene uplifts of the central African plateau 10 to 17 million years ago—and climatic stability have produced a distinctive flora and fauna with very high levels of endemism in the Eastern Arc forests

(Lovett and Wasser 1993). The Taita Hills are made of metamorphic rock covered by a hard quartzite cap; a detailed description of the physical geography of this area and its surroundings can be found in Brooks et al. (1998a). Like the Eastern Arc forests, these hills also have high levels of endemism in many fauna and flora (Beentje and Ndiang'ui 1988). Being a recognized Important Bird Area, they are among the highest priorities for biodiversity conservation in Kenya (Lovett and Wasser 1993; Brooks et al. 1998a; Bennun and Njoroge 1999). The Taita Hills massif is isolated from other highland blocks, the closest of these being 80 km away, by the semi-arid plains of Tsavo West National Park (600-700 m) (Lens et al. 1999b).

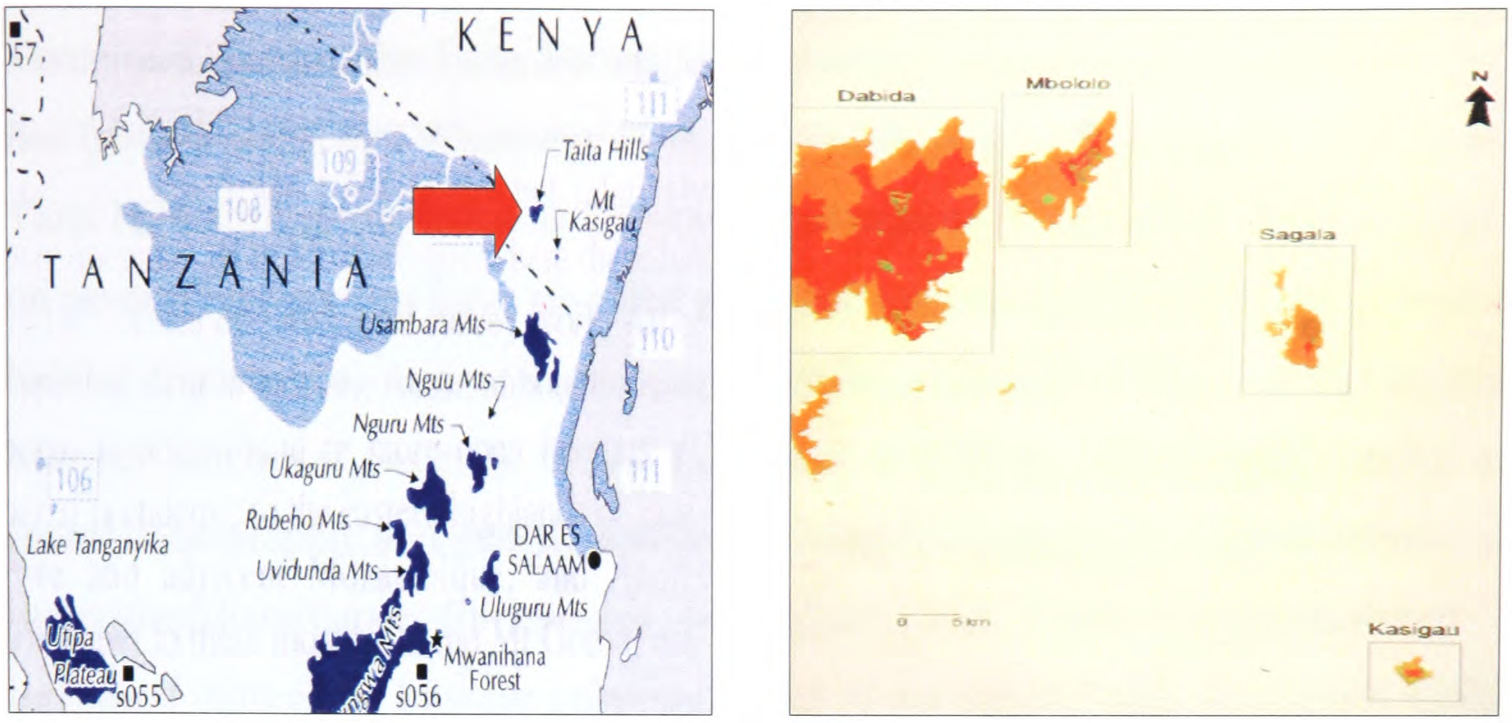
The Taita Hills forests have been fragmented for a long time, but large-scale forest loss has mainly occurred since the 1960s, reaching critical levels in recent years (Brooks et al. 1998a). During this time, the once extensive indigenous forests have been encroached upon leaving only small remnants on hilltops, while the denuded hilltops and hillsides (unsuccessfully cultivated after clearing natural vegetation) have been reforested with exotic trees (Beentje and Ndiang'ui 1988). These indigenous forest fragments were identified as one of the habitats in urgent need of inventorization and protection by the strategy conference for management and protection of Kenya's plant communities held in 1984 (Beentje and Ndiang'ui 1988). While inventories of wild flora and fauna have been fairly well done since then, their gazettement has dragged on for years; they are only protected as Forest Reserves under jurisdiction of the Forest Department. This category permits considerable resource exploitation and manipulation, with little investment in protection (Lovett and Wasser 1993). Thus, multiple threats still persist, including exotic tree plantations, clearance for agriculture and the ever-increasing demands for fuelwood and building poles. This is compounded by the fact that the forests are still little appreciated by the custodians, decision makers and stakeholders, despite their importance for biodiversity and watershed protection (Bennun and Njoroge 1999); disturbance continues with little control (Nummelin 1997).

The present landscape consists of three distinct isolates: Sagala Hill (1,450 m, separated from the rest of the massif by a valley at 700 m), Mbololo Hill (2,209 m, separated from

Dabida by a valley at 900 m) and Dabida Hill (including the highest peak at 2,228 m) (Lens et al. 1999b) (see Fig. 1.1b). Twelve forest fragments are distributed across these three massifs. These patches are scattered on hilltops and ridges and surrounded by a mosaic of human settlements, small-scale cultivation plots and plantations of *Pinus, Eucalyptus, Cupressus* and *Juniperus* spp. as follows: on Sagala Hill: Sagala (*c.* 4 ha); on Mbololo Hill: Mbololo (*c.* 180 ha) and Ronge (*c.* 4 ha); and on Dabida Hill: Ngangao (*c.* 135 ha), Chawia (*c.* 95 ha), Fururu (*c.* 8 ha), Macha (*c.* 2 ha), Mwachora (*c.* 2 ha), Yale (*c.* 2 ha), Kichuchenyi (*c.* 1 ha), Vuria (*c.* 2 ha) and Ndiwenyi (*c.* 4 ha) (area estimates based on GPS readings) (Fig. 1.1c).

(a) Eastern Arc Forests

(b) Taita Hills and Mt. Kasigau



(c) Taita Hills forest fragments

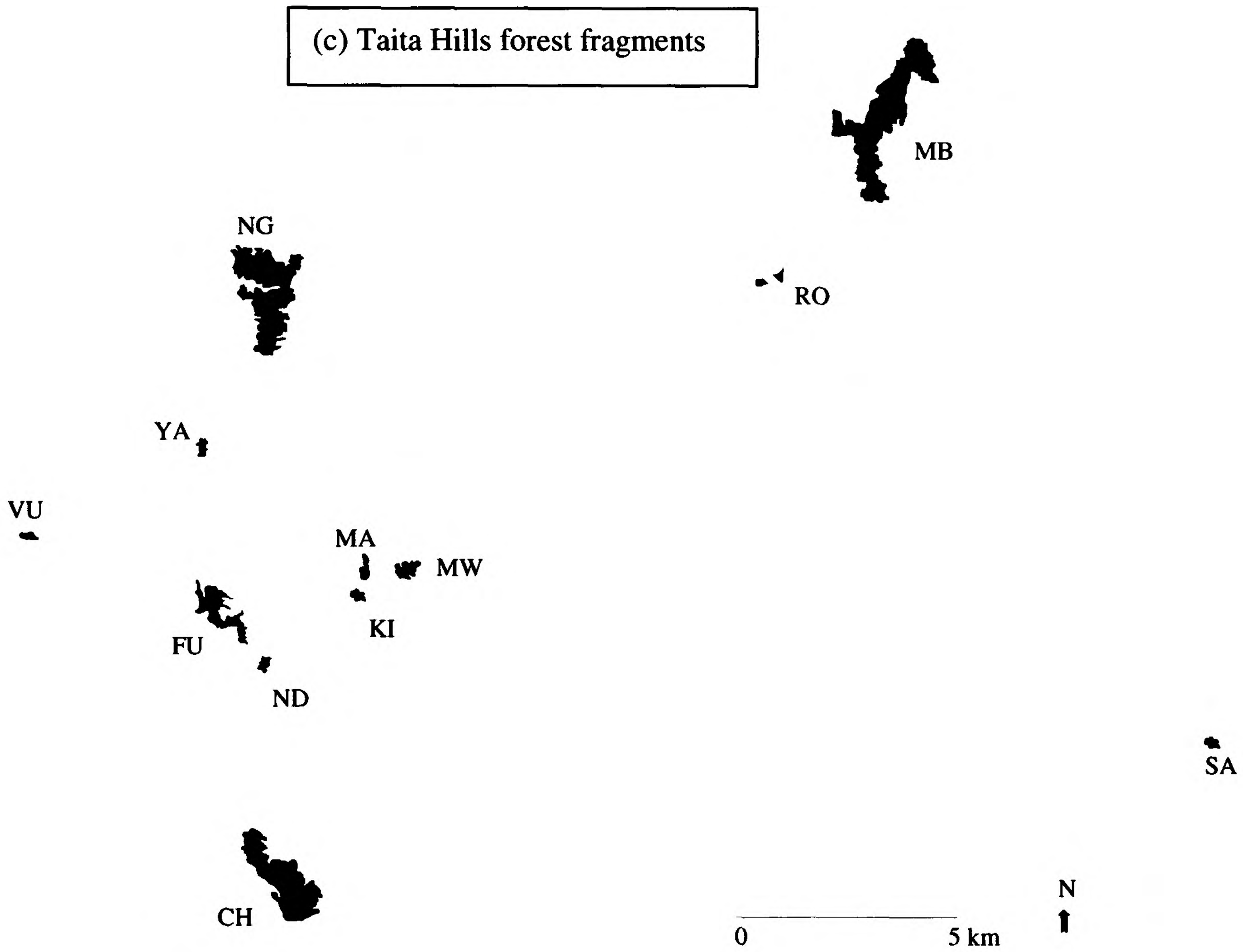


Figure 1.1 Maps of (a) the Taita Hills relative to other Eastern Arc forests, (b) the three main massifs of the Taita Hills together with the adjacent Mt Kasigau, and (c) the forest fragments within which the study was carried out, showing their distribution across the three massifs. [MB = Mbololo, RO = Ronge; SA = Sagala; NG = Ngangao, YA = Yale, VU = Vuria, MA = Macha, MW = Mwachora, KI = Kichuchenyi, FU = Fururu, ND = Ndiwenyi, CH = Chawia].

1.2.1.2 Threats to avifauna

Three bird species, the Taita Thrush *Turdus helleri*, Taita Apalis *Apalis (thoracica) fuscigularis* and Taita White-eye *Zosterops (poliogaster) silvanus*, are endemic to the Taita Hills forests and listed as Critically Endangered (Collar et al. 1994). Recent studies on several bird species have revealed potentially detrimental patterns associated with habitat disturbance, such as increasing fluctuating asymmetry and low dispersal rates between patches (Lens et al. 1999a; Lens et al. 1999b). Species-specific studies have found demographic and genetic problems facing the endangered species themselves with increasing disturbance; for instance, skewed sex ratios, lower survival rates and increased inbreeding in some subpopulations of the thrush (Lens et al. 1998; Galbusera et al. 2000a; Lens et al. 2000; Lens et al. 2002a). Still unclear are both the underlying processes (demographic/genetic/behavioural) that produce these patterns, and the population processes they are disrupting, if any. Moreover, because these previous studies were largely limited to only a few fragments in which the endangered birds still occurred, the role of the other (mostly small) fragments at the landscape level (for example, as pockets holding subpopulations, stepping stones facilitating dispersal or as genetic reservoirs) remains unknown.

All-inclusive studies, incorporating a wide array of potential factors that influence species sensitivity to fragmentation, have been advocated as a means of gaining insights into the main factor(s) causing problems for threatened species in fragmented landscapes (Walters 1998). Only after teasing some of these intricate issues apart can we isolate the different elements that are important in shaping the dynamics of populations (Perrins 1991). From this, we can pinpoint the problems and be able to arrest the declines and/or restore locally extinct populations where necessary (Green and Hirons 1991). These data can only be obtained by studying a relatively common species that occurs in most fragments across the landscape mosaic. By furnishing ample sample sizes, its demographic and genetic aspects can be examined to similar detail in each patch, as well as any interactions between subpopulations in separate patches. For the Taita Hills, such insights, if derived from a forest-dependent species, would enable comparison with the other forest-interior and endangered species for which similar data are available. This would build on our knowledge about how comparable findings from rare and common species are, and hence determine the usefulness of data from common species in formulating conservation plans for the endangered ones (Perrins 1991).

1.2.2 The approach

1.2.2.1 Model species: rationale and selection

Though desirable, it is not normally feasible to study the entire spectrum of species in a habitat to provide the ideal scientific basis for conservation strategies. Realistically, only few species can be studied in sufficient detail to enable making predictions on the effects of habitat destruction at the landscape-level. This has led to use of either the presence or abundance of certain species as models, indicating the general effects of habitat disturbance on related species and general biodiversity in the area (Noss 1990; Hutto 1998); birds and butterflies have been suggested as such 'flagship taxa' (Kremen 1992; Hill and Hamer 1998). These management indicator species are selected for being ecologically representative of the particular environment and/or of other wildlife species also associated with those environments (Morrison et al. 1998). However, due to differences in species sensitivity to forest fragmentation, the applicability of these studies in the precise context of one species representing another remains controversial (Noss 1990; Lawton et al. 1998). This notwithstanding, use of ecological indicator species for monitoring general ecosystem conditions (rather than as representatives of other species per se) is still reasonable (Morrison et al. 1998). In addition, where comparative data on several species are available, applicability of this indicator species approach directly to other species can be explored. These reasons provided the motivation for selecting the white-starred robin *Pogonocichla stellata* (hereafter robin) as a model species in these fragments.

Recently completed studies in the Taita Hills found that the robin was affected by forest disturbance in a manner similar to the related Taita thrush (Lens et al. 1999a; Lens et al. 1999b). Both had higher male-biased sex ratios, while an increase in fluctuating asymmetry between historical (museum) and recent (capture) samples in the most disturbed fragments were parallel, only far more acute for the thrush. [Fluctuating asymmetry, FA, expresses amount of developmental instability, DI, which is the inability of an organism to withstand random perturbations during its development. The underlying assumptions of FA are that the development of both sides of bilaterally symmetrical traits is influenced by identical genes, that non-directional differences between the sides are of environmental origin and reflect accidents during development, and that high levels of FA indicate high levels of DI (Clarke 1993; Palmer 1994; Møller 1997; Lens and Van Dongen 2000).] This suggests a comparable effect of habitat loss and fragmentation on both species. This effect seems less severe for the robin (at least at present), perhaps because it is more adaptable or was more abundant to begin with. Still, in addition to expanding the small database on the effects of habitat loss and fragmentation on small populations in tropical areas, there seems to be a possibility that studying the robin will provide reasonably applicable data for the thrush. Findings might shed some light into why the thrush is absent in all (except one) of the small fragments, or alternatively, why it is present in the one small fragment. The fact that work can be carried out in a wide continuum of forest patches (in most of which the endangered species are not present) is a fundamental advantage in trying to understand the landscape functioning in its entirety. It will allow for a more direct and broader input to future management/restoration plans, than can be accomplished by studying the highly restricted and threatened birds alone.

1.2.2.2 The white-starred robin

The robin is a forest-dependent bird, resident in montane forests of eastern to southern Africa (Keith et al. 1992; Bennun et al. 1996). Of the nine known races, six occur in Kenya and northern Tanzania; sub-species *helleri* is confined to the Taita Hills and Mt. Kasigau (Moreau 1951; Keith et al. 1992; Zimmerman et al. 1996). It is sexually monomorphic, though females are usually smaller in size. It forages at all levels in the forest, most frequently in the undergrowth and at ant trails, but also tosses leaf litter, gleans foliage, makes aerial sallies to capture flying prey and ascends into the canopy for small fruits when available e.g. *Rhus* sp. (Oatley 1982b; Willis 1985; Keith et al. 1992). It is territorial and (apparently) monogamous. The female constructs a domed nest of moss and dead leaves often on sloping ground with a lush herbaceous layer (Oatley

1982c). She lays a clutch size ranging from 2-4 eggs and incubates them alone for 16-18 days. Both sexes feed the young through the 14-day nestling period and 42-day post-fledging period (Oatley 1982c; Keith et al. 1992). Unlike many other forest birds, this species has a quiet song and is seldom aggressive towards conspecifics. Nonetheless, males effectively defend territories during the breeding season, sometimes year-round or even throughout their lifetime in high quality habitats (Oatley 1982a, c; Oatley and Arnott 1998). The robin is also remarkable for its distinctive subadult plumage (separate from the 'spangled'-juvenile and the adult plumages), which has been thought to result in deferment of breeding by both sexes (Moreau 1951; Oatley 1982a). In addition, this plumage appears to confer crypsis, as well as provide a functional social values of enabling immature birds to reside in adult territories without harassment, and reducing competitive stress for the adults (Oatley 1982c). Finally, this species showed high homing ability and site fidelity following translocation in south-central Africa, where it is an altitudinal migrant (Dowsett 1985; Dowsett and Dowsett-Lemaire 1986).

1.3 Overall aim of this study

The overall goal of this study is to examine various demographic and genetic attributes of the white-starred robin *Pogonocichla stellata,* and compare life history characteristics of bird populations in forest fragments of different sizes and habitat quality. It endeavours to provide insights into the crucial stage(s) in the life cycle that influence their persistence. This will facilitate drawing conceptual models predicting the effects of habitat disturbance on birds, both at individual patch and landscape-levels. Conceptual modelling attempts to explain the distribution and abundance of a species through an evaluation of research findings, field observations and general judgement about the species or habitat (Morrison et al. 1998). This also helps predict what will or might happen to populations under a given combination of present or future habitat and spatial conditions (Opdam and Wiens 2002). Because conservation is normally taken into consideration only after socio-economic and financial interests (which are often competing) are fulfilled (see Lande 1988b; Grajal and Stenquist 1998; Bennun 2002), the ability to make clear predictions and informed guesses offers the best chance that the nominal resources provided will be put to their best use.

1.4 Thesis structure and specific hypotheses

This thesis is arranged into nine chapters, with a core of six self-contained result chapters prepared as a basis for future publication. Because of this format, it is not possible to totally avoid some repetition, particularly within the study site and species sections; replication is however kept to a minimum and all references are pooled into a single bibliography at the end. Chapters 2 and 3 provide basic demographic information, chapters 4 and 5 assess the social structure in different patches, chapter 6 evaluates genetic aspects, and chapter 7 examines nest predation. The General Discussion (chapter 8) provides a summary of the key findings and their interpretation on a larger scale, both from scientific and conservation angles, in addition to desired future work. Lastly, an Appendix Chapter (chapter 9) is a recently published collaborative paper, which includes the white-starred robin as one data point in an investigation into overall persistence of bird species in these forest fragments. The general running theme in the chapter hypotheses below is that levels of habitat disturbance are inversely proportional to fragment size; thus habitats within larger fragments are of better quality than those in small ones (Wilder et al. 2000). (NB: all data chapters are presented in their final pre-submission forms. The prefix 'we' is used throughout because they represent multi-authored papers where professional workers were involved in collaboration, particularly for molecular analyses.)

Chapter 2. Demography of the white-starred robin *Pogonocichla stellata* in the Taita Hills forest fragments. I: Population densities, sex ratios and age structure

Hypothesis: in lower quality habitats, reduced bird densities, skewed age and sex ratios may arise maladaptively because of constraints imposed by these habitats, or as a result of adaptive compensations to the constraints imposed by the small fragments.

Chapter 3. Demography of the white-starred robin *Pogonocichla stellata* in the Taita Hills forest fragments. II: Survival and recruitment patterns

Hypothesis: The probability of survival varies with age and habitat quality (fragment size), while recruitment rates and patterns differ with fragment quality and demographic attributes.

Chapter 4. Ranging behaviour and habitat use by the white-starred robin *Pogonocichla stellata* in different-sized forest fragments in Taita Hills, SE Kenya.

Hypothesis: Birds in habitats of lower quality require larger territories to satisfy their needs. Findings will provide insights into the main functions of territories and determinants of their sizes, which could vary for different fragments, for instance, depending on density-dependent effects.

Chapter 5. Relative presence of ‘floaters’ in two isolated populations of an Afrotropical forest bird species: A pilot study

Hypothesis: Habitats of different quality and with different demographic attributes (such as population densities and sex ratios) will have different social structure set-ups leading to different factors regulating the population sizes. Depending on both habitat and individual bird characteristics, adults without breeding opportunities could either become floaters (‘hopeful strategy’ awaiting an empty territory), or disperse and try to breed immediately, albeit in sub-optimal territories.

Chapter 6. Effects of habitat fragmentation on the white-starred robin *Pogonocichla stellata* in the Taita Hills: testing for equilibrium with genetic markers.

Hypothesis: In theory, habitat fragmentation impedes gene flow, such that populations begin to develop some genetic differentiation due to genetic drift. The move from allozymes and mitochondrial DNA to more variable genetic markers such as microsatellites will help track such changes related to recent fragmentation more effectively (Lindenmayer and Peakall 2000).

Chapter 7. Patterns of artificial nest depredation in different-sized Afrotropical forest fragments, SE Kenya.

Hypothesis: Differences in abundance and diversity of predators, or in nest placement sites among habitats of different quality and/or size, result in variation in nest depredation rates.

Chapter 8: General discussion

This summarizes insights from the six result-chapters, and the potential usefulness of the model species approach both to understanding fragmentation effects and for conservation purposes

Chapter 9 (Appendix paper): Avian persistence in fragmented rainforest

Hypothesis: Based on metapopulation theory, patch occupancy by birds across the landscape is a function of both species levels of mobility and sensitivity to forest deterioration.

Paper I

Submitted manuscript [*Oikos*]

Variation in some demographic attributes between subpopulations of a tropical passerine in a fragmented rainforest

Mwangi Githiru & Luc Lens

Paper I

Submitted manuscript [*Oikos*]

Variation in some demographic attributes between subpopulations of a tropical passerine in a fragmented rainforest

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CHAPTER 2

Typical small forest fragment on hilltop

Ongoing degradation within fragment Chawia

"There is nothing in which the birds differ more from man than the way in which they can build and yet leave a landscape as it was before."

Robert Lynd

Chapter 2: Variation in some demographic attributes between subpopulations of a tropical passerine in a fragmented rainforest

Summary

Effective conservation demands careful priority setting and making the right choices in order to get the most out of the few (human and economic) resources available. To facilitate this for the Taita Hills fragmented landscape, we examined various demographic attributes of the white-starred robin *Pogonocichla stellata* metapopulation. Between 2000 and 2001, we collected data (mainly using mistnets) in three forest fragment-size categories within this landscape. We found the highest population densities in the largest and least disturbed patch (NG, *c*135 ha), followed by the small fragments (SF, *c*2-8 ha), and the least in the medium-sized patch (CH, *c*95 ha). Sex ratios did not vary either with age or among the fragment-size categories; typically, between 20 and 30 % of the metapopulation was female. Juvenile to adult ratios, an index of reproductive success, revealed matching high levels in NG and SF, and significantly lower levels in CH. The low density of birds and skewed sex ratios resulted in a scarcity of females in CH, suggesting an inversely density-dependent (Allee) effect. The respective rates of population change (λ) revealed that each subpopulation was stable on average; the metapopulation was also stable ($\lambda = 0.996$). The conservation upshots of these results are twofold. First, they suggest an important role of the small patches in shaping the demographic attributes of the metapopulation, e.g., by acting as a potential source of migrants. Second, though the λ-values suggested each subpopulation was stable, decreased dispersal would probably swiftly endanger the survival of the CH population.

2.1 Introduction

A fundamental concern for conservationists facing problems associated with forest loss and fragmentation is deciding which fragments contain viable populations, and thus warrant priority for conservation. Often, source habitats [based on reproductive or survival rates (Pulliam 1988)] are considered over sinks (e.g., see Trine 1998), although dispersal rates and patterns can also play an important role (Tyre et al. 2001). This has led to the development of habitat occupancy and metapopulation concepts in modelling dynamics in fragmented landscapes (e.g., Hanski and Gilpin 1991; Hanski 1998; Lande et al. 1998), and has motivated discussions about the relative importance of within-patch and between-patch processes in explaining persistence of populations occupying patchy landscapes (Addicott et al. 1987; Sih et al. 2000; Thrall et al. 2000; Flather and Bevers 2002). Understanding the mechanisms that determine metapopulation persistence in fragmented landscapes is useful for predicting the most effective conservation strategies at regional scales (e.g., Desrochers et al. 1999). To achieve this, one needs a good handle on various demographic attributes of individual subpopulations (particularly population density, trends and structure), and how separate subpopulations interact (see Green and Hirons 1991; Perrins 1991).

Recent work revealed that bird species inhabiting the highly-fragmented Taita Hills forests of south-east Kenya show signs of population response to habitat disturbance, such as male-biased sex ratios and increasing levels of fluctuating asymmetry (Lens et al. 1998; Lens et al. 1999b; Lens et al. 2002a). Still unclear are the causes of these patterns and their potential effects on key population processes such as survival and reproduction. For instance, assuming even sex ratios at hatching and fledging (Clutton-Brock 1986), the usual female-biased natal dispersal in birds (Greenwood and Harvey 1982) and associated mortality (Waser et al. 1994) could lead to male-biased sex ratios at the immature and adult stages. Moreover, the facultative nature of adult dispersal (Clarke et al. 1997) could either ameliorate or worsen these biases with ramifications for breeding. At low population densities, acute sex ratio biases could produce a deficiency of mates, thereby disrupting reproduction. Hence, together with population declines resulting directly from habitat loss and degradation, differential mortality of the sexes could impair reproduction (e.g., Peterson and Silvy 1996).

In highly-fragmented ecosystems such as the forest “archipelago” of the Taita Hills, a landscape-level study is necessary to provide insights into the mechanisms that shape individual subpopulations, and how metapopulations are affected by within- and between-patch dynamics. It is therefore essential to conduct studies on forest-dependent species still present in most fragments across the landscape, examining various demographic parameters to a similar level of detail in all fragments. We selected the white-starred robin *Pogonocichla stellata* (hereafter robin) as an ecological model species for such a study, based on its strict forest-dependence (Bennun et al. 1996) and its persistence in most indigenous forest patches across the Taita landscape (Lens et al. 1999a). Robins were captured, marked and released for later recaptures; there were six capture sessions in all. Capture-recapture histories of individual birds were analysed in program MARK (White and Burnham 1999) to obtain estimates of population size and rates of population change. In this paper, we examine if and how adult densities, levels of productivity (ratio of young to adult birds) and sex ratios vary with fragment size and quality.

2.2 Methods

2.2.1 Study species and study area

The white-starred robin is a forest-dependent species found in montane forests of eastern to southern Africa (Keith et al. 1992). It forages at all levels in the forest, most frequently in the undergrowth and at ant trails (Oatley 1982b; Willis 1985). It is territorial, (apparently) monogamous and does not show much antagonism towards conspecifics (Oatley 1982a; Keith et al. 1992). Age (juvenile, immature or adult) was determined according to Jackson (2000). A total of 502 individuals were sexed by analysis of the highly conserved W-chromosome linked gene CHD-W (Ellegren 1996); methodological details in Lens et al. (1998; 1999a). Molecularly sexed males and females differed in wing length: adult male = 84.4±1.9, $n = 222$; adult female = 78.8±1.6, $n = 86$; immature male = 80.6±1.8, $n = 80$; immature female = 76.3±1.5, $n = 31$; juvenile male = 80.9±1.7, $n = 67$; juvenile female = 76.8±1.7, $n = 16$ (ANOVA: Age: $F_{2,496} = 134.0$; Sex: $F_{1,496} = 465.4$; Age*Sex $F_{2,496} = 7.5$; all $P < 0.001$). Because the mean percentages of birds sexed as females by molecular and morphological techniques were highly correlated ($r = 0.68$, $P = 0.0001$, $n = 41$) and did not significantly differ ($t_{39} = 0.4$, $P = 0.67$), sex ratios were based on morphological data as these represented a larger sample size.

The Taita Hills, located in southeast Kenya (03°20'S, 38°15'E, maximum altitude 2,228 m), are an Endemic and Important Bird Area (Stattersfield et al. 1998; Bennun and Njoroge 1999). Geologically they form the northernmost outlier of the Eastern Arc Mountains of Tanzania and Malawi (Lovett 1986; Lovett and Wasser 1993). Extensive forest loss over the last four decades has seen the forest reduced to a network of 12 remnant patches scattered across hilltops and ridges (Brooks et al. 1998a; Lens et al. 1999a). Based on structural qualities of the vegetation measured by Wilder et al. (2000), and on plant species richness and diversity (Githiru 2000), smaller fragments were generally found to be of poorer quality than larger ones. Data for this study were collected from seven patches, grouped into three fragment-size categories as follows: large: Ngangao (NG, *c*135 ha); medium: Chawia (CH, *c*95 ha); and small (collectively referred to as small fragments, SF): Fururu (FU, *c*8 ha), Ndiwenyi (ND, *c*4 ha), Macha (MA, *c*2 ha), Mwachora (MW, *c*2 ha) and Yale (YA, *c*2 ha) (for map, see Galbusera et al. 2000a).

2.2.2 Study design

Five 3-ha plots were randomly selected in each of the larger forest patches (NG and CH). The smaller ones were treated as a single plot each. Within each plot, three permanent mist-net lines each measuring between 54 and 57 metres long, were set up for capturing the robins. Each ringing session involved two days of mistnetting per plot (all three net-lines run simultaneously); mistnetting was done between 0600 h and 1200 h, then between 1500 h and 1800 h on both days. The length of each ringing session per fragment-size category was hence 10 days (excluding net-shifting days). Between May 2000 and December 2001, six separate ringing sessions were conducted in each fragment, corresponding to 6 encounter occasions. Session one run from 12th May to 30th June 2000; session two from 15th July to 28th August 2000; three from 17th October to 3rd December 2000; four 20th March to 3rd May 2001; five 25th June to 8th August 2001; and six 3rd November to 9th December 2001. Thus, the mean inter-session intervals (for each plot) varied as follows: between session 1 and 2, 59 ± 2 days; 2 and 3, 94 ± 2 days; 3-4, 134 ± 23 days; 4-5, 93 ± 2 days; and 5-6, 120 ± 10 days. Because all individuals captured were immediately released back into the population, the encounter histories were based solely on live recaptures (see White and Burnham 1999).

2.2.3 Estimation of adult and juvenile density

We estimated adult population densities, rates of change and recapture probabilities using Jolly-Seber models in program MARK (White and Burnham 1999). There were three groups in the model (Ngangao, Chawia and Small Fragments), while the variation in time intervals between successive ringing sessions was integrated as a multiple of the shortest interval (59 days). Thus, between sessions 1 and 2 the interval was "1", between

2 and 3 "1.6", 3 and 4 "2.3", 4 and 5 "1.6", and, 5 and 6 "2.0". Because recapture data were too sparse to include interactive and additive models, the most parameterised (global) model was — $\Phi_t\ p_t\ \lambda_t\ N_g$, where Φ is the two-monthly survival probability, p the two-monthly recapture probability, λ the two-monthly rate of population change, and N is an the estimate of the population size at the start of the study; subscripts t and g refer to time- and group-dependent probabilities, respectively. When a population is exactly replacing itself, its λ-value = 1; if increasing $\lambda > 1$ and if decreasing $\lambda < 1$ (Leslie 1966; Lande 1988a; Zanette 2000). Program RELEASE (within MARK) was applied to test if the global model adequately fitted the data, i.e. whether the dataset violated the underlying assumptions of the Jolly-Seber model (White and Burnham 1999). This test includes two main component tests: i) TEST 2, which tests the assumption of homogeneity in recapture probabilities among individuals and between occasions – hence it tests for equal catchability and is sensitive to short-term capture effects or non-random temporary migration; and ii) TEST 3, which in general tests the assumption that all marked individuals alive at time (t) have the same probability of surviving to (t+1) (White and Burnham 1999). Lastly, in order to estimate the overall rate of growth of the entire metapopulation, data from all subpopulations were pooled into a single group and a separate Jolly-Seber model was run. Akaike's Information Criterion (AIC) was applied for model selection from the set of candidate models incorporating group and time dependence (Anderson et al. 1994; Burnham et al. 1995). Only when the difference in AIC (ΔAIC) between two models was greater than seven did we consider it compelling evidence for real difference between the models (White and Burnham 1999). When less than seven, Likelihood Ratio Tests (LRTs) were applied to test the significance of individual effects between nested models and avoid omitting any important effects (Lebreton et al. 1992); thus, any significant effect was left in the model irrespective of the model's AIC-value. Because data for juvenile and immature birds were too sparse to allow modelling in MARK, a simpler index was used to estimate their densities, as follows: $N_i = n_i/p_i$, and $SE(N_i) = [(n_i/p_i)^2\ (var(p_i)/\ p_i^2)]^2$, where N_i is the number of individuals at time i, n_i is the total number of birds caught in interval i, and p_i and var(p_i) are the estimated capture probability at interval i and its variance (Loery et al. 1997). As recapture probabilities were not age-dependent (Chapter 3), the estimates from adult

Jolly-Seber models were used. All density estimates were calculated as number of individuals per 15 ha in NG and CH (i.e., five 3-ha plots), and a combined 18 ha for the small fragments.

2.3 Results

2.3.1 Survival and population density

The global model fitted the data (TEST 2: $\chi^2_5 = 3.8$, $P = 0.59$; TEST 3: $\chi^2_7 = 8.8$, $P = 0.27$). Of the candidate set of models, the model with the lowest AIC was $\Phi_c\ p_t\ \lambda_g\ N_g$, indicating constant probability of survival both among groups and over time, temporal variation in recapture probabilities, and differences in population growth rates and sizes among fragment-size categories, respectively. Only one other model, $\Phi_g\ p_t\ \lambda_g\ N_g$, with a group effect on survival probability had a ΔAIC-value less than 7. The LRT testing this effect was not significant ($\chi^2 = 0.3$, df = 2, $P = 0.86$). Thus, the lowest AIC model was retained as the most parsimonious one and was used for further parameter estimation (Table 2.1). Mean population density estimates (over the six sessions) for the three age classes obtained by the Loery et al. (1997) method are also given in Table 2.1. A paired-sample t-test testing the difference in adult density estimates from the two methods was not significant ($t_2 = 2.05$, $P = 0.18$). The overall model revealed that the robin metapopulation was stable with a mean growth rate (λ) of 0.996±0.040.

2.3.2 Sex- and age-ratios

In a logistic regression model with proportion females as dependent variable and factors 'fragment-size class', 'age class' and ' session' as independent variables, neither the main effects nor the two- and three-way interactions were significant (all Wald-values between 0.001-2.3, all $P > 0.13$). On average, 22.7±2.5 % of the total catch was female (Fig. 2.1). The ratio of juvenile to adult birds was lower in fragment CH compared to NG (Fisher's Test: $P = 0.0022$) and the small fragments ($P = 0.0046$); these two were not significantly different ($P = 0.51$).

Table 2.1. Parameters estimated from the Jolly-Seber model for adult *Pogonocichla stellata*, including density estimates for adults, immatures and juveniles by the Loery et al. (1997) method (±SE). [Φ estimates two-monthly survival probability, subscript $_c$ refers to constant probability across all groups, p estimates the two-monthly recapture probability, subscripts $_{2\text{-}6}$ refer to the different ringing sessions, λ estimates two-monthly rates of population change, N estimates population size at the start of the study for entire area studied (density estimates per hectare are given in brackets).]

Parameter	Estimate	Standard Error	Loery et al. method		
			Adults	Immatures	Juveniles
Φ_c	0.94	0.054			
p_2	0.15	0.035			
p_3	0.15	0.033			
p_4	0.061	0.018			
p_5	0.11	0.036			
p_6	0.15	0.058			
λ_{Ngangao}	0.96	0.052			
λ_{Chawia}	1.07	0.059			
$\lambda_{\text{Small fragments}}$	1.06	0.059			
N_{Ngangao}	213 (14)	47	215±61	78±24	126±36
N_{Chawia}	63 (4)	18	91±27	24±8	18±5
$N_{\text{Small fragments}}$	75 (4)	20	117±35	40±13	94±28

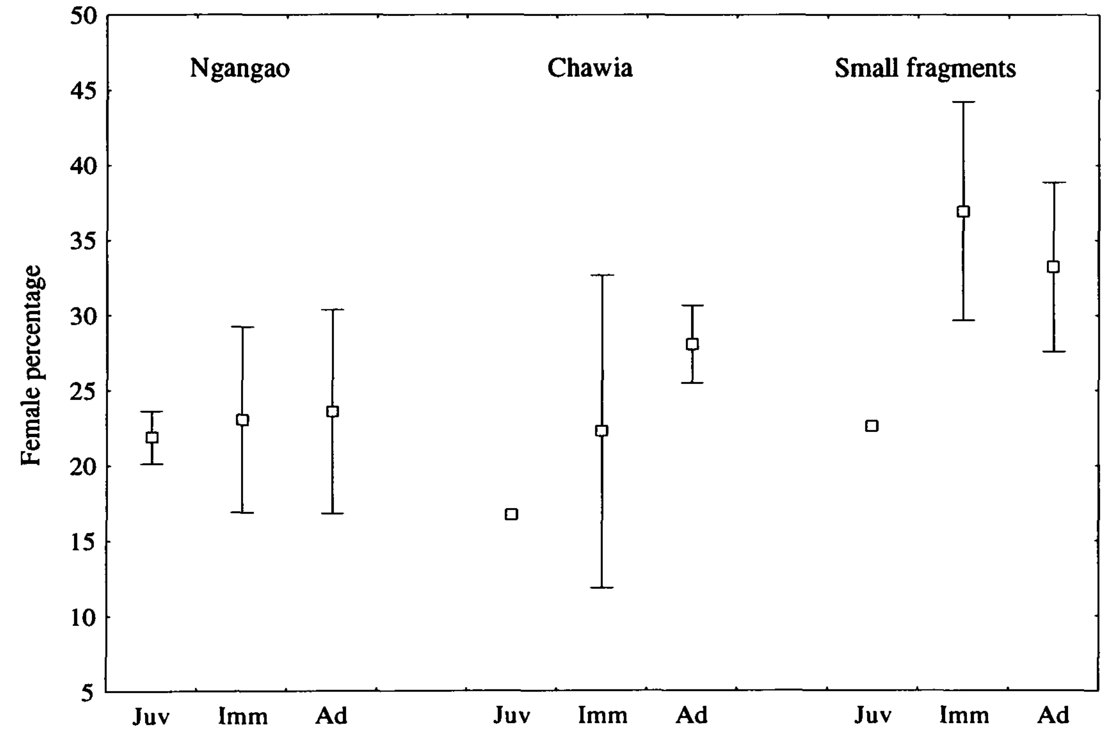

Fig. 2.1. Mean percentage (and SE) over six capture sessions of the total catch of *Pogonocichla stellata* that was female for juveniles (Juv), immatures (Imm) and adults (Ad) per fragment-size category.

2.4 Discussion

Recapture probabilities varied with time but not among fragments, whilst both population size and rate of change varied among different fragment sizes. Lack of variation in recapture probability across fragments validates the use of capture-recapture data to compare population sizes (see Remsen and Good 1996). The temporary drop in recapture probability during the fourth session suggests increased concealment and furtiveness during this period, which, in addition to being the dependency period of the young, was also the main moulting season (M. Githiru & L. Lens, unpubl. data). The highly demanding nature of the moult process in terms of energy and nutrition requirements (Hemborg and Lundberg 1998; Franklin et al. 1999) has been found to lead to increased predation risk, poor flight and feeding efficiencies and general shyness in birds (e.g. Lindstrom et al. 1994; Swennen and Mulder 1995). The largest and least disturbed fragment (NG) showed the highest adult population densities, followed by the small fragments then CH. The estimated density of 14 birds ha^{-1} in fragment NG was slightly higher than expected based on an average of two territories ha^{-1} and up to 3 non-breeding floaters per territory (Chapter 5). This discrepancy might be due to the fact that some of the sampled birds occupied areas extending beyond the boundaries of the study plots.

Despite their small sizes and relatively high levels of disturbance (Wilder et al. 2000), small fragments showed similar density estimates to CH. The likely explanations for this are twofold. First, habitat loss and disturbance has recently escalated in CH to levels much higher than in all other fragments. While this attrition has not reduced the actual fragment perimeter, the degradation has probably led to a decline in habitat quality in terms of availability of food, cover and other resources, as well as an influx of predators from the adjacent landscape matrix as conditions become more favourable for them (Chapter 7). Secondly, the small fragments (particularly FU-ND-MA-MW) are clustered close to one another (see maps in Brooks et al. 1998a; Galbusera et al. 2000a), and could therefore operate as a fine-grained system, rather than independent fragments as would be expected in a proper coarse-grained system (Rolstad 1991). Indeed, recapture data and anecdotal observations revealed that individuals regularly moved, for instance between

FU and ND, within the space of a few days. This could lead to their being able to support higher densities than expected if they were only acting as single, isolated patches (e.g., Quinn and Hastings 1987; Burkey 1988; Nunney and Campbell 1993).

No significant variation in sex ratio skew was found, either between age classes or among different fragment-size categories. Even though ratios were similarly skewed, the real impact could yet be larger at low densities because of female numbers dwindling to levels where territorial males face difficulties in locating a mate, thereby producing a form of Allee effect (e.g., Lande 1987; Wells et al. 1998; Dale 2001). This need not be the case at higher population densities where the skew might just mean fewer numbers of floating females. Indeed, the presence of both male and female floaters in the high population density patch, NG (Chapter 5), suggests there was insufficient space for all adults to hold territories there. Further, the lack of variation in sex ratio skew among age classes shows that the bias was already present at some point during the juvenile stage and remained into the adult stage. Because variation in recapture probability between age groups or sexes was eliminated in the preceding section as a potential cause, this bias was thus caused by either uneven sex ratios at fledging, or higher female mortality at some early stage. Of six successful nests found (each with a clutch of two), five (3 in NG, 1 in CH, and 1 in FU) had a 50:50 sex ratio, while one in NG was all female. Although based on a small sample, this suggests that sex ratios are equal at hatching and fledging, hence pointing towards differential post-fledging mortality as the likely cause. Higher female mortality during the dependency period is a likely factor, though potential reasons for this remain unknown. Additionally, because dispersal in this species was found to be female-biased (Chapter 6), mortality during dispersal could also have some effect. However, five of the seven adult interfragment dispersers were male, possibly indicating the facultative nature of breeding dispersal unlike juvenile dispersal. This suggests that dispersal strategies differed between age groups, fragments and over time (Clarke et al. 1997). More long-term data are required to resolve these issues, particularly monitoring entire families during the dependency period and radio-tracking juveniles in all fragments.

Overall, there were significantly higher ratios of juvenile to adult birds in NG and SF compared to CH, and significantly more individual birds were captured in NG than SF and CH. The higher density estimates of immatures compared to juveniles in CH (Table 2.1) points to low reproductive output together with high rates of immigration. Reproductive success was likely to be impaired by the deficiency of females seen earlier, as well as the higher levels of nest predation found in this patch (Chapter 7). The resulting low juvenile density implies that locally recruiting individuals were fewer in this fragment compared to NG and SF. Yet, dispersal could partly redress this imbalance as young birds and non-breeding adults from NG and SF dispersed to CH. High rates of immigration were feasible because CH was closer to most of the small fragments than NG, and was potentially a bigger recipient of dispersers from them. Indeed, genetic analyses corroborated this assertion by demonstrating potentially greater exchange of individuals between CH and the small patches compared to NG (Chapter 6).

In conclusion, these findings suggest that different processes shaped the population attributes in different fragments. On the one hand, in habitats where large numbers of juveniles were produced (NG and SF), mortality and emigration were probably most important (with little immigration). In CH, in contrast, mortality and immigration (with little emigration) were the most important. This strongly suggests that, while there was some evidence of breeding activity in this patch, the CH population was a net importer of individuals from the other patches indicating it was at least a pseudo-sink. Because of their small sizes, populations in the small fragments may ultimately be unable to hold independent stable source populations. They are likely to be vulnerable to stochastic or human-induced events even at fairly small scales. Hence the only stable and viable source population in the long run would be the NG population ($\lambda = 0.96$). Lande (1988a) reported a similar λ-value for a stable population of the spotted owl *Strix occidentalis*. It would be useful to collect more data on per capita reproductive output from individuals in the different fragments in order to provide solid backing for a source-sink argument. Natal dispersal patterns, together with the likely facultative nature of adult (breeding) dispersal [in terms of rate and sex bias (Clarke et al. 1997)], are also vital future research targets for understanding the influence of social dynamics on the demography and genetics of this metapopulation. Still, the current work has highlighted the important role of the small fragments in maintaining this metapopulation, as well as the negative impacts of habitat degradation even within larger patches. Therefore, while it is crucial to reduce the habitat disturbance going on in the larger fragments (especially CH), it is equally important to conserve the small patches and maintain between-patch processes that sustain the metapopulation as a whole.

Paper II

Submitted manuscript [*Oecologia*]

Survival probabilities and turnover rates in a metapopulation of a tropical rainforest passerine

Mwangi Githiru & Luc Lens

CHAPTER 3

Young boys' trap used to capture various species of small mammals – a delicacy

.... You ask, What is our policy? I will say; "It is to wage war, by sea, land and air, with all our might and with all the strength that God can give us: to wage war against a monstrous tyranny, never surpassed in the dark lamentable catalogue of human crime. That is our policy." You ask, What is our aim? I can answer with one word: Victory - victory at all costs, victory in spite of all terror, victory however long and hard the road may be; for without victory there is no **survival**.

Sir Winston Churchill (1874 - 1965)

Chapter 3: Survival probabilities and turnover rates in a metapopulation of a tropical rainforest passerine

Summary

How well the metapopulation of a species persists in a fragmented landscape largely depends on how well individuals survive within individual patches. Using data from six capture-recapture (ringing) sessions, survival probabilities of the white-starred robin were estimated in seven indigenous forest patches in the highly fragmented Taita Hills 'archipelago', SE Kenya. There were no significant differences in survival probability among age classes (juveniles, immatures and adults) and fragment-size categories (large 135 ha, medium 95 ha, and small 2-8 ha). However, males survived better than females overall. Contrariwise, turnover rates were highest for females in general, but particularly those living in the small and/or degraded patches. Though lower female survival was a general phenomenon, it was likely that actual sources of mortality differed amongst these fragments. On the one hand, mortality associated with female-biased dispersal was probably more important than increased predation in good quality habitats (with high reproductive success). On the other hand, increased predation, especially predation during incubation could have caused the severe increases in female mortality in the more disturbed habitats. In general, these findings imply that conservation efforts are only likely to be successful if they work both within-patches (e.g., to reduce nest predation) and between-patches (e.g., to reduce deaths during dispersal).

3.1 Introduction

Fluctuations in population size – sometimes catastrophic, leading to extinction of species – are governed by changes in survival, reproductive success, recruitment, immigration and/or emigration rates (Perrins 1991; Roth and Johnson 1993; Loery et al. 1997). In particular, the dynamics of populations hinge on mortality and recruitment rates (Lebreton et al. 1993). Habitat loss and fragmentation can affect any or all of these factors. For instance, mortality rates may increase with reduction in forest area and with general habitat degradation. At the same time, successful dispersal between remnant forest patches might decline with increasing distance between fragments and/or reduced connectivity of the landscape matrix due to hostile land uses. Because different effects might require different conservation strategies, it is essential to understand the factors underpinning metapopulation persistence throughout the landscape. In cases where there is shown to be adequate survival and reproduction within individual forest patches, factors affecting chances of long-term persistence are most likely to be associated with isolation and the surrounding (hostile) land-uses (e.g., Andrén 1994; Opdam and Wiens

2002). Alternatively, if reproductive rates are low and/or mortality rates are high, increasing the connectivity (and hence dispersal) will, at best, only have short term benefits (Harrison and Bruna 1999). It is worth noting that both effects could be operating within a metapopulation simultaneously. Only after teasing these issues apart can we pinpoint the problems and be able to arrest the declines and/or restore locally extinct subpopulations where necessary.

Normally, within fragmented landscapes, area-, edge-, or isolation-sensitive bird species (sensu Temple 1990) occur either less commonly in suboptimal (i.e. small and/or degraded) patches, or may have declining populations (e.g., Zanette 2000). Moreover, differences in habitat quality may engender source-sink dynamics within a metapopulation (Dias 1996). Optimal habitats with high reproductive success and survival rates act as source populations, while suboptimal ones act as sinks. As a result, rates of turnover among individuals occupying the suboptimal habitats will be higher than for individuals in better quality patches (Svensson 1999; Boulinier et al. 2001; Zanette 2001). Further, within each subpopulation, age and sex could have additional effects on survival rates. Specifically, female-biased dispersal (e.g., Greenwood and Harvey 1982; Dale 2001) could expose females to higher mortality levels because of the risks associated with dispersal (Waser et al. 1994). In addition, though mainly reported from temperate areas, juvenile survival is often lower than that of adults (e.g., Ringsby et al. 1999; Lieske et al. 2000; Moss et al. 2000). Yet, differences in ecological conditions and social systems of tropical and temperate-zone birds may cause dissimilar life history strategies. For example, the smaller clutch sizes and prolonged natal care found in several tropical bird species could result in higher juvenile survival than expected based on temperate-zone species (e.g., Armstrong et al. 2000; Geffen and Yom-Tov 2000; Stutchbury and Morton 2001).

Capture-recapture data have been used to estimate the survival of bird species for a long time (Cormack 1972; MacArthur and MacArthur 1974; Jolly 1981; Karr 1981; Bibby et al. 2000). Recently developed modelling techniques and programs have improved the robustness, effectiveness and relevance to conservation biology of these studies

(Lebreton et al. 1992; Lebreton et al. 1993). Though studies applying these techniques are becoming more and more common, their use in studying dynamics of populations living in fragmented landscapes has not been explored as much (but see Ringsby et al. 1999), especially in the tropics. Through analysis of individual capture-recapture histories, this study investigates the factor(s) that affect the survival of individuals of small passerine populations in the highly fragmented Taita Hills forests, southeast Kenya. Recent population studies in this area revealed severe sex ratio skews and decreasing survival with increasing levels of habitat deterioration in the globally, critically-endangered Taita Thrush, *Turdus helleri* (Lens et al. 1998; Lens et al. 2002a). Given that this endemic species is entirely restricted to three larger forest remnants, these studies only had a limited landscape scope. The conditions that subpopulations living in small forest patches face, and the importance of these patches for species persistence in a metapopulation context, both remain largely unknown. To assess this, capture-recapture data were collected on the white-starred robin *Pogonocichla stellata* (robin hereafter), a forest-dependent bird species previously shown to occur in all 12 Taita Hills forest fragments (Lens et al. 1999a). This facilitated addressing the following research questions: (i) do survival rates differ between age-classes and sexes within fragments; (ii) do survival rates differ between small and large fragments; and (iii) do turnover or recruitment rates differ between small and large fragments?

3.2 Methods

3.2.1 Study site and species

Extensive forest loss over the last four decades has seen the indigenous forests of the Taita Hills being reduced to three larger fragments (*c*95-180 ha) and nine tiny remnants (*c*2-8 ha) scattered across hilltops and ridges (Beentje and Ndiang'ui 1988; Brooks et al. 1998a; Lens et al. 1999a). Measures of vegetation composition and structure indicated that the smaller fragments were more disturbed and were of poorer quality than the larger ones (Githiru 2000; Wilder et al. 2000). They had lower species richness and diversity, poorer stratification and showed signs of heavy cutting of both old and young trees. Data for this study were collected from seven fragments, grouped into three size-based categories as follows: large: Ngangao (NG, *c*135 ha); medium: Chawia (CH, *c*95 ha); and small (collectively referred to as small fragments, SF): Fururu (*c*8 ha), Ndiwenyi (*c*4 ha), Macha (*c*2 ha), Mwachora (*c*2 ha) and Yale (*c*2 ha) (for map, see Galbusera et al. 2000a). Five 3-ha plots were randomly selected in each of the larger plots (NG and CH), while the smaller ones were treated as a single plot each. Within each plot, three permanent net lines were set up, each measuring between 54 and 57 metres long, where mistnetting was carried out.

White-starred robins occur in montane forests of eastern to southern Africa (Keith et al. 1992). This forest-dependent species (Bennun et al. 1996) forages at all forest levels, most frequently in the undergrowth and at ant trails (Oatley 1982b; Willis 1985; Keith et al. 1992). Upon capture, each individual was aged as juvenile, immature, or adult based on its plumage characteristics (see Jackson 2000). Sex was initially determined through molecular analysis of the highly conserved W-chromosome linked gene CHD-W (Ellegren 1996; Lens et al. 1998). Analysis of a pilot dataset showed that molecularly sexed males and females of all ages differed significantly in wing length as follows: Adult: $\text{male}_{222} = 84.4\pm1.9$, $\text{female}_{86} = 78.8\pm1.6$; Immature: $\text{male}_{80} = 80.6\pm1.8$, $\text{female}_{31} = 76.3\pm1.5$; Juvenile $\text{male}_{67} = 80.9\pm1.7$, $\text{female}_{16} = 76.8\pm1.7$ (Chapter 2). This criterion was subsequently used to sex individuals.

3.2.2 Estimation of survival probability

Between May 2000 and December 2001, a total of 408 individuals (Adult: males 86, 34, 38, females 28, 18, 23; Immature: males 26, 5, 12, females 21, 9, 16; Juvenile: males 31, 5, 21, females 16, 1, 13 in NG [big], CH [medium] and SF [small], respectively) were captured over six separate ringing sessions, corresponding to 6 encounter occasions with only live recaptures (White and Burnham 1999). Each ringing session involved two days of mistnetting per plot, all net-lines run simultaneously. Session one run from 12th May to 30th June 2000; session two from 15th July to 28th August 2000; three from 17th October to 3rd December 2000; four 20th March to 3rd May 2001; five 25th June to 8th August 2001; and six 3rd November to 9th December 2001. The mean intervals between successive ringing sessions per plot were 59 ± 2 days (sessions 1-2), 94 ± 2 days (sessions 2-3), 134 ± 23 days (sessions 3-4), 93 ± 2 days (sessions 4-5) and 120 ± 10 days (sessions 5-6).

Survival and recapture probabilities were estimated using a Cormack-Jolly-Seber (CJS) model in program MARK (White and Burnham 1999). Variation in the time interval between successive capture sessions was integrated as a multiple of the shortest interval (59 days), as follows: '1' (sessions 1-2), '1.6' (sessions 2-3), '2.3' (sessions 3-4), '1.6' (sessions 4-5), '2.0' (sessions 5-6). Because the recapture data for the young birds were too sparse to include all effects in a single model (with age, sex and fragment), we examined the effects of age-class on survival and recapture first in an *Age-model,* where the data for all fragment-sizes and both sexes were pooled into three groups (i.e., adults, immatures and juveniles). Thus, the model had three groups and five time intervals. The saturated (most parameterised) model was $\Phi_{g*t}\, p_{g*t}$, where Φ is the two-monthly survival probability, p the two-monthly recapture probability, and the subscripts g and t refer to age- and time-dependent probabilities, respectively. Second, the effects of sex and fragment-size on survival were explored in a *Sex and fragment model.* Because no significant differences were found among the age-classes (see *Results*), data for all ages were pooled in this model. The model therefore had six groups (3 fragment-sizes and 2 sexes) and five time intervals. The saturated model was $\Phi_{f*s*t}\, p_{f*s*t}$, where the new subscripts f and s refer to fragment size- and sex-dependent probabilities, respectively. Annual survival probability Φ_a was estimated by raising the two-monthly estimates by a factor of six. Finally, mean life span (MLS) was computed as MLS = $1/\text{-}\ln(\Phi_a)$, with the variance $\sigma^2_{MLS} = (1/(\Phi_a * \ln\Phi_a{}^2)^2)^{2*}\sigma^2_{\Phi a}$ (White and Burnham 1999; Lens et al. 2002a).

For each model, the parametric bootstrap procedure in MARK was used to test whether the saturated model adequately described the data and no assumptions were violated. 100 iterations were initially run for each goodness of fit (GOF) test, with each iteration producing a simulation of the model deviance. The number of simulated models (out of the 100) with a deviance equal to or greater than the deviance of the observed model provided the probability of observing a deviance as large as (or greater than) that. Thus, this p-value indicated significance of the departure from adequate fit of the model to the data. Next, overdispersion was estimated using the parameter c-hat ($\hat{c}$) and, if present, corrected for by inflating the variances (Lebreton et al. 1992; Anderson et al. 1994). Under the CJS model theory, $\hat{c} = 1$; $\hat{c}$-values ≤ 3 suggest little overdispersion in the data and can be easily corrected for by inflating variances of parameter estimates, while larger values indicate the model structure is inadequate for the data (Lebreton et al. 1992). $\hat{c}$ was calculated by dividing the observed model deviance by the mean deviance of the simulated models. The goodness-of-fit results for both models show that none violated the CJS model assumptions ($p = 0.10$, $\hat{c} = 1.297$ and $p = 0.50$, $\hat{c} = 1.111$, respectively).

3.2.3 Estimation of recruitment rates

Relative recruitment was assessed by counting the number of individuals of each sex initially ringed as juveniles or immatures and later recaptured in a different stage. Adult turnover rates were estimated from the Pradel Recruitment Only (PRO) model in MARK (White and Burnham 1999). This model estimates the proportion of the adult population that was previously in the population, as opposed to new immigrants or locally recruiting individuals. The parameters estimated in the PRO are gamma, γ, (i.e. the probability that an individual present at time i was in the population at time i-1) and recapture probability (p). Data were arranged into six groups (3 fragment-sizes and 2 sexes), similar to the *Sex and fragment model* above. Because we were interested in differences in turnover among the different groups, we begun with $\gamma_{f*s*t}\ p_{f*s*t}$ as the saturated model, where the new parameter γ is the two-monthly probability that an individual present at time i was in the population at time i-1. Though there is no formal goodness-of-fit test for this model, a $\hat{c}$-estimate of 1.049 was obtained by dividing the deviance of the saturated model by its degrees of freedom. Given that $\hat{c}$-values estimated by this approach are typically biased high (White and Burnham 1999), and $\hat{c}$-values ≤ 3 indicate adequate model structure, the model was considered satisfactory for these data.

3.2.4 Model selection

A fundamental issue in analysis of capture-recapture data is proper model selection (Anderson et al. 1994), i.e. the process of scaling down from a global (saturated) model including all reasonable effects, to the most parsimonious model representing the data most adequately with the least number of parameters (Lebreton et al. 1992; White and Lubow 2002). Starting with the saturated model, all candidate models were run. Models were initially selected based on the Quasi-Akaike Information Criterion QAIC (i.e. applying the quasi-likelihood parameter, $\hat{c}$) (Lebreton et al. 1992; Anderson et al. 1994). The most parsimonious model has the lowest QAIC-value. However, only when the difference in QAIC between two models is greater than 7 is there compelling evidence to support real difference between the models (White and Burnham 1999). Hence, to minimize the chances of excluding significant effects from parameter estimation, all models with ΔQAIC$\leq$7 were further tested using Likelihood Ratio Tests (LRT's). LRT's test the significance of different effects on the survival and recapture probability by contrasting pairs of nested models, one containing the effect of interest with one where it is omitted; all significant effects are retained.

3.3 Results

3.3.1 Differences in survival between age-, sex-, and fragment size categories

In the *age model*, the least QAIC-model was $\Phi_c\ p_t$, where the new subscript c refers to constant probability. LRT results confirm it as the most parsimonious model (Table 3.1). Thus, adults, immatures and juveniles did not differ significantly in their survival and recapture probabilities. In the *sex and fragment model*, the least QAIC-model was $\Phi_s\ p_t$, which was also confirmed by the LRT's as the most parsimonious one (Table 3.1). It was therefore used for estimating survival and recapture probabilities of the study species (see Table 3.2). Overall, the annual survival of males was almost twice as high as that of females.

3.3.2 Recruitment patterns

Except for one female that dispersed from NG to CH, all individuals that were recaptured in a different stage of development from their first capture were recaptured in the fragment of original capture (NG 13, CH 2, and SF 3). All of these individuals, except three (one in NG and two in SF), were juveniles recaptured as immatures. In the PRO, the least QAIC model was $\gamma_s\ p_t$. However, there was a trend towards significance for the fragment effect (LRT of $\gamma_{s+f}\ p_t$ vs. $\gamma_s\ p_t$: $\chi^2 = 7.2$, df = 4, p = 0.13). Because this effect was among those predicted *a priori* to be of probable biological significance, it was retained in the final model (Lebreton et al. 1992). Lebreton and colleagues recommended that a less stringent α-level (e.g., 0.1 or 0.15) in judging the significance of factors known *a priori* to be of likely biological significance. Gamma-values (± SE) estimated from $\gamma_{s+f}\ p_t$ were as follows: NG: 0.95±0.045, 0.83±0.062; CH: 0.87±0.064, 0.64±0.13; and SF 0.87±0.054, 0.66±0.087 for males and females, respectively.

Table 3.1. Modelling survival and recapture probabilities for *P. stellata*. For each model, the number of parameters to be estimated (np), the deviance (DEV) and the Quasi-Akaike Information Criterion (QAIC) values are provided. [Φ is the two-monthly survival probability, p the two-monthly recapture probability, and the subscripts s, f, t and c refer to sex-, fragment size- or time-dependent, or constant probabilities, respectively. The models selected as most parsimonious are marked in bold characters.]

Model	np	DEV	ΔQAIC	Comparison (LRT)
I. Age-structured model				
(1) $\Phi_c\ p_t$	6	172.8	518.86	
(2) $\Phi_t\ p_t$	9	169.2	522.39	Time effect on recapture
				(1) vs. (3): $\chi^2_4 = 15.8$, p = 0.0032
(3) $\Phi_c\ p_c$	2	188.6	522.89	Time effect on survival
				(2) vs. (1): $\chi^2_3 = 3.5$, p = 0.32
II. Sex and fragment model				
(4) $\Phi_s\ p_t$	7	151.6	595.02	
(5) $\Phi_c\ p_t$	6	156.1	596.91	Fragment effect on survival
				(7) vs. (4): $\chi^2_4 = 1.4$, p = 0.84
(6) $\Phi_f\ p_t$	8	156.0	600.98	Sex effect on survival
				(4) vs. (5): $\chi^2_1 = 4.4$, p = 0.036
(7) $\Phi_{s+f}\ p_t$	11	150.2	602.12	

Table 3.2. Two-monthly probabilities of survival (Φ) and recapture (p) estimated from the *sex and fragment model.* Projected probability of annual survival and mean life span (MLS) are also given. [Φ is the two-monthly survival probability, p the two-monthly recapture probability, and $p_{2\text{-}6}$ represent recapture probabilities for the 2nd to 6th ringing sessions, respectively.]

Parameter	Estimate	SE	Annual survival (Φ_a)	Mean Life Span	SE (MLS)
Φ_{males}	0.97	0.046	0.83	5.3	1.41
$\Phi_{females}$	0.87	0.065	0.43	1.2	1.34
p_2	0.180	0.055			
p_3	0.138	0.043			
p_4	0.062	0.027			
p_5	0.139	0.052			
p_6	0.143	0.060			

3.4 Discussion

Probabilities of recapture did not differ between fragment-size categories, ages or sexes. However, recapture probability was lower during the fourth ringing session, possibly associated with secretive behaviour during the dependency period of the fledglings and/or with moult (see also Oatley 1982b). This notwithstanding, lack of variation in recapture probabilities among groups validates any differences among them in other parameters estimated, such as survival and turnover (see Remsen and Good 1996). The survival analysis produced three key findings: first, that survival probability did not differ across different age classes; second, that males survived better than females in general; and third, that there was no significant difference in survival probabilities among fragments of different sizes. Many studies, predominantly conducted in temperate zones (but see Woodworth et al. 1999), have shown juvenile survival rates to be lower than those of adults (e.g., Ringsby et al. 1999; Lieske et al. 2000; Moss et al. 2000). However, differences in both the ecological conditions and the social systems of tropical birds may cause dissimilar life history strategies, which can explain this result found in the Taita Hills study site (e.g., Geffen and Yom-Tov 2000). For instance, most temperate birds lay clutches ≥ 5, while similar-sized tropical species, including *P. stellata*, typically lay only 2 eggs (Stutchbury and Morton 2001). As a consequence, juveniles of tropical species may not suffer similar levels of mortality as their temperate zone counterparts (Armstrong et al. 2000; Geffen and Yom-Tov 2000); there may be less starvation risk, for example. Analogously, prolonged natal care and extended post-fledgling periods enable fledglings of high-elevation (cardueline) finches to remain in their parents' territories for many months after leaving the nest (Badyaev 1997). During this period, juveniles of most passerines are most vulnerable to various sources of mortality, such as starvation and predation (Anders et al. 1997; Yackel et al. 2001). Because of the small clutches and scarce breeding (territory) vacancies in the tropics, reproductive success can be expected to largely hinge upon improving survival and successful dispersal of fledglings (Stutchbury and Morton 2001).

The average survival probability of female *P. stellata* could be lower than that of males if natural processes, such as females being the sole incubators (Oatley 1982c) and female-biased dispersal (Greenwood and Harvey 1982), render them more vulnerable to various sources of risk. Thus, although lower female survival was a feature of all fragments, it was possible that the actual sources of mortality were different among them. On the one hand, mortality related to female-biased dispersal (see Waser et al. 1994) was probably more important in high quality fragments with high reproductive success. On the other hand, in lower quality patches where reproductive success was diminished, this dispersal-effect was possibly relatively unimportant. Female mortality could have been mostly exacerbated by an influx of (nest) predators from the surrounding matrix as forest deterioration created habitats suitable for them (Chapter 7). Because of such differences, simple patterns of higher mortality rates with increasing disturbance, for instance, would not necessarily be expected. Differences in annual survival probability between males (0.83) and females (0.43) were reflected in mean expected life spans, with males living about four times as long as females on average. Life-span estimates reported in this paper fall well within the range of estimates reported for tropical passerines (e.g., Dowsett 1985; Woodworth et al. 1999; Stutchbury and Morton 2001).

The large majority of individuals sampled at different ages were recaptured within the fragment of initial capture. Though this suggests high levels of local recruitment, capture-recapture methods are known to underestimate long-distance dispersal (Barrowclough 1978; Gauthreaux 1996). It was also possible that some of the juveniles were captured after dispersing. Given that survival rates were lower for females than males, turnover rates (i.e. the proportion of adults captured in a session that were not part of the population in the preceding session) were expected to follow a reverse pattern (e.g., Svensson 1999). Our recruitment model corroborated this by demonstrating that fewer 'new' adult males than females entered the population during any single interval. In addition, this analysis revealed a likely fragment-effect, with NG having lower turnover rates than both SF and CH, which suggests higher survival in NG. The lack of a corresponding (fragment) effect from the survival analyses could, by inference, corroborate the argument in the preceding section about differences in sources of mortality across fragments. In particular, when mortality is largely dispersal-related, turnover will be low because resident adults remain within the patch (assuming a large portion of the dispersers are locally born individuals). Conversely, turnover rates are prone to be higher with predator-related mortality, because this is likely to target all birds equally, perhaps even more on adults if they are preyed upon during incubation. Combined with the survival results then, our findings indicate that mortality in NG was predominantly from dispersal (high reproductive success, low turnover rates), in CH primarily from increased predation (low reproductive success, high turnover rates), while in SF it was a combination of both (high reproductive success and high turnover rates). In general, because individuals occupying optimal habitats are expected to show lowest turnover rates (Winker et al. 1995), NG can thus be considered as the best quality habitat. This corresponds to a ranking of fragments based on vegetation composition and structure (Wilder et al. 2000). Increased habitat disturbance in CH in recent years may have rendered it a lower quality habitat compared to SF, albeit still larger in size.

In conclusion, the lower probability of female survival in this robin metapopulation potentially engenders highly male-biased sex ratios (e.g., Lens et al. 1998), further exacerbating its effects on the long-term persistence of this species. Evidently, fewer females survived the dependency period than males, died during (female-biased) natal dispersal or during incubation (Chapters 6&7). This suggests that between- and within-fragment processes are both crucial to the persistence of this metapopulation. Likewise, recent findings reported that overall species persistence across this landscape was linked to their mobility (dispersal rates) and tolerance (adaptability) to deteriorating habitats

(Lens et al. 2002b). Hence, there is a need to advocate for conservation measures that reduce the levels of disturbance, as well as facilitating movement between subpopulations, in order for dispersal to compensate for the low survival rates in some fragments and avoid possible local extinctions.

Paper III

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Ranging behaviour and habitat use by the white-starred robin in the Taita Hills

Mwangi Githiru, Luc Lens & Leon Bennun

CHAPTER 4

Max Chovu [a field assistant] getting ready
to go 'robin-hunting'

> The only reason some people get lost in thought is because
> it's unfamiliar **territory**.
>
> **Paul Fix**

Chapter 4: Ranging behaviour and habitat use by the white-starred robin in the Taita Hills

Summary

The habitats that different species select govern their ranging patterns and play an important role in determining how habitat loss and fragmentation affects species. Using radio telemetry, we explored the ranging behaviour of a small forest-dependent passerine (white-starred robin *Pogonocichla stellata*) in the highly fragmented Taita Hills forests. Thirty-one males were radio-tracked in seven forest fragments of different sizes and disturbance levels in this 'archipelago'. There was no significant difference in home range size or structure among these patches. However, individuals in habitats with higher population densities had greater levels of overlap in their ranges. Throughout all fragments, the robins selected sparse to moderate foliage habitats over open and very dense habitats. The proportion of the home ranges covered by these vegetation types differed across fragments, with the fragments showing highest selection (disparity between use and availability) having the least proportions. This suggests that these forest patches had much less of the preferred habitat in general, and hence could be considered to be of lower quality. Nonetheless, home range size remained similar even when the proportion of the preferred vegetation types within the ranges differed among fragments. A possible deduction from this finding is that, although the robin showed clear preference for certain habitat types, it was fairly adaptable and could survive well with only nominal amounts of the preferred habitat within its home range. This might offer one explanation for its better persistence within this landscape compared to other related species such as the endangered Taita thrush [*Turdus helleri*].

4.1 Introduction

Most organisms restrict their normal activities to specific areas - home ranges - at certain times during their life cycles (Burt 1943; Odum and Kuenzler 1955). Whereas the physical size of a forest is perhaps the single best predictor of the presence of forest-interior species (Rolstad 1991), home range sizes of individuals within the forests is governed by factors related to species requirements, the quality of the habitat (i.e., availability of food, nest site, cover, etc.) and density of conspecifics (Brooker and Roxley 1995; Redpath 1995; Ortega and Capen 1999). Thus, forest destruction, resulting in habitat loss and deterioration, can affect the ranging behaviour of organisms within remnant patches. It is likely that, for forest dependent bird species, a reduction in forest size plus degradation of remaining forest patches could drive them to range more widely to fulfil their normal requirements. In such case, the quality of habitat influences the minimum space each individual requires to fulfil its essential requirements, while the size of the fragment sets the upper limit to the density of birds that the area can hold. This ceiling need not necessarily be attained due to other constraints associated with interactions between the birds themselves (Krebs 1971; Severinghaus 1996), and with their predators. Therefore, independently or in concert, habitat and social aspects affect both home range size and levels of overlap in the ranges.

The way in which organisms use the resources available to them determines how any change(s) in the environment is going to impact on their survival. Forest destruction distorts both the spatial and temporal distribution of resources, which can potentially affect the ranging patterns of organisms dependent on these resources. Specifically, the destruction affects vegetation characteristics in an area, resulting in habitats of different quality. Therefore, a vital question for ecologists is determining the factors that influence species' preferences to certain habitats (Cody 1981). At the heart of habitat selection is a resource being used more (or less) than its availability (Alldredge and Ratti 1986). In selection studies, assessing and estimating availability from an organisms' point of view is fraught with difficulty, both in terms of subjectivity in delineation of study areas, and electing the variables to measure (Johnson 1980; Aebischer et al. 1993; Arthur et al. 1996; Hall et al. 1997). A 'hierarchical approach' to habitat selection studies helps (at least partly) resolve these two problems. Basically, habitat selection can be considered as an hierarchical process, moving from selection at the geographical range of the species (first-order selection), to selection of specific home ranges within the geographical range (second-order) and use of various components within the home range (third-order) (Johnson 1980). This clearly helps resolve the delineation of the study area. In addition, the variables to study are also easier to select. For instance, first-order would mainly focus on general variables such as forest type (e.g., indigenous versus exotic), whilst third-order will mainly focus on specific aspects within these forests such as litter depth or distribution of fruiting trees.

In this paper second- and third-order habitat selection by the white-starred robin is assessed in a series of 2-3 ha study plots in the Taita Hills 'archipelago', southeast Kenya. The Taita forests have been subjected to extreme degradation and fragmentation, and negative effects on the biotic community there have been recently reported (Lens et al. 1999a; Lens et al. 1999b; Wilder et al. 2000). We examined second-order habitat selection by studying ranging behaviour of 31 radio-tagged robins and comparing vegetation values in each home range to those in a larger geographical area within which the range was set. Based on observed movements, all habitats within a study plot were assumed to be accessible to all individuals captured within it (see also Murphy et al. 1985). Hence, abundance of the vegetation components within the plot was assumed to equal availability (sensu Johnson 1980). As the robins derived their feeding, cover and nesting needs from their home ranges, we selected the vegetation parameters deemed most important for provision of these needs (directly or indirectly), based on personal observations and from literature (Oatley 1982a; Keith et al. 1992). Third-order habitat selection was then examined for all 31 ranges by comparing habitat values at individual radiolocations within those for the entire home range (Porter and Church 1987). This allowed us to explicitly address the following two questions: i) whether various attributes of the robin home range (viz. size, structure and overlap) differed among fragments of different size, and among habitats of different vegetation characteristics; and ii) whether the robin selected particular vegetation characteristics when establishing home ranges, and when using their home ranges.

4.2 Study species and site

The white-starred robin is an endemic resident in montane forests of eastern to southern Africa (Keith et al. 1992), and is classified as a forest generalist species, i.e., is dependent on forests but also regularly found in secondary forest, forest strips and edges (Bennun et al. 1996). It forages at all levels in the forest, most frequently in the undergrowth and at ant trails, infrequently tossing leaf litter, making aerial sallies to capture flying prey and ascending into the canopy for small fruits when available e.g. *Rhus* sp. (Oatley 1982b; Keith et al. 1992). It is territorial and (apparently) monogamous, and does not show much antagonism against conspecifics, though males aggressively defend territories during the breeding season and possibly year-round or throughout their lifetime in high quality habitats (Oatley 1982c; Oatley and Arnott 1998). It shows high homing ability and site fidelity in south-central Africa where it is an altitudinal migrant

(Dowsett 1985; Dowsett and Dowsett-Lemaire 1986). Wing length was used to discriminate between sexes, which was confirmed by molecular sexing of most individuals (Githiru 2003).

The Taita Hills forests, located in the south-eastern part of Kenya, are an important area for bird conservation (Bennun and Njoroge 1999). Yet, extensive human destruction over the last 4 decades has reduced these forests to 3 larger fragments (95-180 ha) and 9 tiny remnants (2-8 ha) scattered across hilltops and ridges (Beentje and Ndiang'ui 1988; Brooks et al. 1998a). Data for this study were collected in 7 fragments at Dabida, grouped into 3 fragment-size categories as follows: large: Ngangao (NG, *c*135 ha); medium: Chawia (CH, *c*95 ha); and small (collectively referred to as small fragments, SF): Fururu (FU, *c*8 ha), Ndiwenyi (ND, *c*4 ha), Macha (MA, *c*2 ha), Mwachora (MW, *c*2 ha) and Yale (YA, *c*2 ha) (for map, see Galbusera et al. 2000a). In general, based on structural qualities of the vegetation measured by Wilder et al. (2000), and on plant species richness and diversity (Githiru 2000), smaller fragments were of poorer quality than larger ones. Five 3-ha study plots were randomly selected in the larger fragments (NG and CH). The smaller fragments were treated as a single plot each. Within each plot, 3 permanent net lines were set up, each measuring between 54 and 57 metres long where mistnetting was done. Six ringing sessions were conducted per plot (3 per year).

4.3 Methods

4.3.1 Home ranges

Male robins were captured using mistnets and immediately fitted with transmitters at the ringing site before release. Pip transmitters (manufactured by Biotrack Ltd., UK) with an Ag376 cell and weighing 1.0 g were used. The tags were glued fairly high on the bird's back using Cyanoacrylate ('Superglue') so that they were closest to the centre of gravity, taking care not to glue feathers of nape or scapulae, in the standard attachment procedure (Raim 1978; Sykes et al. 1990; Johnson et al. 1991). Tracking was done in NG and CH between May and October 2000, then in all fragments between March and October 2001. The radiolocations (fixes) for all adult males were analysed in RANGES 6 (Kenward and

Hodder 1996; Kenward et al. 2002). To distinguish between resident and non-resident males ['floaters' (sensu Smith 1978)], residency was ascribed only to individuals that roosted at or around the same site during the entire fix collection period. In contrast, floaters roosted in completely different sites on consecutive nights (often out of the area they spent most of their day), thus often traversed far greater distances than resident males (see also Rohner 1997). Following this, we included 31 individuals in this analysis: 13 in NG, 14 in CH and 4 in SF (Appendix).

Two prerequisite tests were conducted on these data. First, autocorrelation between successive fixes was checked using the Schoener's index, which calculates the degree of independence between distance and time (Swihart and Slade 1985a, b; Kenward and Hodder 1996). On average, fixes showed statistical independence after 106 ± 15 minutes. Because at least 1.5 hrs were allowed between consecutive fixes during tracking, all locations were considered independent. This made biological sense too because it was sufficient time for the birds to traverse their entire home ranges (see also Leary et al. 1998). Second, incremental area plots (IAPs) for individual birds were inspected for asymptotes in home range size (using 100 % Minimum Convex Polygon [MCP] method) as more locations were added. Individual incremental plots are created by drawing an outline around the first three fixes, then plotting successive fixes one by one, and an outline drawn each time, until all fixes in the range have been added (Kenward and Hodder 1996). No proper asymptotes were found even after 100 fixes (see Fig. 4.1 for all individuals combined). This was probably due to the ant-trailing behaviour of this species, where regular scouting for ant-trails outside their respective ranges led to unpredictable increases in home range size. Thus, in order for comparison of range sizes among fragments to be valid, it was necessary to keep number of fixes used in their calculation standard across the fragments. To maximize sample size, we elected to use only those individuals with 20 or more fixes for further analysis; for those with more than 20 fixes, the first 20 were used. This number of fixes was satisfactory for addressing the questions in this paper because home range size at 20 fixes was highly significantly correlated to the size when all fixes were included (MCP: $r = 0.49$, $P = 0.004$, $n = 31$). This indicates that larger ranges were already so at 20 fixes. Fixes were collected over 7 to 10 days. (NB: as a side-analysis, given that there was some levelling off after 30 fixes [see Fig. 4.1], overall mean home range size was calculated using 30 fixes [for individuals with more than 30 fixes, the first 30 were used] to get a better idea of absolute home range size.)

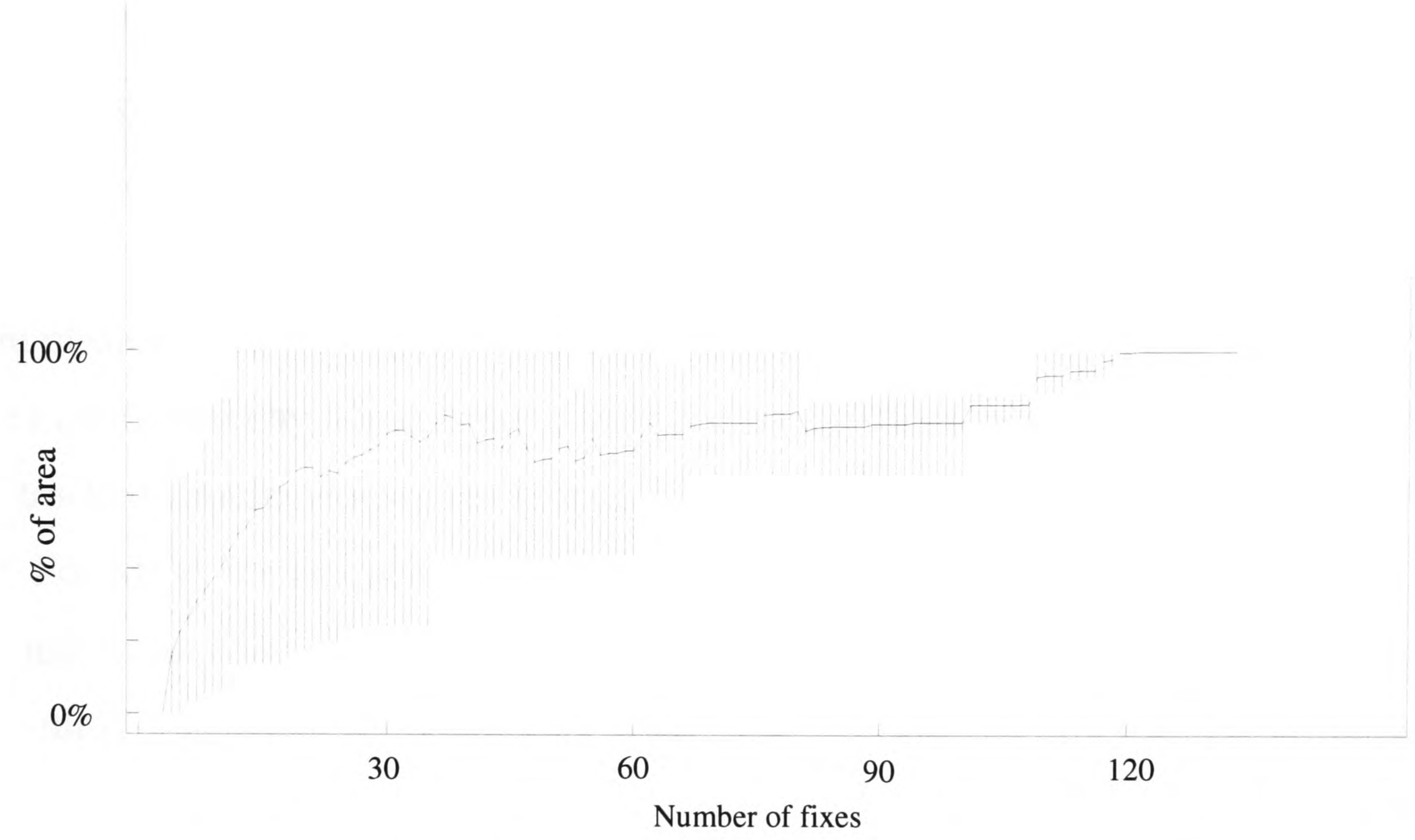


Fig. 4.1. Multiple home range plot of sampling increments (using 100 % Minimum Convex Polygon) for all resident white-starred robin males in the Taita Hills, SE Kenya, 2000-2001. The spread of values (SD) with each additional fix is shown as vertical bars (Kenward and Hodder 1996); $n = 31$ ranges.

Both Kernel and MCP methods were used to estimate home range sizes. For the kernels, utilization plots (Kenward and Hodder 1996) showing progressive changes in range size as the percentage of fixes used in the analyses was increased, were ran for all (31) individuals to set the percentage best describing a core area of activity (Wray et al. 1992; Hodder et al. 1998). This would emphasize the key parts of the range, and hence enable more useful comparisons among fragments (Seaman et al. 1999). Judging from the point of inflexion of individual utilization plots, we found a mean of 81 ± 2 % as best describing the core area, and selected 80 % as the appropriate percentage to describe ranges by this method. [NB: throughout this paper, 'territory' will sometimes be used in reference to these core areas (e.g., Maher and Lott 1995). Though active defence was seldom observed, these areas were fairly exclusive, except when ants were present.]

When calculating actual range size, we used the ad hoc technique (Worton 1989) to select the smoothing parameter, h. This parameter determines how closely the program fits contours to the radiolocations. Further, we used the fixed kernel option that keeps the smoothing parameter constant irrespective of the concentration of locations in the utilization distribution (Kenward 2001). This was important because we were using only a relatively small (and constant) number of fixes (Seaman et al. 1999). Apart from estimation of range size, further utility of the kernel method was twofold. First, it enabled assessing range structure, i.e. whether the range comprised of a single continuous range or several separate cores. Second, it was useful for estimating overlap, where mean overlap for a pair was calculated as the average of the percentage of home range i overlapped by home range j, and vice versa. This was calculated for all possible pairs tracked simultaneously per plot i.e. only those tracked in the same season (and year). For MCP, the frequently used 95 % fix inclusion (Harris et al. 1990) with a harmonic mean center (Kenward 2001) were used. In addition to range size estimation, this method was handy for computing range spans. Range span (in meters) is the furthest distance between any pair of fixes within a home range. Finally, there was no significant season (both MCP and Kernel: $t_{29} = 1.3$, $P = 0.21$) and year (MCP: $t_{29} = 0.5$, $P = 0.61$; Kernel: $t_{29} = 0.8$, $P = 0.41$) effect on range sizes. Thus, ranges from both years and all seasons were pooled when comparing among fragment-size categories.

4.3.2 Habitat quality

4.3.2.1 Principal Factor Analyses (PFA)

All plots were divided into 25 by 25 m grid cells. Also included in the grid system were areas outside the plot where any individual was located during tracking. At each 25-m intersection, vegetation structure was estimated within a 5-m radius circle with the intersection as the center. Each of the three forest strata – canopy cover (CC, >12 m), middle canopy (MC, 2 – 12 m) and undergrowth (UG, <2 m) – was classified into the following four categories: '1' ('OPEN', representing 0 % foliage cover) '2' ('SPARSE', 5 – 25 % cover), '3' ('MODERATE', 30 – 75 %), and '4' ('DENSE', 80 – 100 %). The proportion of the 5-m radius circle represented by each of these four vegetation categories was estimated. A preliminary pilot exercise was conducted to ensure the scoring was consistent; the same person did all estimation. Next, a single value for the grid cell per category per stratum was obtained by calculating the mean of the percentages in the cell's corners. Then, the overall mean values for each category per stratum were computed for each individual's home range.

Using factor analysis (SPSS 2001), the values for these 12 variables (4 categories, 3 strata) in all 31 kernel-based home ranges were explored further to identify principal components (factors) that were more useful descriptors of vegetation gradients. To account for all the variance in the dataset, one needs as many factors as observed variables (in this case, 12). Thus, the number of factors to be extracted demands a trade-off: to retain enough factors for an adequate fit, but not so many such that parsimony is lost. A scree test (observing the inflexion point in a scree plot of the eigenvalues) was used to determine the number of factors to extract. Next, a variance maximizing (varimax) rotation was used to calculate factor loadings (Alsobrook II et al. 1999; Tabachnick and Fidell 2001). Factor loadings – the correlations between the original variables and the extracted factors – were calculated for all 12 variables. To interpret a factor, one tries to understand the underlying dimension that unifies the group of original variables loading on it; as a rule of thumb, only variables with loadings of 0.32 and above are interpreted (Tabachnick and Fidell 2001). Finally factor scores were calculated for further analysis. Factor scores are estimates of the scores individual birds would have received on each of the extracted factors had they been measured directly (Tabachnick and Fidell 2001). These scores are formulated as a normal distribution with a mean of zero (Alsobrook II et al. 1999). Due to the orthogonal nature of varimax rotation, the scores obtained for these factors are nearly uncorrelated. This potentially makes the results much easier to interpret. The relationship between the factor scores and home range size (kernel) was examined using a multiple regression procedure (SPSS 2001).

4.3.2.2 Ant data

Ant-trail incidence in each plot during five ringing sessions (no assessment was done during the first session) was estimated by counting the number of times an ant trail crossed: i) any of the three permanent net-lines (each 54 – 57 m); and ii) an independent

500-m transect criss-crossing the entire plot. Sufficient spacing ensured little chance of single trails crossing any two transects, and careful observations prevented double counting when single trails crossed a transect twice. All ant trails were counted except for the very small ones with few individual ants, as these were deemed not useful to the robins. Hence, for instance, if ants crossed each of these four ant-transects once in every plot during a particular session, given there were five plots per fragment-size category, a value of 20 would be obtained for that fragment-size category for that session.

4.3.3 Habitat selection

From the vegetation measurements described earlier in the factor analysis, the values for each grid cell (per stratum) were imported into RANGES 6 as raster maps (sensu Kenward and Hodder 1996). Vegetation composition per stratum was calculated for each plot and home range. For second-order selection, vegetation composition within home ranges (indicating use) were compared to those for the entire plot (indicating availability) (e.g., Smith et al. 1982; Murphy et al. 1985; Roy and Dorrance 1985). For third-order selection, the home range compositions became the availability values, and were compared to compositions at individual radiolocations (Porter and Church 1987). Throughout the rest of this chapter, thus, 'abundance' is used in reference to the quantity of a vegetation component in the environment independent of the consumer (Johnson 1980), 'usage' is used to refer to the abundance of the component within individual home ranges or at individual fixes, while 'availability' is used in reference to the abundance of the component in the entire plot or home range, for the second- and third-order selection, respectively. All habitat selection analyses using home range data used the more reliable kernel-based estimates only (Seaman et al. 1999).

For the second-order selection, we compared availability to usage values using compositional analyses in Resource Selection for Windows (beta 8.4) (Leban 1999). Using individual birds as the sampling units, this program generates preference rankings for the different vegetation characteristics using the log ratios of utilized to available values. The presence of selection is indicated by a chi-square statistic; where significant it ranks each category indicating the significance of the differences in rank. Selection for the four vegetation types – open, sparse, moderate and dense – was calculated for the three strata (CC, MC and UG) separately for each of the three fragment-size categories. Next, third-order selection was estimated using the Jacobs' index (Jacobs 1974) in RANGES 6 (Kenward et al. 2002). This program computes the preference or avoidance of a vegetation feature/type at individual radiolocations compared to the value in the home range as a whole. Values of the index range between +1 (most preferred) to –1 (least preferred). The mean values were obtained for each stratum in the three fragment-size categories.

4.4 Results

4.4.1 Home range

Based on 20 fixes, neither the home range size nor the range span showed significant variation across the three fragment-size categories (ANOVA: 95 % MCP $F_{2,28} = 0.5$, $P = 0.59$; 80 % Kernel $F_{2,28} = 0.2$, $P = 0.82$; Range span $F_{2,28} = 0.6$, $P = 0.55$; the mean [± SD] sizes were 0.8 ± 0.36 ha, 176 ± 55 m, and 0.7 ± 0.33 ha, for MCP, range span and Kernel respectively: data in Appendix). Based on 30 fixes, the overall mean home range size (80 % kernel) was 0.67±0.28 ha ($n = 20$); there was no difference between NG and CH (SF was excluded because only a single individual had more than 30 fixes) ($t_{17} = 1.3$, $P = 0.22$). Assessment of range structure showed that NG and CH had 1 of 13 and 1 of 14 home ranges, respectively, with more than one core area of activity, while 2 of 4 of those from small fragments did. This difference between the larger (2,27) and smaller (2,4) fragments was not significant (Fisher's exact test: $P = 0.13$), possibly due to a lack of power from small sample size in SF. Lastly, we found a significant difference in home range overlap levels among the three fragment-size categories ($F_{2,13} = 8.95$, $P = 0.0036$). Mean percent overlap was significantly lower in CH (8.4 ± 4.26, $n = 8$) compared to SF (25.4 ± 2.68, $n = 2$) and NG (28.1 ± 4.25, $n = 6$); NG and SF did not differ significantly ($P = 0.71$).

4.4.2 Habitat quality

4.4.2.1 Principal Factor Analysis (PFA)

Three factors were extracted that accounted for 62 % of the total variance. Based on factor loadings, PF1 (individually accounting for 28.9 % of the total variance) represented the 'open' vegetation category in all three strata; PF2 (19.4 % of variance) signified the 'sparse' to 'moderate' categories; and PF3 (13.6 %) denoted 'open' canopy cover, and 'dense' middle and lower strata. Comparing the calculated factor scores for ranges within the three fragment-size categories, we found significant variation in PF2 and 3, and no difference in PF1 (Table 4.1). Ranges in CH had a significantly less PF2 score, while those in SF had a significantly higher score for PF3. None of the principal factors significantly explained differences in home range size ($R^2 = 0.06$; all P-values > 0.25).

Table 4.1. Average factor scores in different fragment-size categories occupied by the white-starred robin, Taita Hills, SE Kenya, 2000-2001. [Larger values indicate more of the vegetation feature represented by the PF; means with different letters in the same row were significantly different; $P = 0.05$]

Principal factor	$F_{2,28}$	P-value	Ngangao	Chawia	Small fragments
PF1	1.6	0.23	0.16^a	-0.31^a	0.57^a
PF2	4.5	0.020	0.13^a	-0.43^b	1.07^a
PF3	4.7	0.018	-0.39^a	0.022^a	1.18^b

4.4.2.2 Ant occurrence

There was no significant variation in the frequency of ant occurrence among the five ringing sessions (Table 4.2) (Friedman's ANOVA: $\chi^2_4 = 3.7$, $P = 0.45$). Thus, we pooled them and found significant differences among the fragment-size categories (Kruskal-Wallis Test: $\chi^2_2 = 6.9$, $P = 0.033$), with NG having significantly lower frequencies than CH ($P = 0.03$) and (though marginally non-significant) SF ($P = 0.07$); CH was not different from SF ($P = 0.9$).

Table 4.2. Total incidence of ant-trails per session in different fragment-size categories occupied by the white-starred robin, Taita Hills, SE Kenya, 2000-2001

Fragment-size category	Session 2	Session 3	Session 4	Session 5	Session 6	**Total**
Ngangao	1	0	2	3	1	**7**
Chawia	7	3	4	4	2	**20**
Small fragments	5	2	2	1	8	**18**

4.4.3 Habitat selection

Compared to the vegetation characteristics (the three strata combined) of the entire plot within which the home range was set (i.e., habitat availability), vegetation features within home ranges (habitat use) revealed that the robin did not establish home ranges at random (NG: $\chi^2 = 33.5$, df = 3, $P < 0.0001$; CH: $\chi^2_3 = 40.9$, df = 3, $P < 0.0001$; small fragments ($\chi^2_3 = 13.5$, df = 3, $P = 0.05$). In all fragments and for all strata, sparse and moderate vegetation types were more preferred than both open and dense categories (Table 4.3).

Table 4.3. Preference rankings of the four vegetation types indicating second-order selection by the white-starred robin, Taita Hills, SE Kenya, 2000-2001. [Rank '3' was most preferred and '0' least preferred; different letters in the same row indicate a significant difference in use of the vegetation types. There is no detectable difference in use (preference) when ranks have the same letter, implying that the order of ranking means little (see Aebischer et al. 1993).]

Stratum	Fragment category	χ^2_3	*P*	Vegetation categories			
				Open	Sparse	Moderate	Dense
Upper Canopy	Large, NG	78.6	0.0001	1^{ab}	3^{a}	2^{b}	0^{c}
	Medium, CH	70.8	0.0001	2^{ab}	3^{a}	1^{b}	0^{c}
	Small, SF	6.8	0.077				
Middle canopy	NG	14.5	0.05	1^{ab}	2^{ab}	3^{a}	0^{b}
	CH	73.3	0.0001	1^{b}	3^{a}	2^{a}	0^{c}
	SF	4.9	0.18				
Undergrowth	NG	6.6	0.087				
	CH	37.6	0.0001	0^{c}	1^{b}	3^{a}	2^{ab}
	SF	8.8	0.05	0^{b}	2^{a}	3^{a}	1^{ab}

Comparisons between habitat availability and use within individual ranges also revealed highest preference for the sparse and moderate vegetation categories, and least for the open and dense categories, for all fragment-size categories and strata. The overall mean values for the Jacob's Index were: Open -0.62 ± 0.41, Sparse 0.64 ± 0.38, Moderate 0.83 ± 0.29, Dense -0.11 ± 0.27 (Table 4.4).

Table 4.4. Mean values of the Jacob's index showing third-order habitat selection by the white-starred robin, Taita Hills, SE Kenya, 2000-2001. [+1 is most preferred and –1 is least preferred.]

Stratum	Fragment category	Vegetation category			
		Open	Sparse	Moderate	Dense
Upper Canopy	Large, NG	-0.32	0.75	0.71	-0.13
	Medium, CH	-0.40	0.62	0.79	0.00
	Small, SF	-0.35	1.00	0.67	0.014
Middle canopy	NG	-0.65	0.50	0.86	-0.012
	CH	-0.77	0.68	0.86	0.00
	SF	-0.73	1.00	1.00	-0.14
Undergrowth	NG	-0.59	0.50	0.63	-0.23
	CH	-0.78	0.095	0.94	-0.46
	SF	-0.97	1.00	1.00	0.069

4.5 Discussion

4.5.1 Home ranges and fragment size

There were no significant differences in home range sizes, shapes or range span among the fragment-size categories. This may be because the smallest fragment (*c*2 ha) was larger than the mean robin home range size (0.67 ha), implying that when fragment size was larger than range size, fragment size per se did not influence range size. However, there were significant differences in levels of overlap in home ranges among the different fragment-size categories, with the medium-sized fragment, CH, having significantly lower overlap than the largest (NG) and smallest (SF) fragments. Lower levels of overlap in CH were most likely to be a result of there being lower densities of birds there compared to both NG and SF (Githiru 2003). It was implicit, therefore, that higher bird densities resulted in higher overlap levels in lieu of smaller (more compressed) home ranges (e.g., Krebs 1971; Severinghaus 1996; Tripp and Collazo 1997). The fact that range-size remained constant but overlap increased could be the result of the robin's reliance on an unpredictable and superabundant resource, ants. It suggests that because of the unpredictability of ants (in space), the birds needed a minimum searching area to guarantee some constant supply over time. Ant-trails, however, provided a superabundant food resource permitting sharing. Contrasting number of adult birds at individual ant-trails, with typically as many as 10 to 15 in NG and SF, and only 2 to 4 in CH, corroborates this argument (M. Githiru, unpublished data). This mean home range size could thus represent the minimum space required to ensure a breeding chance to the holders; simply, an adequate area for feeding and nesting (Burt 1943; Brown 1964). Contrariwise, Oatley (1982a) found that an increase in territory size at lower population densities did not occur in this species, and suggested that its effective song range (approximately 50 m, thus producing a [circular] area of 0.78 ha) might have evolved in response to territory size requirements. Song is an important form of advertisement (Krebs 1971; Morton 1996), and perhaps more so in species such as the robin where agonistic behaviour is rare (Oatley 1982a; Githiru 2003). Thus, song degradation (e.g., Morton and Derrickson 1996) could preclude the occupation (defending) of territories beyond the natural song range where this was expected.

4.5.2 Home ranges and habitat variables

The three principal factors obtained from the PFA correspond to 'openings' (little foliage in all three strata), 'secondary or regenerating forest' (sparse to moderate foliage density in all strata) and 'gaps' (little canopy cover with dense middle canopy and undergrowth). None of these factors significantly explained the variation in home range sizes. Home ranges in the different fragment-size categories contained similar amounts of the open areas, but ranges in CH had significantly less amounts of the secondary forest (intermediate foliage density), while those in SF contained significantly more gaps. Thus, although there were differences in vegetation characteristics within home ranges in different fragment-size categories, home range size did not show parallel variation.

Similarly, Wortman (1997) found territory sizes of Lincoln sparrows [*Melospiza lincolnii*] not to be related to vegetation composition within them. Still, it is logical to predict that with habitat heterogeneity, any variation in the proportion of different habitats within individual home ranges would be reflected in corresponding differences in the structure or size of the ranges. This would be expected if the species shows preference for certain habitats, as did the robin (see further). A range containing more of a preferred habitat (e.g., signifying more food) it would be smaller, and vice versa (e.g., Redpath 1995). When such a relationship between preference and range size is absent, as for the robin, it can be attributed to two potential factors: (i) that differences between different habitats are not crucial for the species – signifying it is adaptable, and/or (ii) the presence of another overriding/limiting factor that precludes such a relationship even if it were desirable – hence the species is mal-adapted. Based on (i), it suggests that the robin was quite adaptable and could survive in different habitats by broadening or switching its diet composition (for instance, as seen in its varying the levels of reliance on either ant trails versus other forms of food in different fragments [M. Githiru, personal observations]). It could also switch between nesting sites; for instance, it successfully nested in abandoned sawpits, stump and boulder bases to gently sloping ground. Based on (ii), an overriding effect of song as proposed in the preceding section could cause such an effect, in case ranges extending beyond the natural song limit were desired but proved too costly to defend. In conclusion, an increase in home range size with increasing habitat degradation has not happened (yet) for the robin, potentially because of its flexibility in feeding and nesting requirements (thus still well adapted), and/or because fragmentation is a fairly recent phenomenon in evolutionary terms (e.g. related to changing the song range). Teasing these aspects out demands detailed behavioural studies looking at foraging behaviour and choice, territory defence mechanisms and breeding success, specifically in relation to differences across fragments.

4.5.3 Habitat selection

Overall, the highest levels of habitat selection at the home range level occurred in CH, then NG; least selection occurred in SF. However, even with different degrees of selection, selection was largely for similar vegetation features, with sparse and moderate habitats being preferred to open and dense ones. Further, within home ranges, the robins preferentially spent more time in the sparse and intermediate habitats compared to the open or densely vegetated ones. This was consistent for all fragments and strata. The fact that the birds ended up with significantly lower proportions of these preferred vegetation types in CH (PFA results in the preceding section), where selection for them was greatest, indicates that they were least common there. This suggests that CH was a poor quality fragment for the robin, which is corroborated by the lower population density, lower index of productivity and higher turnover rates in this fragment compared to NG and SF (Githiru 2003). There are a variety of reasons why birds might select or avoid habitats of certain vegetation attributes. As seen in the preceding section, it was unlikely that food and breeding sites were limiting for the robin, which would imply that they were not key forces driving habitat selection. Differences in type and abundance of both competitors and predators could engender different selection strategies across different habitats or forest patches (Thomas and Taylor 1990). NG was less disturbed than CH, with larger sections of well developed three-strata forest and fewer open areas (e.g., from recent disturbance) (Wilder et al. 2000). In more open habitats, the robins were probably easier targets for goshawks and sparrowhawks (they often hunted at ant-trails too), hence their avoidance of such areas. However, little is known about non-avian predators in these fragments, as well as the levels of inter-specific competition (e.g., with related thrushes). Both are likely to have additional effects on habitat selection. Even so, the ability of the robin to survive in habitats showing signs of previous disturbance could explain why it is one of the most resilient bird species in these fragments, surviving in many small patches where related species are absent. In order to understand habitat selection better, it is essential to follow-up on the effects of predators and inter-specific competition on the distribution of the robins. In particular, whether their territories overlapped with those of related species, and whether predator distribution and hunting behaviour indeed posed a greater risk for robins in open habitats.

4.6 Management implications

Given the constant home range sizes across different-sized fragments, possibly related to the robin's eclectic feeding and nesting behaviour, the robin seems to have been little affected by the ongoing forest loss and fragmentation thus far. This could also be because it was very abundant to begin with, and hence any negative effects take time before they can be reflected in densities and distribution. Still, there are signs that populations in the most highly degraded patches with unrelenting destruction are facing problems and are probably maintained only by immigration from the lesser disturbed patches (Githiru 2003).

Of immediate concern to conservation is the fact that other species might not be as well adapted or flexible as the robin and, therefore, may be affected far more adversely. For example, a reduction in the selected habitats (e.g., from unrelenting forest attrition) may have greater negative impacts on species such as the Taita thrush, which seem not as flexible in their feeding or nesting needs as the robin. Only more data on breeding success will show whether individuals in degraded habitats are having lesser reproductive success compared to those in more intact areas even whilst maintaining similar home range sizes. This would point to a more inherent mechanism maintaining non-adaptive home ranges that do not compensate for habitat degradation, or at least a lag in the physiological processes in mirroring environmental alterations.

Appendix. Home range size (based on both Minimum Convex Polygon and Kernel methods, [ha]) and range span (m) of all adult male white-starred robins used in this paper, Taita Hills, SE Kenya, 2000-2001

Fragment size	Fragment	Individual Code	Estimates using first 20 fixes		
			MCP	Range span	Kernels
Large	Ngangao	7	1.04	177	1.29
Large	Ngangao	8	0.52	116	0.44
Large	Ngangao	11	0.96	270	0.95
Large	Ngangao	20	0.42	120	0.46
Large	Ngangao	22	0.53	140	0.42
Large	Ngangao	25	0.41	141	0.36
Large	Ngangao	3	0.9	157	0.86
Large	Ngangao	18	0.73	139	0.91
Large	Ngangao	19	0.81	230	0.39
Large	Ngangao	5	0.77	145	0.75
Large	Ngangao	6	0.72	150	0.54
Large	Ngangao	15	0.41	111	0.41
Large	Ngangao	16	1.59	231	1.4
Medium	Chawia	40	0.93	230	0.92
Medium	Chawia	36	0.86	219	0.54
Medium	Chawia	37	0.48	117	0.65
Medium	Chawia	41	0.63	243	0.54
Medium	Chawia	42	1.18	183	0.96
Medium	Chawia	43	0.34	119	0.41
Medium	Chawia	45	0.81	159	0.8
Medium	Chawia	46	0.8	130	0.64
Medium	Chawia	33	0.87	235	0.92
Medium	Chawia	35	0.3	112	0.22
Medium	Chawia	30	0.87	292	0.75
Medium	Chawia	27	0.47	111	0.45
Medium	Chawia	28	1.59	234	1.3
Medium	Chawia	29	0.91	242	0.9
Small	Fururu	50	1.28	237	1.06
Small	Fururu	51	1.34	189	1.31
Small	Ndiwenyi	60	0.17	107	0.11
Small	Yale	56	1.08	182	0.82

Paper IV

Manuscript to be submitted [*Animal Behaviour*]

Relative presence of 'floaters' in two isolated populations of an Afrotropical forest bird species: a pilot experiment

Mwangi Githiru, Luc Lens, Leon Bennun & Christopher Perrins

CHAPTER 5

Bernard Amakobe and Max Chovu [field assistants] warm and cosy at a ringing site

> Use what talents you possess: the woods would be very silent if no birds sang there except those that sang best.
>
> **Henry Van Dyke**

Chapter 5: Relative presence of 'floaters' in two isolated populations of an Afrotropical forest bird species: a pilot experiment

Summary

When breeding space is limited within a habitat, territorial behaviour leads to the exclusion of adults that are capable of breeding from the breeding population. These individuals can opt to disperse and attempt to breed immediately elsewhere, or stay and live furtively (i.e., float) within the occupied territories waiting for a chance to arise. The existence of a floating population in two white-starred robin populations in the Taita Hills was explored using a removal experiment. We found a non-breeding adult component in Ngangao (*c*135 ha), the larger and better quality patch, which also had the higher population density. None was found in the smaller fragment, Chawia (*c*95 ha), which was less densely populated. This patch also contained unmated territorial males. In Ngangao, the floating males took over vacated territories within a few days of the residents' removal. Females in Ngangao showed more consistent site fidelity than those in Chawia, while no resident neighbouring males expanded their territories or moved to take over the vacant territories in both fragments. In general, our findings strongly suggest that territorial behaviour was an important factor limiting the number of breeders in Ngangao. In Chawia, poor habitat quality and female scarcity limited numbers before territorial exclusion became a concern. Demonstrating the presence of non-breeding adults could be important for the conservation of threatened species with limited dispersal ability, as such birds may be translocated to suitable habitats. This is discussed with specific reference to this study area.

5.1 Introduction

An important basis for territorial behaviour, besides food supply, is an opportunity to breed. Where breeding space is in limited supply, competition restricts the maximum number of individuals that can hold a territory (Brown 1964). If habitat quality varies from excellent to unsuitable and assuming there are more birds than available breeding territories in the optimal habitat, some individuals will be forced into sub-optimal areas while others may have nowhere to breed (Fretwell and Lucas 1969; Kokko and Sutherland 1998). Adult individuals (male or female) that are capable of breeding but are excluded by habitat saturation form a non-breeding surplus (Brown 1969); typically, they have lower rank and larger home ranges than breeding birds (Smith 1987; Rohner 1997). These non-breeders can opt to disperse in search of immediate breeding space, albeit at the potential cost of increased mortality risk during dispersal and/or reduced chance of territory acquisition in a less familiar habitat. Alternatively, they can choose to wait furtively within the territories of residents [thus forming a floating population (sensu

Smith 1978)] and take up any opportunities cropping up e.g. after death or disappearance of the territory holder. In order to opt for floating and hence delay breeding beyond the age of sexual maturity, it has to offer, ultimately, more hope for higher fitness than dispersing (Zack and Stutchbury 1992). For each individual floater, the promise of acquiring a territory is influenced by the level of intraspecific competition (Smith 1978). This is largely determined by its quality compared to conspecifics of the same sex (Perrins 1990), together with the sex ratio operating within the population and overall density of non-breeding adults.

Behavioural ecology studies in the tropics have shown that individuals born in high quality habitats are less likely to disperse into sub-optimal areas than those born in poor quality habitats; they prefer to float, and sometimes queue, instead (Stutchbury and Morton 2001). Compared to temperate zones, tropical systems are generally characterized by low reproductive success (Stutchbury and Morton 2001) and high adult survival, the latter which results in few openings for territories (e.g., Morton et al. 2000). In this scenario, improving chance of survival is likely to be the best strategy for maximizing lifetime reproductive success (Morton et al. 2000). If so, non-breeding adults, particularly ones in high quality habitats, can be expected to adopt a 'hopeful dominant strategy' (e.g., Smith 1984; Zack 1990) rather than disperse into hostile habitat. On the other hand, non-breeding adults in low quality habitats might consider dispersal as the best alternative to either enhance their chances of immediate breeding or increase their survival probability by floating in high quality habitat. As a consequence, high quality habitats can be expected to host more floaters than low quality habitats.

Studying the presence of floaters, and more generally the effects of territorial behaviour in regulating breeding density, often requires experimental removal of individuals with known territorial status (e.g., Watson and Jenkins 1967; Krebs 1971; Knapton and Krebs 1974; Smith 1978; Newton 1992). We used removal experiments to investigate the presence and behaviour of non-breeding adults in two populations of the white-starred robin *Pogonocichla stellata,* a forest-dependent resident of montane forests in eastern to southern Africa (Keith et al. 1992, Bennun et al. 1996). One study population inhabited a relatively intact forest patch, Ngangao, while the other one occupied a smaller and more disturbed one, Chawia. Analyses of vegetation composition (Wilder et al. 2000), population trends and survival rates (Chapter 4) in these fragments indicated that Ngangao was generally a better quality habitat for the robins than Chawia. This suggests there were more resources available in Ngangao that would allow furtive existence of non-territorial individuals within breeder's territories while awaiting a breeding vacancy, without diminishing the survival and reproductive potential of the breeding birds. The converse would hold for Chawia, where the combination of a lack of sufficient promise of future reproduction and hostility from territorial holders could make floating an unlikely strategy. In this paper, we address two main questions with respect to differences between the two populations: i) was there any evidence of the presence of a non-breeding adult component; ii) were there differences in the behaviour of floaters, females and neighbouring males after removal of territorial males?

5.2 Methods

5.2.1 Study Species and Site

White-starred robins forage predominantly in the undergrowth of montane forest and at ant-trails. Although levels of antagonism against conspecifics are moderate to low, males aggressively defend territories during the breeding season, possibly year-round or throughout their lifetime in high quality habitats (Oatley 1982a; Oatley and Arnott 1998). This species has previously shown homing ability and site fidelity after translocations in south-central Africa where it is an altitudinal migrant (Dowsett 1985; Dowsett and Dowsett-Lemaire 1986). Adult males and females are largely sexually monomorphic, but males are slightly larger in size (Zimmerman et al. 1996).

The Taita Hills are one of the Important Bird Areas in Kenya (Bennun and Njoroge 1999). Extensive forest loss over the last four decades has reduced the forests on these hills to three larger fragments (*c*95-180 ha) and nine tiny remnants (*c*2-8 ha) scattered across hilltops and ridges (Beentje and Ndiang'ui 1988; Brooks et al. 1998b). Data for this study were collected in two of the larger fragments: Ngangao (*c*135ha), and Chawia (*c*95 ha) [for map, see Galbusera et al. (2000a)]. Based on structural qualities of the vegetation and on plant species richness and diversity (Githiru 2000; Wilder et al. 2000), Chawia was considered to be of poorer quality than Ngangao.

Data were collected from a 16-ha plot in each fragment. Fieldwork was broken into two main sessions, pre-removal (15/08/ to 27/08/2001 in Chawia, 15/09 to 25/09/2001 in Ngangao), and post-removal (29/08 to 09/09/2001 in Chawia, 27/09 to 09/10/2001 in Ngangao). Because two individuals returned to Chawia after translocation (on 05/09 and 06/09/2001), where relevant, a separate short third session running between 05/09 and 09/09 was considered for this fragment. During all sessions, the main methods used to collect data on the social system of the populations were radio telemetry and records of dawn calls together with intensive behavioural observations.

5.2.2 Radio Telemetry

Individuals were captured in standard mistnets and fitted with radio transmitters at the ringing site before release. Using superglue, one-gram pip transmitters (manufactured by Biotrack Ltd., UK) with an Ag376 cell were carefully attached on to the birds' back so that they were closest to the centre of gravity, in the standard attachment procedure (e.g., Raim 1978; Sykes et al. 1990; Johnson et al. 1991). Seven and six individuals were initially fitted with radio transmitters in Ngangao and Chawia, respectively. One individual in Ngangao disappeared almost immediately after release and was excluded from further analysis. In Chawia, a transmitter was retrieved from a male before translocation and fitted on a female-mate to another translocated male. Program Ranges 6 (Kenward et al. 2002) was used to calculate home range size and overlap between pairs of ranges. Because at least 90 minutes was allowed between consecutive fixes, and statistical independence (sensu Swihart and Slade 1985a) was obtained after 106 ± 15 (Chapter 4), all fixes were considered independent. The Kernel method was used to estimate range size and overlap. Utilization plots, showing progressive changes in range size as the percentage of fixes used in the analyses was increased (Kenward and Hodder 1996), were ran for all individuals (see Appendix) to set the percentage best describing a core area of activity (Wray et al. 1992; Hodder et al. 1998). Judging from the point of inflexion of individual utilization plots, we selected 80 % as an appropriate percentage to describe home range size. This would emphasize the key parts of the range, and hence enable more useful comparisons among fragments (Seaman et al. 1999). [NB: throughout this paper, we use '*territory*' in reference to these core areas (e.g., Maher and Lott 1995)]. Next, the mean overlap between a pair of ranges was calculated as the average of the percentage of home range i overlapped by home range j, and vice versa.

5.2.3 Dawn Calls and Observations

Permanent transects crisscrossing each study plot were walked daily at constant speed between 0600 and 0730h, tallying all individuals heard calling or singing. Following Oatley (1982a), three different vocalizations were distinguished: '*rattle calls*' indicating high-intensity stress/anxiety; '*piping calls*' used to maintain contact between a pair and as warning system; and '*song*' seemingly used in a territorial context, but by both sexes. For the purposes of this paper, only piping calls and song were analysed. Mean number of calls per territory per day was used as the dependent variable in an ANOVA design with fragment, removal status and session as independent variables. In addition, song and piping calls were used for targeted playbacks where necessary to provide additional information on territory occupancy and help resolve owner identity. Lastly, during the entire experimental period we recorded all aggressive (i.e. chasing and fights) and non-aggressive (i.e. displaying behaviour and synchronized calling/singing) interactions between individually-marked adults, with special focus on behaviour at ant-trails.

5.2.4 Assessment of Territorial Status (Pre-removal)

Throughout this paper, '*resident*' refers to any territorial bird with a known mate and/or constantly roosting at a particular site within his/her territory; '*quasi-resident*' refers to any territorial bird without a confirmed mate and/or that roosted outside his/her territory; '*floater*' refers to any adult without a proper territory, mate or roosting site, and/or whose home range encompassed more than one *resident* bird's territory. Consistency in singing and/or making piping calls at dawn also confirmed residency. Because the maximum distance the birds travelled to ant trails remained unknown, information on possible status of individuals at ant-trails was treated as tentative before verification by either dawn calls or playbacks. Thus, as a caveat, residency was only ascribed when it was verified by two or more different methods. When only one method indicated residency, quasi-resident status was assigned. Typically, territories of residents and quasi-residents were less than 1.0 ha [Appendix; see also Chapter 4] and were partly or wholly overlapped by one or more floater's home range(s) (Fig. 5.1a&b). Overall, more adult individuals were captured or observed in Ngangao compared to Chawia (Table 5.1).

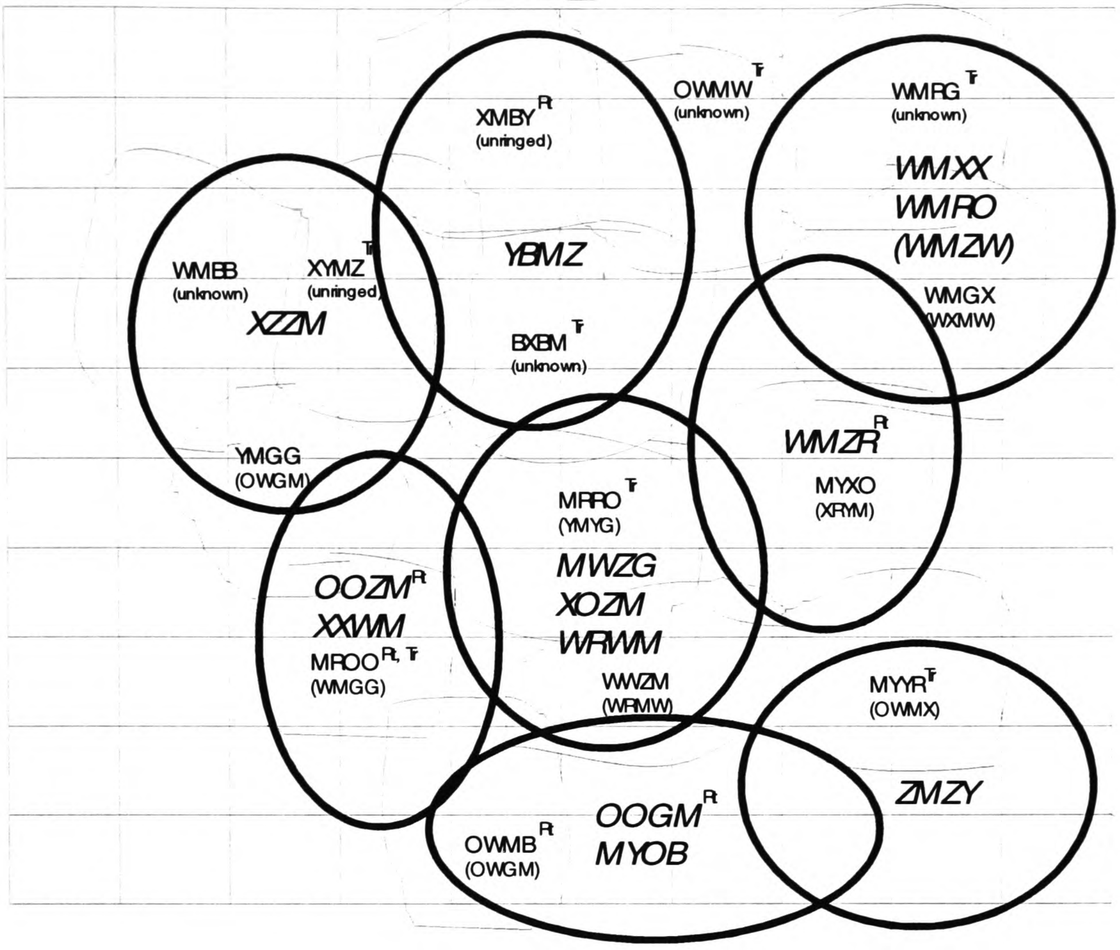
Table 5.1. Total number of adult *P. stellata* per 16-ha study plot (based on equal search effort): 'resident' refers to known territory holder; 'quasi-resident' refers to unconfirmed resident; 'floaters' refers to known non-territorial adults

Fragment	Total	Residents		Quasi-residents		Floaters	
		Males	Females	Males	Females	Males	Females
Ngangao	38	10	8	4	2	13	1
Chawia	14	6	4	2	--	2	--

5.2.5 Translocation and Monitoring (Post-removal)

After establishing the status and home ranges of individuals within each study plot, resident and some quasi-resident males were targeted for translocation to fragment Fururu (*c*8 ha), located approximately 6.6 km south and 5.0 km north of Ngangao and Chawia, respectively. A total of seven individuals were translocated from Ngangao: resident males MRRO, MROO, MYYR and XYMZ, and quasi-resident males BXBM, OWMW and WMRG (Fig. 5.1a). In Chawia, four individuals were translocated: resident males BMXG and MBYG, quasi-resident male OOXM, and resident female ZMGW (inadvertently removed after being mistaken for a male) (Fig. 5.1b). Individuals were translocated immediately after capture. They were moved by car, carefully held in bags by a passenger to reduce stress from shaking. All individuals translocated flew off as normal immediately after release. In each plot, at least two resident individuals were left intact as controls. Following each removal, radio tracking, dawn calls (plus targeted playbacks) and observations were performed in all territories identical to the pre-removal stage.

a) Ngangao



b) Chawia

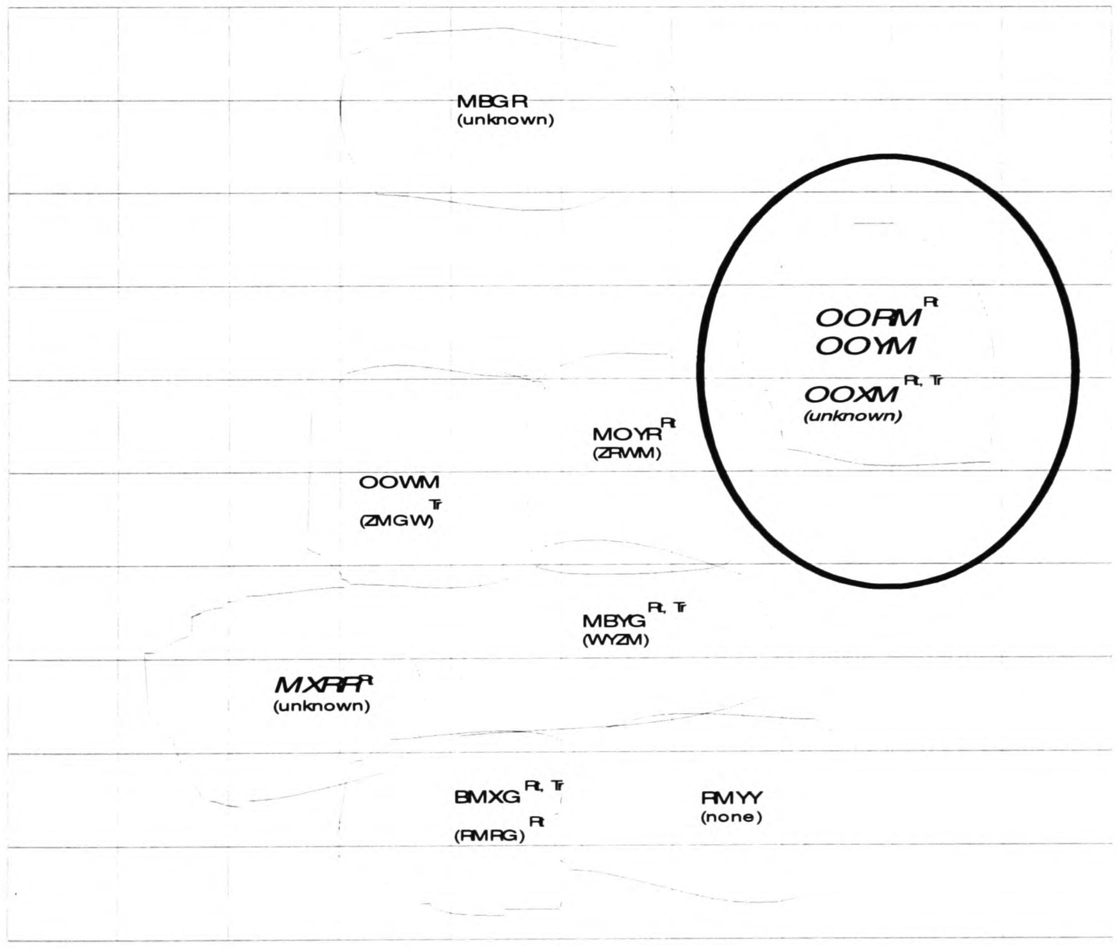


Figure 5.1. Territories and home ranges of 50 individually marked *P. stellata* in Ngangao and Chawia. Hairline figures with small fonts refer to resident and quasi-resident birds, while thick-lined ellipses with large fonts are floaters. Females (both resident and floating) are shown in brackets. ^{Rt} = radio-tracked individuals, ^{Tr} = translocated individuals; grid squares are approximately 40 x 40 m.

5.3 Results

5.3.1 Calling Behaviour

Over all the known territories, birds called significantly more in Ngangao than in Chawia ($F_{1,26} = 6.4$, $P = 0.018$), with a general trend indicating more calls in the post-removal than pre-removal session ($F_{1,26} = 2.6$, $P = 0.12$) in both study plots. The increase in number of calls in the post-removal session was greater in territories where removals were done than ones without removal in Ngangao, while the reverse was the case in Chawia; however, both interactions were not significant ($P > 0.28$).

5.3.2 Behaviour of Floaters

In Ngangao, there was confirmed response from floaters in three territories where known residents were removed. The second day after removal, floaters OOZM and MWZG (Fig. 5.1a) began calling and singing in the main territory within their home ranges, including singing from points the translocated residents often sang from. They increased the calling and singing intensity towards the end of the study. Even when several floaters had been identified at a single territory (see Fig. 5.1a), only a single floater was observed calling after the removals, except in one territory where a different floater was observed making piping calls. In the territory previously occupied by MYYR, two aggressive fights were observed involving floater ZMZY and an unidentified adult(s). Observations and radio tracking in fragment Chawia after the removals did not yield any floating individuals around the vacant territories.

5.3.3 Behaviour of Mates

In Ngangao, all three colour-ringed mates of the translocated resident males remained within their territories throughout the post-removal session. Females WMGG and YMYG were seen with the invading floaters (OOZM and MWZG, respectively, [see Fig. 5.1a]). Occasionally they called and responded to targeted playbacks together. In Chawia, female WYZM stayed within her territory while the female RMRG moved to the neighbouring territory of the previously unmated male RMYY. Partner OOWM of female ZMGW (which was accidentally translocated, [Fig. 5.1b]) remained in his territory and began calling and singing intensively on the third day after removal of his mate. No female was associated with him by the end of the study.

5.3.4 Behaviour of Neighbours

In Ngangao there was no evidence of neighbouring males attempting to move into the vacant territories or expanding their territorial boundaries into these areas. For instance, the percent overlap between territories of MROO (removed) and OWMB (intact) declined between session one and two: 11.2 and 2.4 %, respectively (this was the proportion of MROO's territory that was overlapped by OWMB). Likewise, there were no take-overs of, or expansions into, vacated territories in Chawia; the percent overlap between territories of BMXG (removed) and MXRR (intact) declined between sessions one and two: 15.2 and 2.0 %, respectively. Compared to Ngangao, however, neighbouring males in Chawia slightly increased their calling rate after the removals. Further, the female RMRG that was tracked after translocation of her mate apparently moved into the territory of a previously unmated male RMYY. This male increased his calling intensity when the translocated male (BMXG) returned; the female remained with RMYY until the end of the study (2 days after the return of BMXG). Another previously unmated male MXRR (a quasi-resident) was subsequently seen with female WZMW whose previous status was unknown. He increased his singing and calling frequency, slightly contracted his home range (see Appendix), and though he still roosted away from his territory, he began roosting within it on some nights (which had not been observed pre-removal).

5.4 Discussion

This study revealed four general findings. First, fragment Ngangao had a higher density of floaters than fragment Chawia. At least for the males, there seemed to be more than one floater in some territories, suggesting that some form of dominance and queuing strategies could have been operating among the floating population (e.g., Smith 1978; Kokko and Sutherland 1998). Second, in Ngangao, new males ventured to replace the translocated males soon after the removals; resident females always remained within their territories. In contrast, there was no evidence of attempted occupation of the vacant territories in Chawia, even when the female opted to stay after removal of her mate. Besides, females in Chawia apparently adopted mixed strategies, with one female shifting into a neighbouring territory occupied by an unmated male. Third, in both populations, there was no indication that neighbouring males attempted to move into the vacant territories or expanded their territorial boundaries into these areas. Finally, as found hitherto (Dowsett and Dowsett-Lemaire 1986), the robin revealed considerable homing ability, with the translocated individuals finding their way back to their territories in Chawia within about a week, and slightly longer for Ngangao. In Ngangao, the returning male MROO drove out its hopeful replacement OOZM and successfully bred with its former mate WMGG in the subsequent breeding season. In Chawia, MBYG was seen with his former mate WYZM. Yet, individual OOXM had not returned to Chawia more than two months after translocation, which was probably not so surprising since he was a quasi-resident. He might have found better prospects of breeding (or surviving) in the new fragment, or indeed was more willing to take a chance, given he was coming from a low quality fragment (see Komdeur 1992). Though these results are based on only a few samples, this being a pilot study, it is worth endeavouring to shed some light into these (likely) differences in social structure and individual behaviours between the two populations, and develop provisional arguments to possible factors underlying such differences.

As expected, Ngangao, being a better quality habitat (Wilder et al. 2000), had a substantial non-breeding population. Plausibly, this was a result of there being less aggression from resident individuals (because resources were sufficient), and ample promise for successful breeding and recruitment later. On the contrary, Chawia possibly lacked both factors vital in motivating floating as a strategy, viz., high survival probabilities and/or the promise of successful breeding (Smith 1978). Likewise, previous studies noted that non-territorial birds in high quality habitats opt to stay and float, while those in sub-optimal areas are more willing to accept the risks involved with dispersing and attempting breeding elsewhere (Komdeur 1992; Stutchbury and Morton 2001). Thus, corroborating the finding of Smith and Arcese (1989), the fragment with the higher number of breeders (Ngangao), also had the higher number of floaters, which suggests that floaters were a by-product of the regulation of numbers of breeding individuals by territorial behaviour (Tompa 1962).

The responses by females were tied in with both floater-related aspects and population attributes. Three qualities in particular made female site fidelity a more sensible option in Ngangao than Chawia. First, because there was always a male floater ready to take up the territory almost immediately, the female just chose to stay in the home range she was best acquainted with (e.g., had knowledge of the best nesting sites). Second, due to the presence of some female floaters, maybe moving out would immediately invite another female into the territory, necessitating some form of a contest to re-acquire it (if need be). Third, there was little probability that by moving out she would encounter an unmated male in a good quality territory, owing to the presence of the female floaters. Conversely, in Chawia the lack of male floaters ready to usurp the vacant territories perhaps made it a better gamble by some unmated females to shift territory and seek unmated males rather than wait. Indeed, parallel to previous findings (Smith and Arcese 1989), the unmated territorial males in Chawia were perhaps advertising their presence and breeding potential in some ways, such as singing and displaying. The unmated territorial males were possibly the upshot of skewed sex ratios coupled with low population densities in this fragment (Chapter 2). In other tropical populations, similar behaviour has been found to result in extra-pair copulations (Morton 1996; Morton and Derrickson 1996). It would be interesting to follow this (extra-pair fertilization phenomenon) up in these forest patches, given the social structure differences in the two populations.

In conclusion, we found little evidence of territorial behaviour limiting breeder densities in Chawia, which were most likely limited by scarcity of females and poor habitat quality. In Ngangao, however, both sexes were found to be floating [NB: the fact that there were more male than female floaters was most likely just an artefact of the overall robin metapopulation, which was only 20-30 % female: Chapter 2]. This strongly suggests that territorial behaviour was, at least, one important factor regulating this population; specifically, that habitats were saturated with breeding birds in Ngangao but not Chawia. Consequently, one would expect a social structure in Ngangao chiefly driven by territory acquisition, and mate acquisition to be more important in Chawia. Our removal experiment demonstrates that this was likely to be the case. Clearly, the decision whether to breed or not affects the reproductive potential of the entire metapopulation (see Kokko and Sutherland 1998). In addition, it has implications for conservation, because the floaters can be translocated to other fragments where they can switch from floating to breeding (e.g., Komdeur 1996). This is useful where there exists potentially suitable patches across the landscape but low dispersal ability makes their (re)colonization improbable. A germane case for this study area is that the low persistence of the highly threatened Taita thrush *Turdus helleri* across forest patches this landscape was recently shown to be partly caused by low dispersal ability in this species (Lens et al. 2002b). Thus, if similar removal experiments can demonstrate the presence of a non-breeding adult component for the thrush, translocations into some potentially favourable small patches [such as Fururu] might become a realistic conservation strategy.

Appendix. Radio-tracking data for *P. stellata* showing the unique colour codes of the radio-tracked individuals, their residency status, the total number of fixes collected per individual per session, and the 80 % Kernel-based home range size estimate (ha)

Fragment	Individual	Status	Session 1		Session 2		Session 3	
			Fixes	Size	Fixes	Size	Fixes	Size
Ngangao	MROO	Resident	47	0.6	-	-		
	XMBY	Resident	41	0.9	21	1.6		
	WMZR	Floater	37	1.3	50	2.0		
	OOZM	Floater	50	1.2	76	1.0		
	OWMB	Resident	50	0.5	71	0.7		
	OOGM	Floater	38	1.7	52	0.9		
Chawia	MXRR[1]	Quasi-Resident	58	1.1	51	0.7	24	0.9
	BMXG	Resident	50	1.0	-	-	30	1.9
	MOYR	Resident	46	0.5	47	0.6	24	0.6
	OORM	Floater	39	1.4	46	1.4	12	2.2
	MBYG	Resident	46	1.1	-	-	-	-
	OOXM[1]	Quasi-Resident	40	0.7	-	-	-	-
	RMRG[2]	Resident	-	-	41	0.7	24	0.3

[1] were unmated territorial males that often roosted outside their territories

[2] was the female to BMXG that was tracked after translocation of its mate

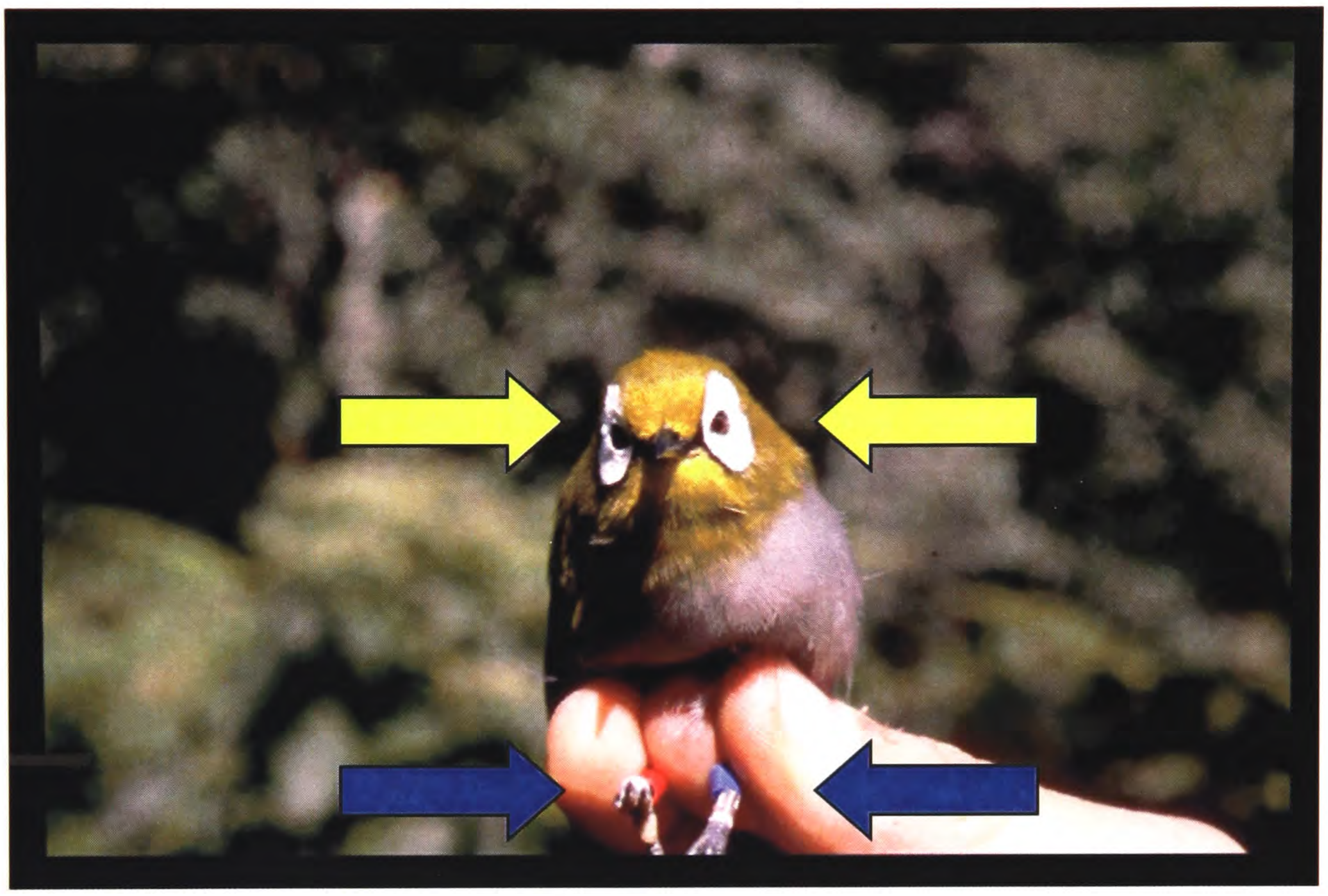
Paper V

Submitted manuscript [*Molecular Ecology*]

Species-specific effects of habitat fragmentation on the population equilibrium of an Afrotropical bird

Peter Galbusera, Mwangi Githiru, Luc Lens & Erik Matthysen

CHAPTER 6



The Taita white-eve *Zosterops silvanus*

...democracy can be interpreted to assert not only equality before the law but also essentialistic identity in all respects. This is expressed in the claim, "All men are created equal," which is something very different from the statement, "All men have equal rights and are equal before the law." Anyone who believes in the **genetic uniqueness** of every individual thereby believes in the conclusion, "No two individuals are created equal."

Ernst Maur

Chapter 6: Species-specific effects of habitat fragmentation on the population equilibrium of an Afrotropical bird

Summary

Because of the variation in species' responses to habitat loss and fragmentation, establishing general patterns remains elusive, even within the same study area. A better grasp of the mechanisms producing differences among species can help formulate such general patterns. Here, we examine the effects of habitat fragmentation on the genetic diversity of the white-starred robin *Pogonocichla stellata* metapopulation in the Taita Hills forest 'archipelago'. Using seven microsatellite markers, we analysed the robin's genetic structure, and tested for equilibrium between migration and drift (fragmentation effects) as well as between mutation and drift (i.e. bottlenecks). This metapopulation was found to be in migration-drift equilibrium, suggesting that increased isolation between fragments has not had much effect on the dispersal patterns between them. Further, in contrast to previous findings on the related and sympatric Taita thrush *Turdus helleri* (which is critically endangered), there were no indications for bottlenecks in any of the robin subpopulations. This difference can be attributed to the higher dispersal capacity of the robin compared to the thrush (deduced from both the genetic and capture-recapture data), corroborating the assertion that the effects of habitat loss and fragmentation on genetic diversity are clearly influenced by species mobility; in this case, the ability of the species to traverse a landscape matrix with different land uses.

6.1 Introduction

Habitat loss and fragmentation threatens the survival of many species; small and isolated populations are most prone to extinction (e.g., Frankham 1998; Saccheri et al. 1998). The actual impacts on demographic and genetic structure of natural populations depend on both landscape aspects (level of habitat isolation, degradation, and surrounding land uses) and species characteristics (natural population size and density, dispersal power and stress tolerance) (Matthysen et al. 1995; Newton 1998; Bohonak 1999). In particular, these parameters govern the migration-drift and mutation-drift equilibria, both central in shaping the population's genetic attributes. On the one hand, migration and mutation generally preserve genetic variation, and are mainly dependent on the dispersal rates and effective population size, respectively (Vucetich et al. 1997). On the other hand, genetic drift removes genetic variation at a rate inversely proportional to population size (Lande 1995; Gilligan et al. 1997). This triangle of genetic drift, mutation and migration (gene flow) is basic to our understanding of neutral theory on population genetics (Hartl and Clark 1997).

Spatially structured populations inhabiting severely fragmented habitats are often found to be in migration-drift disequilibria because decreased interfragment dispersal cannot compensate for rising levels of genetic drift as subpopulations become smaller and more isolated (e.g., Slatkin 1987; O'Ryan et al. 1998; Uimaniemi et al. 2000). Recent studies in the Taita Hills, a severely fragmented tropical rainforest and biodiversity hotspot in southeast Kenya (Bennun and Njoroge 1999; Myers et al. 2000), revealed rising levels of fluctuating asymmetry, mortality, male-biased skew in sex-ratio and a genetic bottleneck with increasing levels of habitat disturbance in the critically endangered Taita thrush *Turdus helleri* (Lens et al. 1998; Lens et al. 1999b; Galbusera et al. 2000a; Lens et al. 2002a). Coupled with diminished dispersal, this can disrupt genetic processes, resulting in migration- and/or mutation-drift disequilibria. There remains a pressing need to pin down the mechanisms that shape the genetic structure of such small populations at the landscape level. This need necessitates a metapopulation-level study focusing on a species that, unlike the thrush, persists throughout the landscape. To achieve this, we studied the effects of habitat fragmentation on the white-starred robin *Pogonocichla stellata*, a relatively common and forest-dependent bird species occurring in most of the indigenous forest patches of the Taita Hills (Bennun et al. 1996; Lens et al. 1999a). The isolated nature of this forest archipelago (it is surrounded by plains) allows the sampling of a complete metapopulation with little chance of individuals dispersing to or from other populations. We sampled and analyzed between 11 and 30 individuals from eleven subpopulations using 7 polymorphic microsatellite DNA markers. Based on previous capture-recapture data for this species (Lens et al. 1999a), we expected rates of dispersal between subpopulations of the robin to be sufficiently high to counter the effect of random genetic drift.

To test for migration-drift equilibrium, we applied a method that explores the most probable demographic and genealogical histories consistent with the sample of chromosomes typed (Ciofi et al. 1999; Beaumont 2001). In addition, we used direct (current) and indirect (historical or genetic) methods to evaluate changes in dispersal patterns over time. Indirect methods measure only effective dispersal over many generations (e.g., Monaghan et al. 2001), while direct methods give a more instantaneous picture and include dispersal events not necessarily resulting in successful reproduction of the individuals in their new population (Greenwood and Harvey 1982; Crochet 1996). Direct methods have been described as inadequate (e.g., Koenig et al. 1996) because of their dependence on the proportion of the total population sampled and limited ability to locate long-distance migrants (Barrowclough 1978). Yet, even the indirect methods are not without their share of problems (e.g., Bossart and Prowell 1998); indeed, Bossart and Prowell conclude that direct assessment of movement remains the most valid approach. The application of both direct and indirect methods, because they possess complementary resolution power and concern different time and geographical scales, will improve our understanding of dispersal in natural populations (Crochet 1996). Current patterns of gene flow were assessed by assignment tests (Cornuet et al. 1999; Pritchard et al. 2000; Waser et al. 2002), while historical patterns were obtained by the coalescent method (Beerli and Felsenstein 1999). Lastly, because both the underlying mutation rates of the genetic markers and magnitude of change in effective population size were unknown, presence or absence of mutation-drift equilibrium could not be predicted a priori. Therefore, the assessment of this equilibrium was achieved by estimating effective population sizes based on established mutation rates (Ellegren et al. 1995; Saino et al. 1997), as well as by comparing observed and expected heterozygosities (Cornuet and Luikart 1996).

6.2 Methods

6.2.1 Study area and species

The Taita Hills are divided into three distinct isolates (massifs): Sagala Hill (SA), Mbololo Hill (MB), and Dabida Hill (DA). Geographically, DA is separated from MB by a large valley at least 11 km across, while SA is separated from both DA and MB by the Voi River and at least 25 km of dry plains (see Fig. 1.1b in Chapter 1). These hills are isolated from other highlands by over 80 km of semi-arid plains in any direction (Lovett 1986). The indigenous cloud forests on these hills have suffered substantial loss and degradation since the early 1960s (Beentje and Ndiang'ui 1988). At present, the forest persists in a scatter of 12 patches across the three isolates – one (Sagala) is located on SA, two (Mbololo and Ronge) on MB, and nine (Ngangao, Chawia, Fururu, Ndiwenyi, Mwachora, Macha, Yale, Vuria and Kichuchenyi) on DA – embedded in a mosaic of human settlements, small-holder cultivation plots and plantations of exotic trees (Brooks et al. 1998a). Slightly over 400 ha of original forest are retained in these patches: Mbololo (*c*179 ha), Ngangao (*c*136 ha), Chawia (*c*94 ha) while the rest (nine) are tiny remnants (*c*1-4 ha, one of *c*8 ha). An analysis of patch size, biomass, stem density, canopy cover, shrub density, stratification and extent of herbaceous ground cover (Wilder et al. 2000), when compared to earlier data (Beentje and Ndiang'ui 1988), showed that Mbololo suffered the least disturbance and forest loss. Ngangao suffered intermediate levels, while Chawia and the small patches were most heavily impacted, e.g., with between 95% and 99% deforestation in Sagala and Vuria, respectively (Lens et al. 1999a).

The white-starred robin *Pogonocichla stellata* occurs in montane forests of eastern to southern Africa (Keith et al. 1992). Currently, nine races are recognized, six of which occur in Kenya and northern Tanzania. Sub-species *helleri* is confined to the Taita Hills and Mt. Kasigau (Moreau 1951; Keith et al. 1992; Zimmerman et al. 1996) where it is relatively common in patches of indigenous forest. It is forest dependent (Bennun et al. 1996), and forages at all forest levels, most frequently in the undergrowth and at ant trails (Oatley 1982b; Keith et al. 1992). It is territorial and showed homing ability and site fidelity after translocations in south-central Africa (Dowsett 1985; Dowsett and Dowsett-Lemaire 1986). Upon first capture, all robins were ringed, colour-banded, aged, measured and blood sampled. All genotyped individuals were sexed through examination of the highly conserved W-chromosome linked gene CHD-W (Griffiths et al. 1998); Lens et al. (1998; 1999a) describe the methodology in greater detail.

6.2.2 Genotyping

Blood samples were collected by puncture of the brachial vein and stored in 95% ethanol or DMSO. DNA was obtained either by boiling in a 5% Chelex solution (BIORAD) after incubation for 90 min at 55°C in the presence of 100 μg proteinase K (ethanol storage)

(Walsh et al. 1991), or by a normal phenol-chloroform extraction also in the presence of 100 μg proteinase K (DMSO storage). PCR amplification was achieved in a 10 μl reaction volume containing approximately 100 ng DNA, 1x buffer (75 mM Tris-HCl pH 9.0, 20 mM $(NH_4)_2SO_4$, 0.01% Tween 20), 0.5 U Taq polymerase (Eurogentec), 200 μM dNTPs (GIBCO), 1.0-3.0 mM $MgCl_2$ (see Addendum A) and 250-500 nM of seven highly variable microsatellite DNA markers (Galbusera et al. 2000b). These markers were originally developed for the following passerines: *Parus atricapillus* (Pat14; Otter *et al.* in prep.), *Chiroxiphia linearis* [Ltmr6; (McDonald and Potts 1994)], *Plocepasser mahali* [WBSW2 and WBSW9; (McRae and Amos 1999)], *Malurus cyaneus* [Mcyμ4; (Double et al. 1997)], and *Geospiza fortis* [Gf5B and Gf6; (Petren 1998)]. Starting from the original PCR conditions, variable $MgCl_2$ and template DNA concentrations and annealing temperatures were tested in a gradient PCR device (PC-960G Gradient Thermal Cycler, Labortechnic). Optimal reaction conditions and PCR product size ranges are summarised in Addendum A. Genotypes were scored on a 6 % acrylamide gel in an automatic sequencer (ALF express, Pharmacia Biotech).

6.2.3 Analyses

6.2.3.1 Partitioning of genetic variation and estimating N_e

Genetic variation was explored at both fragment and isolate levels. Allelic richness was calculated with FSTAT (Goudet 1995), while allele frequencies, observed and expected heterozygosity, mean number of alleles per locus and genetic differentiation among the isolates were calculated using GENEPOP Version 3.1d (Raymond and Rousset 1995a). For each pair of isolates, we estimated pair-wise F_{ST} using parameter θ (Weir and Cockerham 1984), and applied a Markov Chain method to calculate significance levels using 10000 permutations in an exact test for population differentiation (Guo and Thompson 1992; Raymond and Rousset 1995b). Approximate confidence limits for F_{ST} were obtained as 2.5% and 97.5% quartiles after bootstrap sampling over all loci for 1000 times [GDA: (Lewis and Zaykin 1999)]. Isolation by distance was explored by comparing the genetic (F_{ST}-based) and geographic distances using a Mantel's test. Principal Component Analysis (PCA) in PCAGEN http://www.unil.ch/izea/softwares/pcagen/html was used to illustrate the genetic structure.

Though the commonly accepted microsatellite mutation rate for a wide range of animal taxa is $5x10^{-4}$ (Ellegren et al. 1995), there is some evidence that birds might have higher mutation rates. For instance, based on 1000 meiotic events in three *Hirundo rustica* microsatellite loci, Saino et al. (1997) calculated mutation rates of $1x10^{-3}$, $5x10^{-3}$ and $36x10^{-3}$, respectively. We chose the intermediate rate ($\mu = 0.001$) to estimate effective population size, N_e, in MIGRATE (Beerli & Felsenstein 1999). Finally, future levels of genetic diversity were predicted in GENELOSS (England and Osler 2001), based on current allelic frequencies and the calculated N_e -values.

6.2.3.2 Estimation of gene flow

In order to estimate the levels of gene flow, it is essential to establish that different populations are indeed genetically discrete. To check this, we estimated the number of subpopulations (K) in our total sample assuming no substructuring a priori (i.e. without effect of sampling locality) using STRUCTURE (Pritchard et al. 2000). Based on the structure found, the numbers of current migrants and/or descendants from migrants were then estimated using assignment tests in STRUCTURE (Waser and Strobeck 1998; Davies et al. 1999). Each individual was assigned to the subpopulation for which the probability of random sampling the individual's multi-locus genotype (based on knowledge of the gene frequencies of the progenitor populations) was highest. The number of 'misassigned' individuals (i.e. those that are assigned to a population other than the one where they were captured) reflects the dispersal rate between each pair of subpopulations (Haig et al. 1997; Waser et al. 2002). Variation in dispersal rates between sexes was tested in FSTAT (Goudet et al. 2002), using the assignment indices (AI) pooled for males and females (e.g., see Favre et al. 1997; Dallimer et al. 2002). Given an average AI value for a population is zero, individuals with negative AI values are less likely than average to belong to that population, and vice versa for positive AI values (Dallimer et al. 2002).

We then estimated the levels of historical gene flow using the coalescence theory in MIGRATE (Beerli and Felsenstein 1999). Uni-directional gene flow estimates were calculated by running this program ten times (the estimates from each run were used as starting values for the next run). Unlike traditional F_{ST}-methods, coalescent methods are more robust because they compute directional gene flow taking differences in subpopulation sizes into consideration (Luikart and England 1999; Beerli and Felsenstein 2001; Neigel 2002).

6.2.3.3 Equilibrium testing

Program 2MOD http://www.rubic.rdg.ac.uk/~mab/software/html (Beaumont 2001) was used to test for migration-drift equilibrium. This program identifies populations subjected to genetic drift and gene flow as opposed to those under genetic drift only, through estimation of the relative likelihood of the two models using a Markov Chain Monte Carlo procedure (Ciofi et al. 1999; Goodman et al. 2001; Palo et al. 2001). The interaction between drift and gene flow was further assessed using the gene flow model, $M = (1\text{-}F) / (2F)$, where F is the probability that two genes shared a common ancestor within a population and M the number of migrants per generation (Ciofi et al. 1999). Finally, we used BOTTLENECK (Cornuet and Luikart 1996) to test whether the level of heterozygosity derived from the observed allele frequencies per forest fragment and for each isolate differed from the heterozygosity expected under mutation-drift equilibrium. As mentioned previously, the mutation model underlying the microsatellite markers was unknown. Thus, we analyzed the data under three different model assumptions: the Infinite Allele Model (IAM), the Two-Phase Model (TPM) and the Stepwise Mutation Model (SMM) (Jarne and Lagoda 1996).

6.3 Results

6.3.1 Hardy-Weinberg equilibrium

No linkage was detected between any pair of loci (all $p > 0.05$). All locus-forest fragment combinations were in Hardy-Weinberg equilibrium, except for the following combinations (significant after Bonferroni correction): LTMR6 in Ronge, WB9 in Macha and Vuria, GF5B in Mbololo, Fururu and Vuria, and Pat14 in Yale. All were heterozygosity deficits. Grouping the forest fragments according to isolate did not alter deviation from Hardy-Weinberg equilibrium. A lack of substructuring within forest fragments excludes a spatial Wahlund effect as an explanation for these heterozygosity deficits. Likewise, because F_{is} values (not shown) were much higher than F_{st} values, a temporal Wahlund effect, i.e. subunits of individuals reproducing at different times (Morand et al. 2002), seems unlikely, albeit breeding activity in different patches within DA peaked at slightly different times over the six month (October-March) breeding period. Inbreeding in some forest fragments might also cause such heterozygosity deficits. Yet, if so, a deficit would be expected for all loci, which was not the case in our study. Alternatively, the use of cross-specific markers might have caused the lack of amplification of some alleles (i.e., null-alleles). Yet, no null-homozygotes were observed which suggests low frequencies of null-alleles, if any.

6.3.2 Current and predicted genetic diversity and effective population size

The mean number of alleles per locus (MNA) averaged 7.8±0.29 per forest fragment (Table 6.1). Mwachora had the smallest sample size and the lowest MNA-value, followed by Sagala, Mbololo and Ronge. Excluding Mwachora, Ngangao and Macha had lowest values within DA. The expected heterozygosity H_{exp} ranged from 0.63 (Sagala) to 0.71 (Chawia). Again Macha and Ngangao had intermediate values, while Sagala, Mbololo and Ronge had lowest values. The confidence intervals of both H_{exp} and MNA for the least diverse populations (Sagala, Mbololo and Ronge) did not overlap with those for the most diverse ones (Chawia, Fururu, Ndiwenyi, Yale and Vuria). When we grouped forest fragments into their isolates (i.e. by subpopulation [see further]) and reanalysed the genetic variability, DA retained highest H_{exp} and MNA (Table 6.1). The difference in allelic richness (genetic diversity) between DA and the other isolates was significant, but MB and SA did not differ (see Table 6.1). Estimates of N_e were 400 individuals for DA, 90 for MB, and 40 for SA. Simulations of future genetic diversity (MNA and H_{exp}) for each isolate indicated that, proportionally, MNA dropped faster than H_{exp}, and increasingly so in the smallest subpopulation (SA) (Table 6.1).

Table 6.1. Estimates of allelic diversity and heterozygosity both per forest fragment and per subpopulation of *P. stellata*. N = number of individuals genotyped, MNA= mean number of alleles per locus, H_{obs}= observed heterozygosity, H_{exp}= expected heterozygosity. Numbers in brackets are predicted estimates in 5 generations per subpopulation, while different letters per column indicate significant differences, p = 0.05.

Fragment or Subpopulation	N	MNA	Allelic Richness	H_{obs}	H_{exp}
Chawia	30	8.7	6.5	0.65	0.71
Mbololo	31	7.3	5.6	0.57	0.64
Ngangao	30	7.4	5.7	0.60	0.67
Fururu	32	8.4	6.3	0.62	0.68
Macha	30	7.9	6.0	0.60	0.66
Ndiwenyi	33	8.9	6.5	0.66	0.70
Ronge	30	7.3	5.6	0.58	0.65
Sagala	31	6.7	5.3	0.60	0.63
Vuria	32	9.1	6.5	0.63	0.69
Yale	30	8.3	6.3	0.62	0.69
Mwachora	11	6.1	6.1	0.61	0.65
Dabida	228	11.6 (10.5)	6.3^{a}	0.63	0.70^{a}(0.69)
Mbololo	61	8.3 (6.9)	5.6^{b}	0.58	0.65^{b}(0.63)
Sagala	31	6.7 (5.3)	5.3^{b}	0.60	0.64^{b}(0.60)

6.3.3 Population structure and dispersal

We found significant population substructuring (K = 3) corresponding to the three isolates (DA, MB & SA). This substructure remained evident even when correlation in allele frequencies was allowed. Albeit no significant further structuring was found within the DA fragments when this isolate was analysed separately, there was significant pairwise genetic differentiation between Ngangao and three other fragments: Fururu, Macha and Ndiwenyi. Overall F-statistics revealed substructuring at both fragment and isolate levels ($F_{ST} = 0.0179$, $p < 0.001$, 95% CI: 0.0114-0.0257 and $F_{ST} = 0.0343$, $p < 0.001$, 95% CI: 0.0184-0.0495, respectively). Pairwise analyses for the isolates showed relatively high θ-values all which were significant after Bonferroni correction (Rice 1989): DA-MB, 0.034; DA-SA, 0.025; and MB-SA, 0.051. This significant differentiation of the isolates was illustrated by the PCA, where Mbololo and Ronge were separated from the rest on the first axis (37 % inertia; p= 0.010), and SA from DA by the second axis (18 % inertia; p = 0.080) (Fig. 6.1a). The third axis separating the fragments within DA was not statistically significant (10 % inertia; p = 1.00), although it showed that Ngangao was fairly differentiated from the rest (Fig. 6.1b). Lastly, there was a significant correlation between the geographic distance and F_{ST}-values (Mantel-test; p = 0.042) for the entire study area, but no such correlation was evident among the forest fragments within DA by themselves.

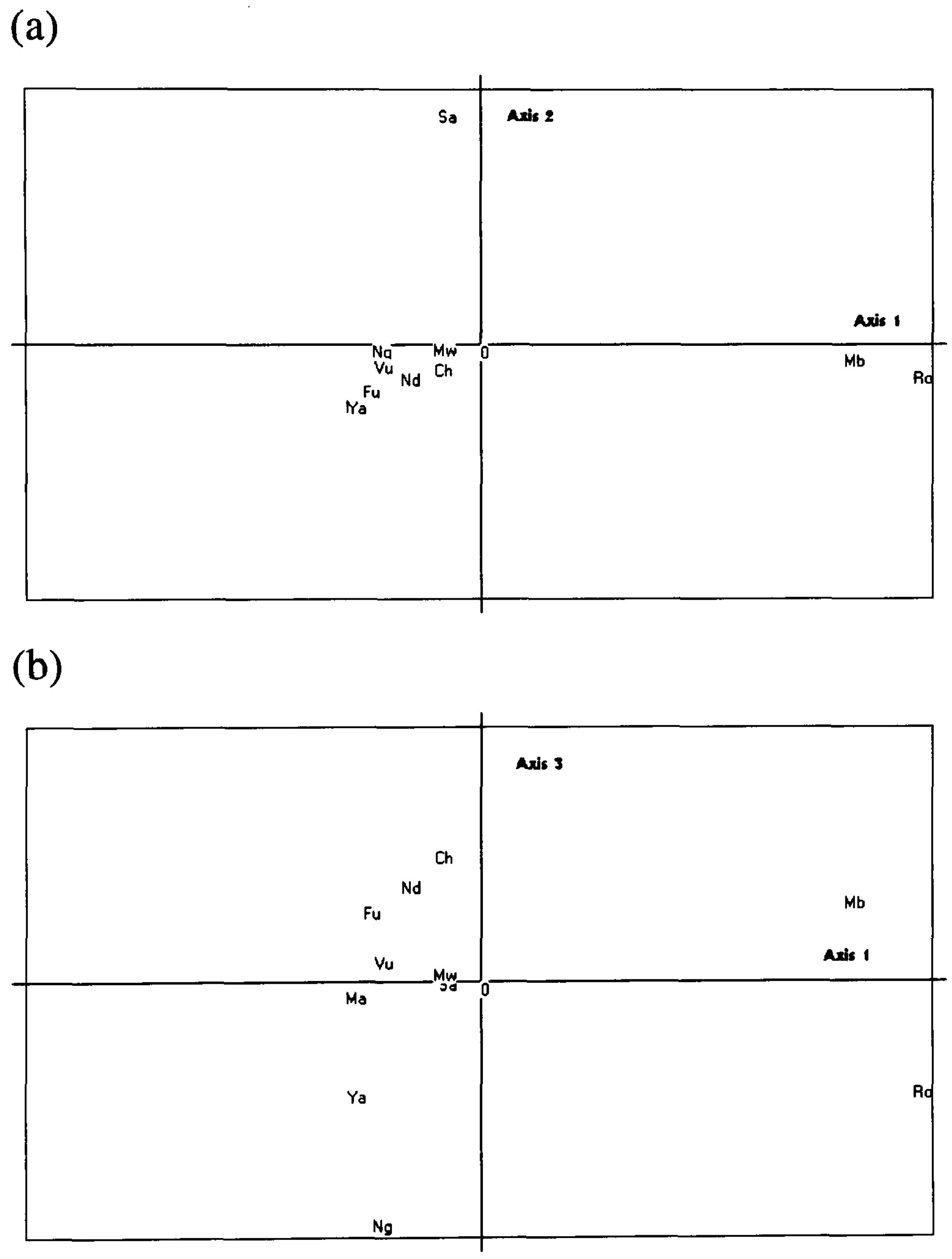


Figure 6.1. Principal Component Analysis (PCA) based on genetic data (7 microsatellite markers) of white-starred robins showing separation (differentiation) of the different fragments (Ro Ronge, Mb Mbololo, Sa Sagala, Ng Ngangao, Ch Chawia, Nd Ndiwenyi, Fu Fururu, Vu Vuria, Mw Mwachora, Ma Macha, Ya Yale, Ng Ngangao)

Current gene flow: we probabilistically assigned individuals to their subpopulation of origin based on the three-subpopulation structure (corresponding to the isolates). Six individuals were classified as probable migrants or offspring of migrants: one individual (#12) was likely to be an offspring of a migrant from SA to DA; four individuals (#c43, #318, #27 and #167) migrated from MB to DA, and one individual (#53) from DA to MB (Fig. 6.2). However, a lack of sufficient power in our analysis because of the relatively small number of markers used (see Pritchard et al. 2000) meant that only one of these individuals (#167) had such a low probability ($p < 0.05$) of being assigned to its subpopulation of origin that it could be confidently classified as a migrant. Overall, the mean assignment index was lower than average for females (-0.019) and higher than average for males (0.008), suggesting female-biased dispersal. This difference approached significance ($p = 0.06$; 1000 randomizations). Finally, direct capture-recapture data yielded eight dispersers: a juvenile female, 2 adult females and 5 adult males, all dispersing within DA except one of the adult males that moved from DA to SA.

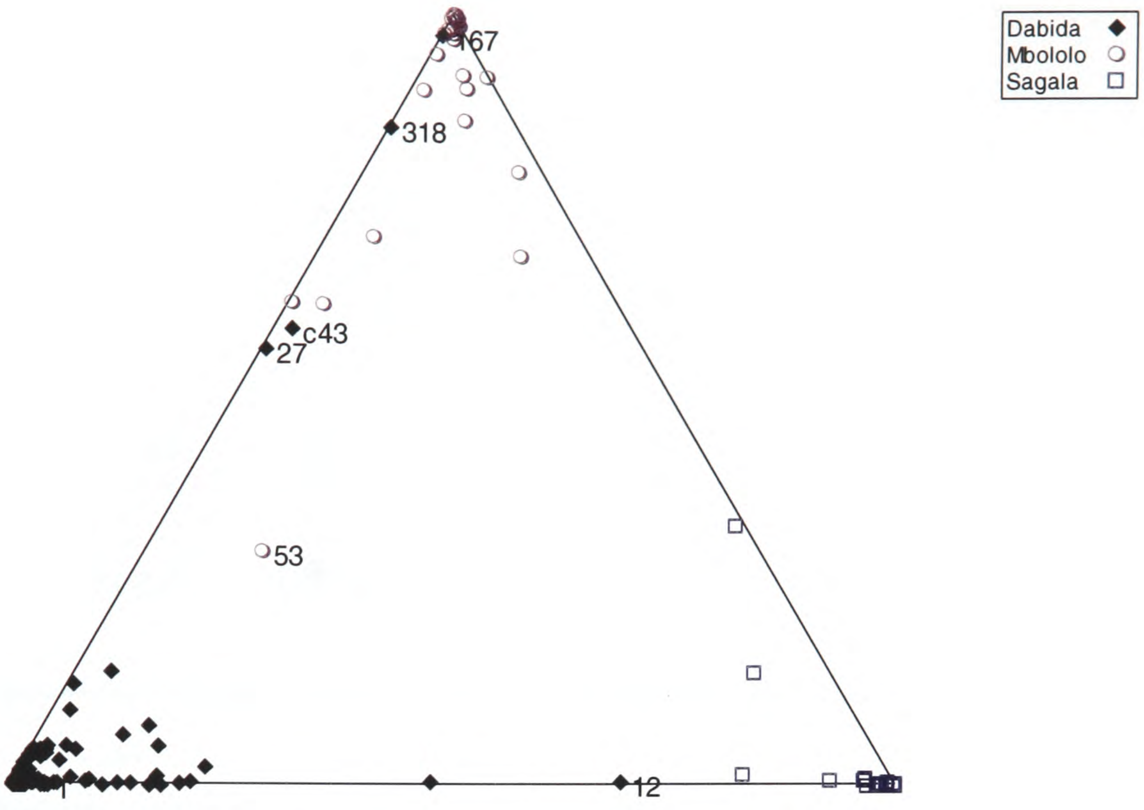


Figure 6.2. Summary of the assignment test assuming three subpopulations of *P. stellata*. Each point shows the mean estimated ancestry for an individual in the sample, based on the individual's genotype and the estimated allele frequencies per subpopulation. Position on the axes shows the genetic affiliation of each individual, symbols refer to their site of first capture: Mbololo Hill (open circles), Sagala (open squares), Dabida (filled diamonds). Numbered individuals are suspected as migrants or of migrant ancestry; only individual 167 had such a low probability ($p < 0.05$) to be assigned to its subpopulation of origin that it could be strictly labelled as a disperser (see text for details).

Historical gene flow: the uni-directional estimates of number of migrants (Nm) between subpopulations are given in Table 6.2. Highest mean dispersal rate was between DA and MB (6), followed by between DA and SA (2.7), and lowest rates between MB and SA (0.5).

Table 6.2. Uni-directional estimates of gene flow (Nm) between the three white-starred robin subpopulations calculated using MIGRATE. (The single [confirmed] misassigned individual detected by STRUCTURE is in brackets)

		To		
	Subpopulation	Sagala	Dabida	Mbololo
From	Sagala	-	2.5 (0)	0.6 (0)
	Dabida	3 (0)	-	8 (0)
	Mbololo	0.5 (0)	4 (1)	-

6.3.4 Equilibrium testing

Migration-drift equilibrium: the gene flow-drift equilibrium model was a thousand times more likely than the pure drift model, implying that gene frequencies were determined by a balance between genetic drift and immigration. The probability (F) that two alleles were identical by descent was at least twice as high in Sagala, Ronge and Mbololo (F = 0.082, 0.059 and 0.061, respectively) compared to the forest fragments within DA (F ranging from 0.001 in Vuria to 0.03 in Ngangao). This denotes a larger immigrant-effect relative to drift within DA compared to the other isolates, which is also demonstrated by a higher estimate of number of migrants per generation in this isolate (M = 16.2 to 500 in DA, and M = 6 to 8 for MB and SA).

Mutation-drift equilibrium: we did not detect any recent (or severe) bottleneck: under the IAM, all allele frequency distributions were L-shaped. In addition, neither the sign test nor the Wilcoxon test detected more heterozygotes than expected under mutation-drift equilibrium. Assuming the SMM and TPM (95% SMM) there was no significant deviation from expectation in all fragments except Vuria, where a significant deficiency of heterozygotes was found (sign test: $p = 0.002$; one-tailed for H-deficiency Wilcoxon test $p = 0.0039$).

6.4 Discussion

6.4.1 Genetic diversity and differentiation

We found significant differences in genetic variability within subpopulations (isolates), as well as significant genetic differentiation between the subpopulations. The large number of patches within DA potentially generated the higher genetic variability and effective population size in this isolate compared to MB and SA. Indeed, the probability that two alleles were identical by descent was twice as high in MB and SA compared to the DA, implying a greater exchange of individuals within DA compared to MB and SA. This was corroborated by capture-recapture data. Whereas the history of the area might have had some additional effect (for instance, if the DA forest originally consisted of a larger area than the other isolates), this finding demonstrates the importance of several fragments (including small ones) for conservation purposes, as long as ample exchange of individuals occurs between them (e.g., see Quinn and Hastings 1987; Burkey 1988; Nunney and Campbell 1993).

Both the Mantel's test and the PCA reveal an isolation by distance effect (sensu Bossart and Prowell 1998), where the genetic structure is influenced by isolate juxtaposition and topographical features separating them. In addition, our data suggest probable additional substructuring within DA, with Ngangao on one side and the other fragments on the other. Indeed, Ngangao was significantly differentiated from 3 of the small fragments, and was distinctly separated on the third PCA-axis, though not significantly so because of the effects of other fragments lying in the middle. The location of a town in between Ngangao and the other fragments (see map in Brooks et al. 1998a) might present a barrier to (straight-line) movement. A similar explanation was invoked to explain the pattern of seed dispersal by the silvery-cheeked hornbill *Bycanistes brevis*, and the resultant distribution of the *Maesopsis eminii* tree in these forest fragments (Githiru 2000).

6.4.2 Gene flow and migration-drift equilibrium

We found strong indications that the robin population was in migration-drift equilibrium, suggesting limited impact of fragmentation on dispersal. The positive correlation between geographic and genetic distances (see preceding section) suggests that the influence of migration is greater than that of genetic drift (Slatkin 1993). The following evaluation of estimates of current and historical gene flow suggests dispersal patterns have not been greatly disrupted, thus supporting this inference. The current and historical numbers of migrants between subpopulations were estimated to be 0-1 and 0.5-6, respectively. However, it is likely that due to the small number of markers we used, we lacked sufficient power to definitely label all individuals (except the single one) as current migrants or having migrant ancestry (Pritchard et al. 2000). Hence, current dispersal was probably underestimated. Furthermore, like capture-recapture, the estimate of number of migrants by the assignment method is dependent on the proportion of the total population sampled; additional samples could yield more dispersers. By capture-recapture we found, besides the 7 dispersers within DA, one disperser from DA to SA but none between DA and MB. In contrast, estimates of gene flow based on the genetic data were the highest between DA and MB. (It is noteworthy that most of the misassigned individuals not confirmable possibly due to limited number of markers, were also between DA and MB [see Fig. 6.2].) These 'omissions' by the capture-recapture method were probably related to sampling after dispersal, a common feature in species with juvenile dispersal (Van Treuren et al. 1999). Moreover, methods based on direct observations are often limited in geographical scope, frequently missing many long-distance dispersal events (e.g., Barrowclough 1978; Crochet 1996; Gauthreaux 1996). In general, low dispersal between SA and both DA and MB could be attributed to the presence of Voi River and extensive plains between them, in contrast to only a valley/ridge between MB and DA. Extra effects of fragment juxtaposition on dispersal will become clear once a digitised GIS map (under preparation) is available. From this, various features can then be associated to enhancing or restricting movements. Thus, the discrepancies in current and historical gene flow (0-1 vs. 0.5-6) can probably be explained by an underestimation of current gene flow. Nonetheless, there was potential congruence between relative estimates of current and historical gene flow (i.e., number of migrants), with both methods revealing the highest exchange between DA and MB. Together with the isolation by distance effect already discussed, this suggests that the migration-drift equilibrium deduction we make is correct, because dispersal patterns seem not to have been drastically altered by fragmentation. Yet, we cannot completely exclude the possibility that there has been a slight decrease in absolute gene flow over time i.e., slightly lower current compared to historical estimates, but whose effects are still minor for this species.

6.4.3 Mutation-drift equilibrium

The subpopulations seemed to be in mutation-drift equilibrium; no recent bottlenecks were detected. This was not surprising because strong bottlenecks are only expected in subpopulations that have been drastically reduced to effective population sizes much lower than the least value we obtained (40 in SA) (Pimm et al. 1989; Gilligan et al. 1997; Spencer et al. 2000). However, in Vuria, we found fewer heterozygotes than expected at mutation-drift equilibrium. This might signify a 'sink' population, plausible if most individuals in the original population there were extirpated (because it underwent a 99 % reduction), and the present population consists of recent immigrants originating from separate populations with different alleles and allele frequencies. These alleles might not have had the chance yet to produce the number of heterozygotes expected under equilibrium conditions.

6.4.4 Conclusions

Overall, the robin metapopulation revealed high genetic diversity (i.e. allelic richness and heterozygosity) and was evidently at both migration- and mutation-drift equilibria. This suggests that habitat loss and fragmentation have not yet significantly disrupted dispersal or drastically reduced the effective population size (numbers of breeders). However, the simulations on future diversity, especially for MB and SA isolates, warn for fairly swift reductions in genetic diversity through drift as effective population sizes decline and landscape permeability is lost through increasing habitat loss, patch isolation and intensification of land uses in the surrounding matrix. Though our simulation is a 'worst-case' scenario because it is based on the assumption of closed populations, female-biased dispersal (if associated with high mortality) will severely decrease the number of females making such a scenario realistic. Presently, however, it seems that any loss of alleles through drift (and deleterious mutations) is successfully countered by dispersal. Sustaining dispersal is thus key to defusing the impact(s) of habitat fragmentation on genetic diversity for the robin, and consequently forestalling any negative impacts on the metapopulation (see also Andrianarimisa et al. 2000). Practically, this implies that focusing conservation action only within the indigenous forest patches themselves is insufficient to maintain the entire metapopulation (see also Desrochers et al. 1999; Baillie et al. 2000; Opdam and Wiens 2002). Finally, higher dispersal capacity yielded higher genetic diversity for the robin compared to the Taita Thrush in these forests (see Galbusera et al. 2000a). This boosted the effective population sizes and helped avert bottlenecks such as that found for the thrush subpopulation in fragment Chawia (Galbusera et al. 2000a). This strongly suggests that the inability to traverse this landscape matrix and successfully establish themselves in the new populations is at least one of the difficulties facing the thrush populations in these fragments, as confirmed by Lens et al. (2002b).

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Appendix: Product size range and optimal reaction condition per microsatellite primer set.

Locus	PCR product size (bp)	Annealing temp. (°C)	$MgCl_2$ conc. (mM)
Pat14	147-171	50	1.5
Mcyμ4	130-160	55	1.0
Gf5B	195-213	57	1.5
Ltmr6	186-194	54	2.0
Gf6	142-150	56	2.5
WBSW 2	127-131	54	1.5
WBSW 9	102-112	54	1.5

Paper VI

Submitted manuscript [*Journal of Tropical Ecology*]

Patterns of artificial nest predation in afrotropical forest fragments, SE Kenya

Mwangi Githiru, Luc Lens & Will Cresswell

CHAPTER 7

B. Amakobe holding an African wood owl *Strix woodfordii*
in one of the small fragments, Ndiwenyi

"If there are any marks of all special design in creation, one of the things most evidently designed is that a large proportion of all animals should pass their existence in tormenting and devouring other animals"

J.S. Mill, 1874

I want to find a voracious, small-minded predator and name it after the IRS.

Robert Bakker, paleontologist

Chapter 7: Patterns of artificial nest predation in afrotropical forest fragments, SE Kenya

Summary

Nest predation accounts for a substantial share of nest failure in most tropical songbirds, leading to low reproductive success. Often, forest loss and fragmentation lead to an increase in nest predation pressure due to reduced cover, fewer (and poorer) nest sites and predator influxes from the surrounding habitats. To test this hypothesis, we studied natural nesting behaviour and nest success of the white-starred robin in seven Afrotropical forest fragments differing in level of habitat disturbance. On average, 29 % of the natural nests initiated survived to produce fledglings. Data on natural nests were complemented by experimental data on artificial eggs, revealing low rates of nest survival in the most heavily disturbed fragment. This was most likely down to an influx of mammalian predators from the surrounding habitats as escalating forest degradation created suitable habitats for them. Both nest placement and microhabitat did not significantly affect depredation levels. This suggests that depredation was predominantly incidental, with the likelihood of encountering a nest largely depending upon the diversity, abundance and distribution of small mammals.

7.1 Introduction

Successful reproduction and sufficient immigration are key to the persistence of metapopulations in fragmented landscapes (Robinson *et al.* 1995). Population declines of many forest birds living in fragmented and degraded habitats have been attributed to a reduction in reproductive success (Chalfoun *et al.* 2002). Nest predation is often cited as a cause of such reproductive failure in songbirds (e.g., Wilcove 1985; Martin and Roper 1988; Trine 1998), perhaps even more so in tropical than temperate areas, because levels of nest predation are generally higher in the tropics (Skutch 1949; Robinson et al. 2000b; Stutchbury and Morton 2001).

Rates of nest depredation are dependent on habitat-, prey- and predator- characteristics. First, the depredation levels can vary with placement and concealment of the nests (Yahner and Scott 1988; Latta et al. 1995; Schmidt and Whelan 1999) or between forest edge and interior (Small and Hunter 1988; Chamberlain et al. 1995). Second, certain aspects of the behaviour and evolutionary traits of birds are geared towards minimizing the predation risks, for example, parental defence (Cresswell 1997; Weidinger 2002), nest density (nest spacing) (Martin 1988; but see Salonen and Penttinen 1988) and clutch size (Skutch 1949; Martin et al. 2000). Third, the abundance and diversity of predators could affect rates of depredation (Chalfoun *et al.* 2002), for instance, because some predators actively hunt for nests using visual or olfactory cues while others incidentally stumble upon nests when foraging for other food items (Vickery et al. 1992; Yanes and Suarez 1996; Schmidt et al. 2001a). When data on natural nest predation are available, well designed experiments can help increase sample sizes and/or help tackle specific questions (e.g., Salonen and Penttinen 1988; Yahner 1996; Cresswell 1997). The validity of such data, however, hinges on how closely experimental set-ups resemble the natural systems they are intended to model (Storaas 1988). Careful modelling of the artificial experiments around natural systems, together with judicious interpretation of the findings, is therefore essential (Haskell 1995; Major and Kendal 1996; Wilson et al. 1998).

Between 2000 and 2002, we collected data on the nesting behaviour of the white-starred robin *Pogonocichla stellata* Vieillot a forest-dependent tropical passerine, in seven forest remnants of the Taita Hills "archipelago" in southeast Kenya. The potential nest predators include birds (silvery-cheeked hornbill *Bycanistes brevis* Rüppell), large mammals (Syke's monkeys *Cercopithecus mitis* Wolf and olive baboons *Papio anubis* F. Cuvier), small mammals (rodents, shrews and mustelids), and reptiles (snakes). Recent studies (Githiru 2000; Malonza 2001; Odhiambo 2001; Oguge 2001) have shown spatial heterogeneity in presence and abundance of these nest predators among the fragments under study. The most degraded forest patch (Chawia) contained the largest and most consistent population of *B. brevis* and *P. anubis* (absent or only transient in the other fragments); it also showed the highest number of rodents and shrews and the highest trapping success of *Praomys taitae* Heller. The largest and most pristine forest patch (Ngangao) showed the lowest incidence of predators, while the smallest and more disturbed fragments showed intermediate levels of predator incidence. Based on these findings, we predict nest depredation levels to be highest in Chawia (poor cover and most predators), lowest in Ngangao (good cover and fewest predators), with the small fragments falling in between (poor to intermediate cover, few to intermediate predators).

An artificial-nest experiment was then also conducted in these fragments to boost the sample sizes from natural nests, and facilitate studying the relationships between predation rates and fragment-, nest site- and microhabitat characteristics. The experiment simulated natural conditions in season, nest shape, site and placement. However, because plasticine eggs were used, it was not possible to simulate natural egg smell. Because fairly constant rates of nest depredation were expected over the incubation and fledgling periods (Johnson and Shaffer 1990), probabilities of nest failure and survival were estimated following the methodology outlined by Mayfield (1961). To summarise, by using both natural and artificial nests, this paper investigates whether rates of nest survival differed amongst i) different fragment-size categories, ii) various nest sites and iii) different microhabitat classes.

7.2 Study site and species

The Taita Hills forest fragments are listed as one of the key areas for biodiversity conservation in Kenya, based on both high endemism of flora and fauna and high threat levels (Bennun and Njoroge 1999). Widespread forest loss over the last four decades has seen the forest being reduced to a series of 12 remnant patches scattered across hilltops and ridges (Beentje and Ndiang'ui 1988; Brooks et al. 1998a). Data for this study were collected in seven fragments: Ngangao (NG, *c*135 ha, 'large-sized'); Chawia (CH, *c*95 ha; 'medium-sized'); and Fururu (*c*8 ha), Ndiwenyi (*c*4 ha), Macha (*c*2 ha), Mwachora (*c*2 ha) and Yale (*c*2 ha) (collectively referred to as 'small-sized', SF) (see Galbusera et al. 2000a for map). Based on structural qualities of the vegetation (Wilder *et al.* 2000), and on plant species richness and diversity (Githiru 2000), fragment quality was highest in NG, intermediate in SF, and lowest in CH. Five 3-ha plots were randomly selected for study in each of the larger plots (NG and CH), while the smaller ones were treated as a single plot each. All 15 study plots were searched for natural nests. Artificial nest experiments were conducted in all five plots within each of the larger fragments, while, for logistic ease, Fururu and Ndiwenyi were used as representatives of the small fragments.

P. stellata is a forest-dependent resident bird in montane forests of eastern to southern Africa (Keith et al. 1992; Bennun et al. 1996); sub-species *helleri* is confined to the Taita Hills and Mt. Kasigau (Zimmerman *et al.* 1996). It builds a domed nest with a side entrance, often well concealed and mostly placed on a sloping ground at the base of a small tree or mossy rock, or occasionally slightly above the ground on fallen tree trunks, top or side of boulder or on herbaceous undergrowth (Oatley 1982c; Keith et al. 1992). The female alone builds the nest and incubates. Eggs are laid on consecutive days; incubation starts immediately after clutch completion and lasts for 16-18 days (16.5 days average) (Keith *et al.* 1992). Nestling period lasts for 14-16 days (14.3 average), and parental care for 40-42 days after fledging (Oatley 1982c; Keith et al. 1992).

7.3 Methods

7.3.1.Background data: natural nests

Nest searches were conducted during the breeding season (September to March) of 2000-2001 and 2001-2002. Each fragment-size category was allocated two separate 2-week search sessions, one between October and December, and another between January and March. For each successfully-hatched nest, nestling-stage period was between day of first egg-hatching until young fledged or predated upon, or until the end of the study (e.g., Cresswell 1997). All nests discovered during the egg stage were checked every day. After the eggs hatched or where nests were found during the nestling stage, at least 2-hour daily observations were conducted at each nest.

When estimating the probability of nest survival, we accounted for varying exposure periods by counting ‘nest-days’ (sensu Mayfield 1961), which controls for the fact that nests found at a later stage are more likely to be successful because they survived part of the required time. This method uses only information from the period during which nest are actually under observation, and thus places all nests on a comparable basis (Johnson 1979; Aebischer 1999). For the nests whose fate was unascertained by the end of the study, the last observed active date was used to calculate number of days of exposure, and was thus assumed successful for that duration (see Manolis *et al.* 2000). Daily nest mortality rate, *m*, was obtained by dividing the number of nests that were destroyed by the total number of days they were exposed for in total (i.e., nest-days). Thus, the probability of survival, *s*, for one day was (1-*m*), while the respective probabilities of surviving the 16-day incubation and 14-day fledgling periods were $(1\text{-}m)^{16}$ and $(1\text{-}m)^{14}$ (Mayfield 1961). Overall nest survival (from the start of incubation to fledging) was estimated as the product of the two probabilities (Mayfield 1961). Standard errors for the survival estimates were calculated according to Johnson (1979).

7.3.2 The experiment: artificial nests

During the breeding season of 2002 (January to March), we randomly placed 80 artificial nests (either natural white-starred robin nests or reshaped nests of other species) in four microhabitats known to be used by the robins: (i) gentle slopes with fern tussocks, (ii) sawpits, (iii) base of logs, and (iv) base of boulders (see Appendix). Six nests were placed within each plot of the larger fragments, while in the two smaller fragments, six were set in Ndiwenyi and 14 Fururu. A minimum of 50 meters was allowed between a nest and its nearest neighbour, which approximated the radius of an average robin territory: 0.75 ha (Oatley 1982a; Githiru 2003). Mean distance between nests was 81 ± 24 m in Ngangao, 76 ± 26 m in Chawia, and 62 ± 19 m in the small fragments. Two plasticine eggs were placed in each nest. Identity of the potential predators was inferred from the imprints left on the plasticine eggs (Nour et al. 1993 for comparable methodology; see Haskell 1995), together with level of disturbance on and around the nest. Deep and shallow small mammal-like marks on the eggs were assigned to shrews and rodents, respectively. They both often left fur on the eggs, occasionally removed eggs from the nest, but very rarely destroyed the nest with only some minimal disturbance around the mouth when it occurred. Missing eggs with nest disturbance was attributed to birds, while without nest disturbance to snakes or mustelids (e.g., Pärt and Wretenberg 2002). Lastly, complete destruction of nest plus mutilation of eggs was attributed to monkeys or baboons. During nest placement and monitoring, rubber boots and fresh rubber gloves were used to minimize human scent (Small and Hunter 1988).

Assuming the day of nest (and egg) placement was Day 0, the nests were monitored on five occasions at 3-day intervals over the next 15 days, akin to the normal incubation period for this species (Oatley 1982c; Keith et al. 1992). When a nest was disturbed, the number of nest-days (sensu Mayfield 1961) was calculated by summing the complete 3-day intervals it was intact for, then adding 1.5 days [midpoint of the exposure interval within which it was disturbed (see Mayfield 1961; Manolis et al. 2000)]. The daily mortality rate, m, of the nests was calculated as for the natural nests; thus, the probability of surviving the 15-day incubation period was $(1-m)^{15}$. Standard errors and confidence limits for the survival estimates were calculated according to Johnson (1979). The degree of concealment of a nest (microhabitat effect) was assessed by the presence of climbers/vines, ferns, logs, boulders and/or sawpits within a 5-m radius with the nest as the center (scores ranged from 1-5; for instance, if all five were present at a specific nest, it got a score of 5).

7.4 Results

A total of 12 natural nests were located and monitored – nine at the egg-stage and three at nestling-stage (Table 1). All nests were on the ground, either at the base of a log or boulder (2), along a gentle slope usually at the base of a fern tussock (6) or inside abandoned sawpits (4). Except for one nest in Ngangao with a single egg, all nests had a clutch of two. Two nests were lost in 59 egg-stage nest-days and two in 41 nestling-stage nest-days, resulting in daily estimated mortality rates of 0.034 and 0.049, respectively. Thus, the respective daily survival probabilities (± SE) were 0.966 ± 0.0236 and 0.951 ± 0.0336. The probability of a nest surviving through the entire incubation and nestling periods was 0.58 and 0.50 respectively, while the probability of surviving both stages was 0.29.

Table 7.1. Fates of the 12 natural nests of *Pogonocichla stellata* in the Taita Hills at the incubation (egg) or nestling (chick) stage and the respective exposure periods for each

Nest	Fragment category	Egg-stage		Nestling-stage	
		Fate	No. of days	Fate	No. of days
1	Small	Successful	3	Predated	7
2	Large	Predated	10		
3	Large	Successful	14	Predated	4
4	Large	Successful	14	Uncertain	4
5	Large	Successful	8	Uncertain	4
6	Large			Successful	1
7	Small			Successful	2
8	Medium	Uncertain	5		
9	Large	Successful	2	Uncertain	3
10	Large	Deserted$^{\alpha}$	2		
11	Large			Uncertain	2
12	Medium	Successful	1	Successful	14

$^{\alpha}$ this was a nest found with a single egg; a pair of adults was seen around it for two days before deserting it.

Based on the experimental nest data (see Appendix), a binary logistic regression model (SPSS 2001) was used to assess the best predictors of nest failure amongst the three main independent effects – Fragment size, Nest site and Microhabitat – and interactions between them. Probability of nest survival varied among the fragment-sizes ($\chi^2_2 = 8.0$, $P = 0.018$) but not between nest-sites or microhabitats ($P = 0.87$ and 0.82, respectively); all interactions were not significant (P-values between 0.10 and 0.23). Frequency of nest disturbance differed among the three fragment-size categories (Cochran Q test: $Q_2 = 7.9$, $P = 0.019$), with significantly higher frequencies in Chawia (83 % of nests disturbed) compared to Ngangao (53 % disturbed) and small fragments (50 %) (Exact tests: $P =$ 0.0002 and 0.0003, respectively). Ngangao and the small fragments were not significantly different ($P = 0.67$). The probability of nest survival for artificial nests over the egg-stage for each fragment-size category is shown in Table 7.2.

Table 7.2. Probability of daily survival (and SE) of the artificial nests, and survival over the entire egg-stage (and CI) for the three fragment-size categories

Fragment size	Failed nests (of total)	Nest-days	Daily survival rate (s)	SE of s	Overall survival rate	Confidence interval
Ngangao	16(30)	306	0.948	0.0127	0.426	0.650-0.275
Chawia	25(30)	211.5	0.880	0.0222	0.129	0.284-0.056
Small fragments	10(20)	204	0.951	0.0151	0.448	0.739-0.267

Following the predator assignment protocols outlined earlier, all depredation of nests was attributed to small mammals – shrews and rodents, except for 2 nests in Chawia destroyed by monkeys or baboons, and a single one in Ngangao likely to be a snake or mustelid (see Appendix).

7.5 Discussion

Overall, 29 % of all natural nests initiated fledged young, i.e. survived both the egg- and nestling- stages. This estimate is similar to the mean success rate reported for open-cup-nesting forest birds in Panama (Robinson et al. 2000b), despite the fact that white-starred robins have closed nests with a side entrance, so are perhaps better concealed (Oatley 1982c). Similar open cup nesters in the temperate regions averaged a 53 % success rate (Stutchbury and Morton 2001), suggesting that nest success rates are, indeed, lower in the tropical than temperate areas (Stutchbury and Morton 2001 and references therein). Higher nest success rates reported for the South African race of the white-starred robin (Oatley 1982c) are likely to be overestimated, due to the fact that the number of successful nests was simply divided by the total number under observation. Nests found at later stages are, however, more likely to be successful as they already survived part of the required duration (Mayfield 1961; Johnson 1979; Aebischer 1999). Further, similar to several previous studies (e.g., Gottfried and Thompson 1978; Cresswell 1997; Wilson et al. 1998; Valkama et al. 1999), the estimated survival rates during egg-stage were lower for artificial nests (36 %) compared to natural ones (58 %). Artificial nests simulated natural ones in timing, nest density and nest-sites but not in smell and parental effects. Thus, the depredation levels of the experimental nests were satisfactory only as relative estimates comparable across the different fragment-size categories, but not as absolute estimates of nest failure for natural nests (e.g., Wilson *et al.* 1998).

Based on results from the artificial nest experiment, nest-site or microhabitat (concealment index) did not significantly affect the probability of nest survival. Several other studies found nest concealment and nest site selection to be of little importance to predation levels (Vickery et al. 1992; D'Eon 1997; Söderström et al. 1998; Robinson et al. 2000a). Predator effects overriding those related to habitat and nest-site characteristics suggest incidental predation. Because the major predators were ground-foraging mammals, most nests were probably located incidentally, or perhaps by olfactory cues but not by visual ones (e.g., Rangen *et al.* 2000). It is likely that predation attempts were partly thwarted by parental attentiveness and defence (e.g., Schmidt et al. 2001b; Weidinger 2002), hence the lower predation on natural nests found above. The unpredictable nature of incidental depredation constrains the development of effective anti-predator mechanisms, thereby rendering nest-site selection and concealment less important (Vickery *et al.* 1992).

Nest predation rate in the most-disturbed fragment (Chawia) was three times higher than the predation rates in Ngangao and the small fragments. Based on vegetation characteristics (Wilder *et al.* 2000), Chawia could be expected to offer the worst in terms of concealment opportunities because it was undergoing the highest level of human-induced habitat deterioration. However, this explanation is not exhaustive by itself as nest site characteristics and habitat immediately around the nest did not significantly affect nest survival rates, and predation levels in the small fragments were as low as in Ngangao despite higher disturbance. Alternatively, higher predation incidences in Chawia could be attributed to the higher diversity and abundance of potential nest predators (particularly small mammals and baboons) invading from the adjacent grassland habitats (Odhiambo 2001). Likewise, an increase in avian predators associated with habitat fragmentation has been found to increase predation on small passerine nests (Fulton and Ford 2001). A phenomenon akin to 'mesopredator release' (sensu Soule *et al.* 1988) may have additionally increased predation levels in Chawia relative to the small fragments. Mesopredator release occurs when top predators disappear from an area, thereby causing an increase in the number and activity of smaller predators (e.g., Terborgh 1988). Predation on small mammals by owls (e.g. *Strix woodfordii* Smith, A.) could have kept the number and activity of these predators down in the small fragments where the owls were most predominant (M. Githiru, unpubl. data).

Overall, this study suggests that nest depredation was primarily incidental in these forests, where the likelihood of encountering a nest was largely dependent upon the diversity, abundance and distribution of potential predators – predominantly the small mammals. Both immediate cover around a nest and site of nest placement had little effect on the probability that the nest would be disturbed. Thus, predator proliferation produced elevated nest predation rates in the most disturbed forest patch.

Appendix. Pattern of disturbance of artificial nests over the 15-day study period, indicating 'Status' of each nest ('0' = intact and '1' = disturbed), number of 'Nest-days' (duration till disturbance) and the 'Potential predator'

Ngangao				Chawia				Small Fragments			
Site	Status	Nest-days	Predator	Site	Status	Nest-days	Predator	Site	Status	Nest-days	Predator
Ground	0	15		Ground	1	4.5	Shrew	Ground	1	4.5	Rodent
Ground	1	1.5	Shrew	Saw-pit	1	7.5	Rodent	Saw-pit	1	1.5	Shrew
Ground	0	15		Ground	0	15		Ground	0	15	
Log	0	15		Ground	1	4.5	Monkey	Ground	1	7.5	Rodent
Saw-pit	1	1.5	Rodent	Ground	0	15		Ground	0	15	
Ground	1	1.5	Rodent	Saw-pit	1	4.5	Rodent	Ground	0	15	
Boulder	1	1.5	Rodent	Ground	0	15		Boulder	1	7.5	Shrew
Ground	1	13.5	Shrew	Ground	1	1.5	Monkey	Log	1	4.5	Rodent
Saw-pit	0	15		Saw-pit	1	10.5	Rodent	Boulder	1	1.5	Shrew
Saw-pit	1	4.5	Rodent	Log	1	13.5	Shrew	Log	1	10.5	Rodent
Saw-pit	0	15		Saw-pit	1	1.5	Shrew	Boulder	0	15	
Boulder	1	10.5	Rodent	Saw-pit	0	15		Saw-pit	0	15	
Log	1	1.5	Rodent	Ground	1	1.5	Shrew	Ground	0	15	
Saw-pit	1	7.5	Rodent	Saw-pit	1	1.5	Rodent	Boulder	0	15	
Saw-pit	1	1.5	Shrew	Ground	1	1.5	Rodent	Ground	1	4.5	Rodent
Saw-pit	0	15		Saw-pit	1	10.5	Shrew	Ground	1	10.5	Rodent
Saw-pit	1	13.5	Shrew	Ground	0	15		Ground	1	1.5	Rodent
Saw-pit	0	15		Ground	1	1.5	Shrew	Ground	0	15	
Saw-pit	1	1.5	Shrew	Ground	1	13.5	Rodent	Boulder	0	15	
Saw-pit	0	15		Saw-pit	1	1.5	Rodent	Log	0	15	
Boulder	0	15		Ground	1	13.5	Shrew				
Saw-pit	0	15		Ground	1	4.5	Shrew				
Saw-pit	1	10.5	Shrew	Boulder	1	10.5	Rodent				
Ground	1	10.5	Snake/Mustelid	Ground	1	10.5	Rodent				
Saw-pit	0	15		Ground	1	4.5	Shrew				
Saw-pit	0	15		Ground	1	1.5	Rodent				
Ground	0	15		Saw-pit	1	1.5	Shrew				
Boulder	1	4.5	Rodent	Ground	1	1.5	Rodent				
Ground	0	15		Log	1	7.5	Shrew				
Saw-pit	1	10.5	Rodent	Ground	1	1.5	Shrew				
Total	**16**	**306**			**25**	**211.5**			**10**	**204**	

Paper VII

Manuscript

Metapopulation or Source-Sink system: Does it matter? A case study, SE Kenya

Mwangi Githiru

CHAPTER 8

Local forest conservation youth group learning more about their birds and research in general

More hands-on experience for the local forest group; this time: radio-tracking

"In the end we will conserve only what we love; we will love only what we understand; and we will understand only what we have been taught."

Baba Dioum

Chapter 8: General discussion

Summary

This study set out to investigate some demographic and genetic aspects of a metapopulation of the white-starred robin *Pogonocichla stellata* living in forest fragments of different sizes and disturbance levels in the Taita Hills forest 'archipelago'. The robin was used as a model or ecological indicator species (sensu Landres et al. 1988; Morrison et al. 1998), to provide insights into the general status of birds living in this landscape. These data were deemed pertinent for understanding the mechanisms that underlie the negative effects of habitat loss and fragmentation on small populations, such as those seen in the endangered Taita thrush *Turdus helleri*. The discussion starts with a synthesized summary of the key findings from the study, followed by a theoretical description of the current and expected status and distribution of the robin. There then follows an assessment of the applicability of the indicator species approach, both in terms of the scale at which conservation activities need to be focussed, and the possibilities of extrapolating results from one species to broader avifaunas (specifically, how these robin data compare to those of *T. helleri*). A separate aspect of this study on interaction with the local community is then briefly looked at. Finally, a range of management requirements and potential strategies for conserving this landscape, together with some potential avenues for future work in the Taita Hills, both from a research and conservation point of view, are proposed.

8.1 Synthesis of the key findings

Overall, the findings from the six core result chapters can be integrated into two key themes, based on (i) metapopulation theory and (ii) social structure.

8.1.1 Metapopulation structure: sources and sinks

Source-sink dynamics are a direct consequence of differences in habitat quality, where local births exceed deaths in better habitats, with the surplus dispersing to poorer habitats – the latter thus becoming net importers of individuals (Pulliam 1988; Dias 1996). Demographic data from this study point to higher levels of productivity for the subpopulations in large- (Ngangao, NG) and small-sized fragments (Fururu, Ndiwenyi, Macha, Mwachora and Yale combined, SF) than in the medium-sized one (Chawia, CH). This is deduced from the higher juvenile to adult ratios (an index of reproductive success) in NG and SF (Chapter 2), together with higher nest predation rates in CH (Chapter 7). The high levels of turnover of females in CH and SF are indicative of substantially more adult females disappearing due to death or dispersal compared to NG. With the high reproductive success in SF, such individuals were probably replaced by locally recruiting birds. Conversely, the very low reproductive success in CH points towards most replacement being from immigrants. This claim is backed up by the large mean number of alleles and high heterozygosity level in CH (Chapter 6), indicative of an assortment of individuals from populations with different alleles and/or allele frequencies. In addition, two other findings demonstrate that there was considerable dispersal between these subpopulations, necessary to maintain such a source-sink scenario. First, the speed and success at which translocated adults found their way back to CH from Fururu (Chapter 5) shows that interfragment dispersal was possible. Second, direct capture-recapture data confirmed relatively ample exchange of individuals between these fragments, both for the robin (Chapter 6) and for bird species in these forests in general (Appendix). Overall, thus, the NG population seemed a potential source population at very low risk of extinction, while the CH population seemed highly dependant on migrants either to sustain it or at least maintain it at the current carrying capacity; because there was some evidence of breeding activity, the latter was possibly the case, thus making it a pseudo-sink (Harrison 1991; Hanski 1999; Sutherland et al. 2002). The SF were peculiar in that, though they had relatively high reproductive success (thus were potential sources of emigrants), they had much higher turnover rates than NG, and so cannot be considered as stable as NG. Further, their small size consigns them to high levels of stochastic risk (Caughley 1994). Even so, direct capture-recapture data (Lens et al. 1999a, Appendix), together with the typically high levels of heterozygosity and large mean number of alleles in the SF-subpopulations (Chapter 6), suggests that some of them – such as Fururu-Ndiwenyi-Macha-Mwachora – partly functioned as fine-grained systems (e.g., Rolstad 1991; Harrison 1994; Wiens 1996), connected by (and perhaps dependent on) high levels of inter-fragment dispersal. Indeed, anecdotal field observations revealed individuals moving back and forth between these patches in the space of a few days. This could have enabled them avert the problems caused by habitat loss and fragmentation (see Quinn and Hastings 1987; Burkey 1988). Lastly, on the degree of area-sensitivity of the robin, there was no evidence yet of any absolute threshold in fragment size below which subpopulations were not viable anymore (even with the tiny fragments). Even if such a threshold exists, other factors unrelated to fragment size, such as increased nest predation rates, seemingly play a more important role, impinging on productivity and survival before the effects of area per se, became significant (see also Zanette 2000).

8.1.2 Social systems

Different subpopulations of the robin had different social structures (Chapter 5). On the one hand, direct density-dependent territorial behaviour seemed to limit the densities of breeders in the high quality and high population density fragment, NG. This created a non-breeding adult component, with some individuals opting to remain within the territories and 'float' awaiting a vacancy; others probably dispersed and sought immediate breeding elsewhere (e.g., see Smith 1978; Zack and Stutchbury 1992). It is still not clear what factors related to the individual, the population's attributes or the habitat influenced this choice. On the other hand, Allee effects [inversely density-dependent effects (Allee et al. 1949; Stephens and Sutherland 1999)] were likely to be the principal factors limiting the population in CH. In this fragment, lower female survival, possibly related directly to habitat degradation and/or to predation or competition from matrix species with increasing disturbance, resulted in male-biased skew in sex ratios (Chapter 2). Combined with low population density, this caused a scarcity of females as demonstrated by the presence of unmated territorial males (Chapter 5). This is a real cause of concern because it could have a dramatic negative effect on the effective population sizes (Hartl and Clark 1997). Though no removal experiments were carried out in SF, their small sizes and relatively high population densities (Chapter 2) suggest that they were limited more by direct density-dependent behaviour than inverse density-dependence.

8.2 Responses to continued forest destruction

At present, the white-starred robin metapopulation in the Taita Hills does not appear to be very adversely affected by the degree of fragmentation. Together with previous findings (Lens and Van Dongen 1999), these results indicate that this species is relatively tolerant to forest disturbance and fragmentation, thereby rendering its current persistence in this landscape [i.e., both the wide-ranging patch occupancy reported by Lens et al. (2002b), and stable overall metapopulation size ($\lambda = 0.996$) seen in Chapter 2] unsurprising. Food and nest-site availability, two key requirements, apparently were not limiting even for subpopulations living in disturbed environments. This is deduced from the robin's diverse feeding and nesting tendencies. First, despite ant-trailing being clearly predominant, it also forages from various other sources including gleaning for insects from foliage at all forest levels and feeding on the forest floor. Besides, although it is primarily forest-dependent (Bennun et al. 1996), it occasionally forages at forest edge and in thickets outside the forest, both for insects and fruits such as those of *Lantana* sp. and *Maesa lanceolata*. It also shows considerable diversity in nesting sites, successfully nesting on gently sloping ground, in abandoned sawpits and at the bases of stumps and boulders. As mentioned previously, other findings provide direct and indirect evidence that the robin traverses the landscape matrix fairly regularly and rapidly. Moreover, evidence from breeding activity and the presence of juveniles suggest that it breeds in most patches in which it occurs. Hence, at present, both its adaptability and ability to disperse between patches offsets any potential within- and between-habitat problems associated with forest loss and fragmentation. Three features of habitat loss necessitate some caveats to this 'no-effect' argument: non-linearity, time lags and equilibrium patch occupancy (Wiens 1996; Hanski 1998; Newton 1998). First, effects of fragmentation may be strongly non-linear such that after some threshold, further habitat loss may have more dramatic effects than would be predicted from initial trends. Second, time lags may occur between habitat loss and manifestation of the effects on populations. Lastly, though this was not a 'classic' metapopulation (sensu Levins 1970; Hanski 1991), it requires a minimal patch occupancy at equilibrium to maintain overall population size and dispersal between populations. Thus, the least we can do is maintain the status quo if the metapopulation is at equilibrium patch occupancy and/or is close to the threshold; in case of it being an 'extinction debt' due to a time lag, we have to do more as active management is required to ameliorate the long-term negative effects on the entire population.

Assuming that fragmentation and degradation of habitat patches proceeds as it has been for the last few years, CH will suffer the most severe destruction, followed by SF, the least degradation being in NG. First, the SF shall have lower reproductive rates due to an increase in the diversity and abundance of predators from the matrix, which will lead to a decline in potential emigrants. Stochastic processes might also gain more prominence because of the reduction in the amount of overall habitat and decreased dispersal between patches (Caughley 1994). Since dispersal was found to be an important feature determining persistence of this metapopulation, this could engender the first threshold described by Newton (1998), where the equilibrium is maintained at only partial occupancy of the suitable fragments i.e., the metapopulation will persist occupying only a proportion of the suitable patches across the landscape. Further, a disruption of the high levels of exchange of individuals between the cluster of small fragments – Fururu, Ndiwenyi, Macha and Mwachora [see Appendix] – might jeopardize some of these subpopulations. While this seems ominous only for potential sink (or pseudo-sink) populations, it is noteworthy that they are also important in ensuring that some of the emigrants survive and occasionally reproduce, thereby playing an influential role in reducing the probability of regional extinction by boosting the overall population size and maintaining the gene pool (Newton 1998; Hanski 1999). The interplay between impaired reproduction and diminished dispersal greatly affects the persistence of metapopulations (Urban and Shugart 1986). Indeed, a recent study demonstrated that species mobility/dispersal (an among-patch process) and tolerance to habitat deterioration (a within-patch process) were the key factors influencing persistence of eight bird species in this landscape (Lens et al. 2002b). Eventually, as more forest habitat is lost or degraded, and dispersal through the matrix becomes more difficult, spatial cohesion of the network will pass the second and final threshold, where high levels of both deterministic and stochastic risk will make the long-term persistence of the metapopulation untenable (Opdam and Wiens 2002). Patches will become too small to support local populations individually due to low reproduction and survival, and too isolated to facilitate dispersal owing to larger distances and hostile land-uses. At this point, a synergistic effect, resulting from the combination of reduced population sizes, loss of genetic variation and increase in recessive genes from increased inbreeding might ensue (e.g., Daniels et al. 2000; Oostermeijer 2000). This could accelerate the extinction process by impinging on the NG population too. As a caveat, it is essential to recognize that a combination of the highly dynamic nature of most ecosystems, the human element and stochasticity, leaves most predictions tentative (Opdam and Wiens 2002). These scenarios are summarized in Figure 8.1.

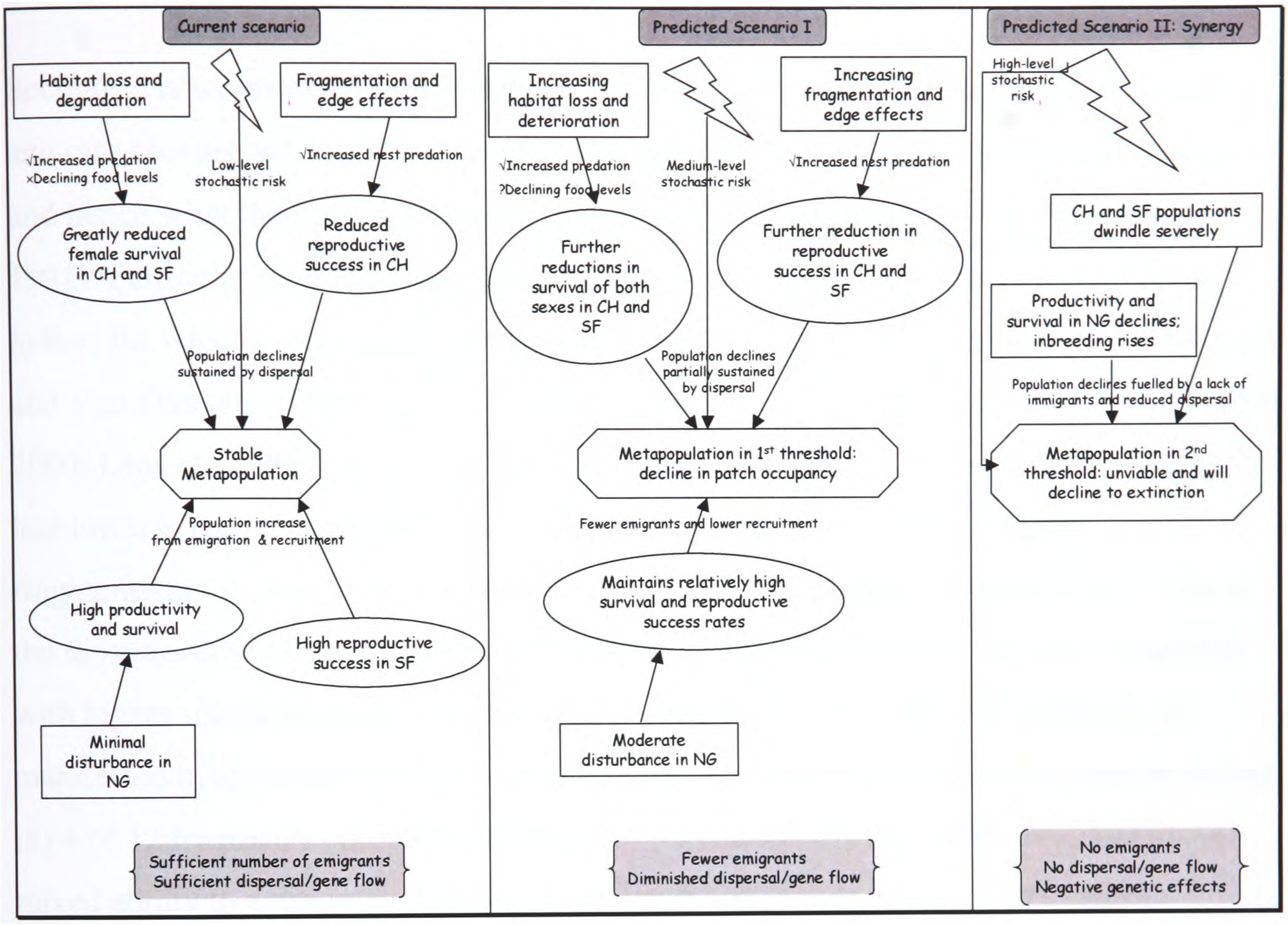


Figure 8.1 A diagrammatic representation of the concept model for *P. stellata* showing both the present and future status with increasing habitat destruction; NG = Ngangao, CH = Chawia and SF = the five small fragments together ['√' = confirmed effect, 'x' = no effect, and '?' = potential/inferred effect].

8.3 Usefulness of the ecological indicator species approach

The applicability of this method is twofold. First, it provides a good sense of the most appropriate scale of conservation for this landscape. It is obvious that given the metapopulation (together with potential source-sink) scenario found, conservation activities must focus on both within- and among-population processes (e.g., Thrall et al. 2000; Lens et al. 2002b). Besides, the effects of surrounding landscape matrix on processes within patches shown (for instance, in increasing the density and diversity of nest predators in CH), clearly advocate for a landscape solution (e.g., Forman and Collinge 1996; Opdam and Wiens 2002). Overall, thus, an exchange of information between the within-patch (small) and between-patch (broad) scales is vital for any conservation measures to be successful (Lima and Zollner 1996; Desrochers et al. 1999; Wu and Qi 2002).

Second, it is worth examining whether by comparing life history strategies of common and rare species, we can gain insights into root causes of problems for the rare species, and hence what the most appropriate conservation measures would be (Perrins et al. 1991). Particular reference here will be given to the endangered Taita thrush *Turdus helleri* for which comparable data are available (Lens et al. 1998; Lens et al. 1999a; Lens and Van Dongen 1999; Lens et al. 1999b; Galbusera et al. 2000a; Lens and Van Dongen 2000; Lens et al. 2000; Lens et al. 2002a). Simple comparisons revealed that the thrush had lower effective population sizes, was more sensitive to habitat loss and fragmentation (assessed by fluctuating asymmetry), had more male biased sex ratios in the most disturbed forests, had a lower dispersal capacity and lower genetic variability with higher inbreeding and evidence of a genetic bottleneck. These differences are manifested in lower persistence of the thrush in this landscape, occupying (and breeding in) 4 of 12 fragments compared to the robin's 11 of 12. Overall, these findings show a mixed ability to extrapolate findings from the robin's work directly to the thrush. Differences in responses of the two species highlight the problems of directly applying data from common species for formulating conservation action of rare ones (Wiens 1996). This emphasizes the assertion that unless the actual mechanisms by which disturbance affect species are clear, any general models are unlikely to be useful for across species application (Newton 1998). Still, when underlying mechanisms are known, they can facilitate making logical and pragmatic statements – informed guesses – about problems likely to be facing species under threat but not directly studied. This is clearly vital if the species in question has been extirpated from the landscape and efforts are being made to establish the likely factors liable for its extirpation. The following two examples from this study endeavour to illustrate the potential application of the knowledge of actual mechanisms. First, the inverse density-dependent effects proposed for sparse robin populations suggests that for many thrush subpopulations, because of their lower population densities and the extremely skewed sex ratios in the most disturbed fragments, the negative effects of skewed sex ratios (Allee effects) would have happened earlier and more severely than for the robin. This could have dramatically reduced effective population sizes (Gilpin 1991; Hartl and Clark 1997), thus engendering the genetic bottleneck found in CH (Galbusera et al. 2000a). Secondly, since lower reproductive success (e.g., due to increased nest predation) caused a reduction of numbers of potential emigrants and relegation of habitats to likely sink or pseudo-sink status for the robin, a similar mechanism could have caused population declines in the thrush. The few thrush nests that were located were more than three metres from the ground and in habitats with fairly similar vegetation characteristics. This suggests that the thrush was not as eclectic as the robin in terms of selecting nest sites. Therefore, in addition to higher nest predation, they may have been limited by a scarcity of nest sites in disturbed habitats too. It is worth noting that the applicability of such comparisons explaining patch occupancy between species can be confounded by other factors, for instance species being absent in areas where conditions are favourable (e.g., due to previous stochastic events), or present in habitats that are essentially unfavourable (e.g., as sink populations and/or because of time lags) (Hanski 1998; Newton 1998). Only more long-term detailed studies can elucidate such aspects.

8.4 Other aspects of the study

During the course of the study, I took some time to engage in formal and informal conversations with the local elders and students in various primary and secondary schools in the area. These were broad and simple discussions about forests and the fundamental importance of conserving them, for both biodiversity and human sustenance. In addition, better and more prudent use of forest products (mainly firewood) was discussed. Despite the simplicity of these discourses, given the enthusiasm they elicited, it was obvious how some effort into this angle of conservation biology is essential for the survival of these fragments. In particular, future projects need to embrace the local community as much as possible through various activities such as formal and informal dialogue, employment, education and training and/or ploughing money back into the local economy by purchasing local produce. This will help to avoid being treated with contempt, foster the local communities' appreciation of the resource, and perhaps most importantly, emphasize the threats facing the forests and biodiversity and the consequences of losing them, about which they are often oblivious (see e.g., Balmford et al. 2002). It is crucial that future projects integrate this socio-economic or educational dimension in their planning if there is to be hope for conserving these patches and their biodiversity! The contribution of small research projects to this end is vital because huge mainly socio-economical or education-based projects are uncommon in this area. Unfortunately, this is most likely to be the case for most other fragmented tropical landscapes as well.

8.5 Recommendations for the conservation of these habitats

The main conservation-related conclusion from the findings of this study is that the Taita Hills forest fragments are habitats at an ominous juncture. On the one hand, there is good evidence that the birds (and possibly other faunas too) living there are facing problems, some critical, associated with habitat degradation and fragmentation. On the other hand, it is evident that all is not lost (yet); small as some of the patches may be, they still retain many species and are important for conservation, especially in their entirety. From this, two wide-ranging perspectives for remedial action can thus be proposed: patch- and landscape-level action.

- Patch-level action aimed at reducing habitat loss and degradation: habitat destruction involves both reduction in size and the insidious process of degradation that ensues in the remnant habitats (Temple and Wilcox 1986). Both habitat loss and degradation evidently play a role in determining overall species persistence in these fragments (Lens et al. 2002b, this study). As indicated by Hanski (1998), metapopulation dynamics notwithstanding, the primary aim in conservation should always be to preserve as much habitat as possible. Realistically, in the Taita Hills, this can only be accomplished at present by regulating the harvesting of forest products – mainly firewood, and by halting agricultural-based encroachment into indigenous forests. As mentioned in the introduction, the current Forest Reserve status of these patches permits considerable resource exploitation and manipulation and has little investment in protection (Lovett and Wasser 1993). On the ground, this translates to underpaid forest guards, not very motivated to fight for the conservation goal. Clearly, it is crucial to have proper legislation conferring these patches the legal protection status they deserve, in addition to having well trained and motivated forest guards. Nevertheless, good education and awareness programs must accompany this endeavour so as not to generate negative attitudes within the local communities.

- Landscape-level action aimed at reducing fragmentation and enhancing connectivity: the key role of dispersal in species persistence (Lens et al. 2002b, this study) emphasizes the importance of reducing the physical distance that birds have to cross between remnant patches. Together with reducing the distances between patches, having stepping-stones between them could further facilitate movement. Thus, accompanying the within-patch recommendations, there should be greater emphasis on encouraging activities outside the forest fragments that enhance movement between patches. For instance, not cutting down all trees (there are still substantial numbers of indigenous trees and thickets scattered throughout this landscape) and/or growing more indigenous trees. In addition, agro-forestry could go a long way in ensuring landscape permeability is maintained, while simultaneously reducing the dependency on forest products by the local populations, e.g., by providing them with alternative sources of firewood and fodder for their livestock. Provision of essential agro-forestry and indigenous saplings in tree nurseries is needed. Such 'forest-friendly' approaches would also reduce the direct impacts of the surrounding matrix on the habitats i.e., edge effects demonstrated in this study. As noted by Opdam and Wiens (2002) 'The major conservation issue, in fact, is land use... solutions to the threat of habitat fragmentation may be ineffective unless they are placed within a broader framework of changing land use and its impacts on entire landscapes'.

8.6 Potential topics for future work in the Taita Hills fragments

There are still several pending issues pertaining the Taita Hills forest fragments, both from a research (science) and a conservation (applied) point of view. Following on from this study, four key broad areas of research are proposed. However, even more pressing are the conservation-related pending issues; four of these are offered.

8.6.1 Research

- Dispersal: to obtain a better grasp of how within-population processes affect and are affected by among-population processes, we need a better grasp of the factors influencing movements within and between patches. Radio-tracking together with continued colour ringing, particularly of nestlings will greatly boost our presently patchy knowledge of this very difficult area of study. An understanding of the patterns of juvenile and adult dispersal, and the facultative nature of either (in terms of differences in sex ratios and the timing of movements), is needed.
- Breeding behaviour and social structure: observation of natural breeding behaviour remains one of the most challenging research subjects in the Taita Hills. (Though an attempt was made to collect these data in this study, data obtained were not sufficient for any detailed analysis to obtain a good grasp of the system.) Breeding success (hatching, fledging [sex-ratios at these stages], post-fledging [i.e. per capita reproductive success]), rates of predation on natural nests (at both egg and chick stages) and investigating the presence/absence of extra-pair fertilization (EPF), will help elucidate individual-level behaviour and choices. This is especially important bearing in mind the potential variation in social structures found between fragments; for instance, do more floaters result in more EPFs? Further, accompanying breeding studies should be a more detailed removal experiment as a follow-up to the pilot one conducted in this study. It should aim at (i) increasing the number of individuals and fragments studied in addition to removing females, (ii) lengthening the period of the study in order to obtain a better handle of the system pre-removal and to enable the fates of replacement pairs to be monitored until the following breeding season, (iii) having proper controls and (iv) evaluating individual bird quality and assessing how this affects patterns of territory acquisition, dispersal decisions and prevalence of EPFs.
- Phenotypic development: the chief focus here would be the primary function of the immature plumage, and consequently what governs the switch to adult

plumage remains. Moreau (1951) reported that some races of *P. stellata* moved directly from the juvenile to adult plumages, while others had much longer immature periods than others. It would be interesting to find out if such patterns could occur within a single race, for subpopulations in different fragments and with different social structures. This would demonstrate an interesting facultative nature of this process.

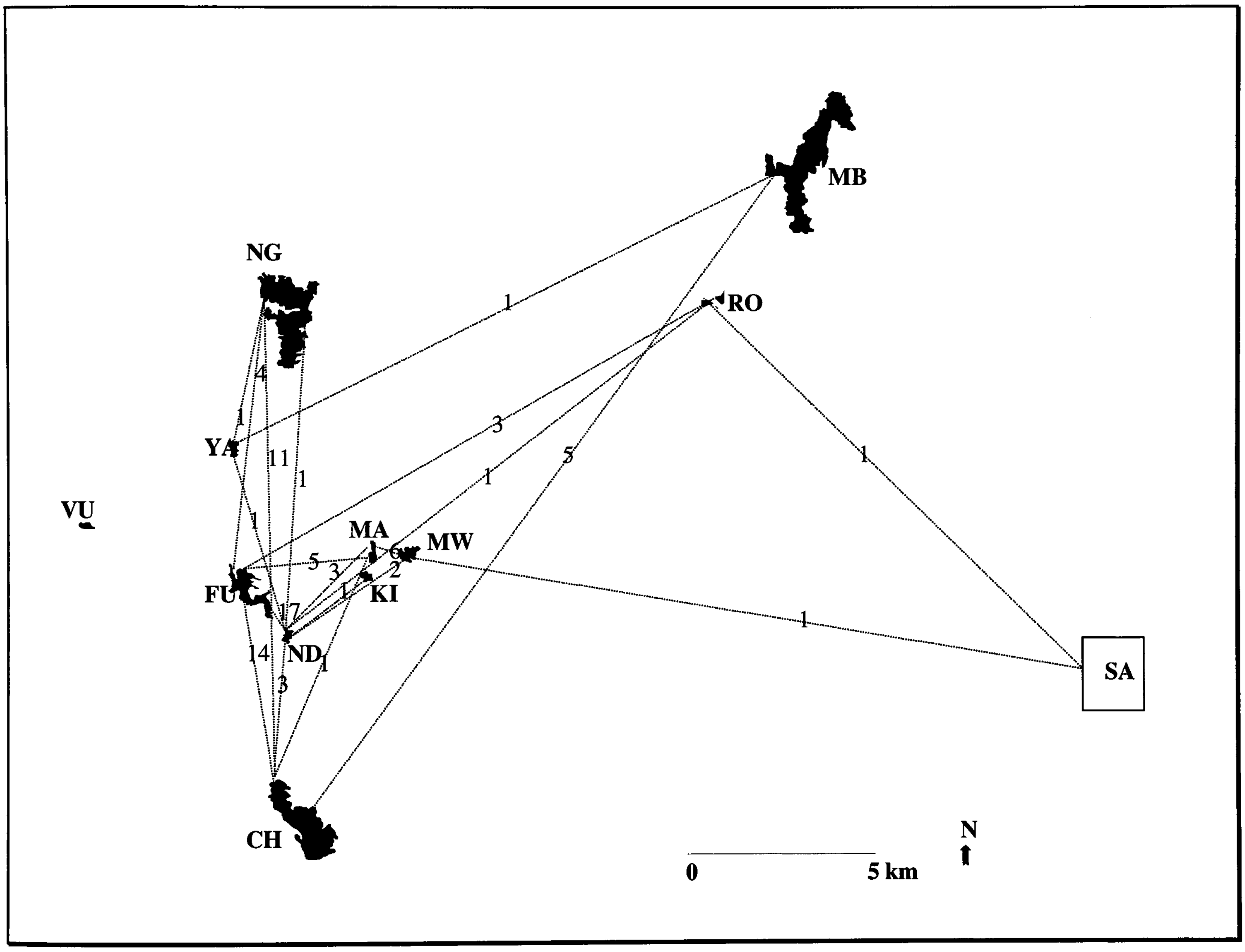
- Evolution and selection: the potential differences in social structure and reproductive success among the fragments (Chapters 2&7) could yield different selection forces across fragments. In turn, these could affect processes such as timing, rate and sex ratio of juvenile and adult dispersers (e.g., Clarke et al. 1997), mating systems, or the timing of plumage switch from immature to adult (e.g., Moreau 1951). Incidence of such habitat-dependent compensatory behaviour is logical because it would leave each subpopulation best adapted to its respective habitat. For instance, individuals in CH might have a shorter immature-stage so as to facilitate earlier breeding, whereas delayed breeding would best suit NG individuals, in order to reduce competitive stress between residents and floaters. Or have differences in breeding behaviour in response to different predator pressures. It would be interesting to explore the genetic component of such adaptability, which represents a paradoxical scenario for the sink populations because the dispersal that sustains them also brings the gene flow that eclipses any attempts they make to adapt to their habitats (Kawecki 1995; Holt 1996; Hanski 1999).

8.6.2 Conservation

- Translocations: this study revealed the presence of non-breeding adults in some fragments, and the suitability of the small fragments for the robin. It is possible that fragments with high population density and more even sex ratios for the thrush [such as Mbololo and perhaps Ngangao (Lens et al. 1998)] contain non-territorial adults that cannot disperse successfully due to hostile land uses. It is also likely that one small fragment, Fururu, is suitable for the thrush but is not occupied due to a lack of colonizers. This is deduced from the fact that a small subpopulation persists and breeds in another small fragment, Yale. It would be interesting to translocate some floaters to this fragment and see how they perform. This would be a good use of the removal experiment's findings for direct conservation purposes, somewhat analogous to the work of Komdeur (1992) on Seychelles warblers *Acrocephalus sechellensis*.

- Next, building from the conceptual and diagrammatic models from this study, further work should harness the extra information contained in the detailed digitised maps under preparation, to assess landscape effects to greater detail and build spatially explicit models (e.g., Dunning et al. 1995; Turner et al. 1995). This would offer a practical tool for management planning in this landscape mosaic (e.g., see Akçakaya et al. 1995; Wahlberg et al. 1996), especially when important behaviour components [now becoming clearer] are included in the models (Morales and Ellner 2002).
- Further, education initiatives need to be encouraged across all age groups. This is vital because ultimately, people will only care for and conserve what they *know* (Balmford et al. 2002). These schemes can build on the basic work already initiated under this study in schools, making the teaching more comprehensive, interactive and participatory; for instance, by students making visits to the forest for more practical learning. This can then be expanded to other target groups e.g. youth and elder groups.
- Finally, there is a long-term need to find alternatives for forest products. On the short-term however, there is a need to regulate firewood harvesting from indigenous forests, not only in terms of amount collected, but also when and what is collected. This demands funding alternative sources of fuelwood; for example, selective and systematic harvesting of exotic trees to provide the local people with 'free' firewood, together with the aforementioned agro-forestry schemes. Ultimately, the Utopian ideal solution is obviously the provision of different means of cooking to ease the pressure on the forests for this basic resource. Major short-term (economic) sacrifices need to be made from the Government-level down if we are to see any long-term (environmental and basic human living standards) gains (James et al. 1999).

Appendix 8.1. Evidence of interfragment dispersal events obtained from capture-recapture of eight bird species in the Taita Hills: stripe-cheeked greenbul *Andropadus milanjensis*, Cabanis's greenbul *Phyllastrephus cabanisi*, Taita thrush *Turdus helleri*, olive sunbird *Nectarinia olivacea*, Taita white-eye *Zosterops silvanus*, Taita apalis *Apalis (thoracica) fuscigularis*, yellow-throated woodland warbler *Phylloscopus ruficapillus* and white-starred robin *Pogonocichla stellata*. The numbers indicate the number of dispersal events between the respective pair of fragments. [MB = Mbololo, RO = Ronge; SA = Sagala; NG = Ngangao, YA = Yale, VU = Vuria, MA = Macha, MW = Mwachora, FU = Fururu, KI = Kichuchenyi, ND = Ndiwenyi, and CH = Chawia]



Paper VIII

Paper Published

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Chapter 9: Avian Persistence in Fragmented Rainforest

Summary

What factors determine the persistence of species in fragmented habitats? To address this question, we studied the relative impacts of forest deterioration and fragmentation on bird species in twelve rainforest fragments in Kenya - combining six years of individual capture-recapture data with measurements of current captures and museum specimens. Species mobility, as estimated from species-specific dispersal rates, and tolerance to habitat deterioration, as estimated from change in fluctuating asymmetry with increasing habitat disturbance, explained 88% of the variation in patch occupancy among eight forest bird species. Occupancy increased with mobility and with tolerance to deterioration, where both variables contributed equally to this relationship. We conclude that individual-level study, such as of dispersal behaviour and phenotypic development, can predict patterns of persistence at the species level. More generally, for conservation tactics to stand a high chance of success, they should include action both within sites, to minimise habitat deterioration, and across landscapes, to maximise dispersal.

Anthropogenic habitat deterioration is imposing new selection pressures on organisms, increasing local extinction rates (*1*). Simultaneously, reduced movement among remnant patches lowers colonisation rates, which further negatively affects demographic and/or genetic population parameters (*2*). From a conservation perspective, impacts of habitat deterioration and impacts of habitat fragmentation might demand different strategies. Whereas the former often requires management of populations within local (protected) areas, the latter may require conservation at the landscape level, e.g. within a metapopulation framework *(3)*.

We evaluated the impact of habitat deterioration and fragmentation on the persistence of eight forest-restricted small- to medium-sized bird species within 430 ha of rainforest remnants in south-east Kenya. Three species are endemic to the Taita Hills forest, which is part of the Eastern Arc biodiversity hotspot (*4*). Over the last decades, the forest has been reduced to twelve patches, of which only the three largest ones (Chawia, 94 ha; Ngangao, 136 ha; Mbololo, 179 ha) are inhabited by all study species. The nine other remnants are tiny (1-8 ha) and heavily disturbed, and host breeding populations of a subset of species only (*5*). At a landscape level, pronounced heterogeneity in habitat quality, such as among the Taita forest fragments, may give rise to source-sink dynamics within a metapopulation (*6*). From metapopulation theory, we hypothesised occupancy of the smaller forest patches (*7*) to be a function of both species-specific levels of mobility, affecting (re)colonisation rates from the three large patches, and sensitivity to forest deterioration, affecting local extinction rates.

Species-specific levels of mobility were estimated with program MARK (*8*), from capture-recapture histories of 3089 individuals trapped and individually marked in the large fragments Mbololo, Ngangao and Chawia between 1996-2002 *(9)*. Monthly probabilities of between-fragment dispersal were estimated from multi-strata mark-recapture models and corrected for between-species heterogeneity in survival and/or recapture rates (*10*). Initially, we estimated species-specific rates of dispersal by assuming a constant dispersal probability for each species. This resulted in four candidate models: $\Phi_g p_g \Psi_c$, $\Phi_c p_g \Psi_c$, $\Phi_g p_c \Psi_c$, $\Phi_c p_c \Psi_c$, where Φ = monthly survival probability, p = monthly recapture probability, Ψ = monthly dispersal probability, and the subscripts *g* and *c* refer to fragment-dependent or constant probabilities respectively. From these models the most parsimonious one was selected for each species. However, since distances differed between pairs of fragments (Mbololo-Ngangao, 11.3 km; Mbololo-Chawia, 19.4 km; Ngangao-Chawia, 10.9 km) estimates of dispersal might be biased by differences in abundance between fragments for the different species. We therefore constructed multi-strata models that estimated monthly dispersal probabilities between each pair of fragments irrespective of the direction of dispersal, by allowing Ψ to vary between fragment pairs *(11)*. The process of selecting the most parsimonious model among the new candidate set was then repeated for each species. In a final step, we regressed pairwise dispersal probabilities against pairwise distances between the three forest fragments for each species, and used the intercept of each regression equation as the species-specific measure of dispersal (mobility) for further modelling. The multi-strata models and dispersal probabilities estimated for each species are listed in Table 1. All methods of estimating species-specific dispersal produced comparable between-species differences in mobility.

Species-specific levels of stress tolerance were estimated from levels of fluctuating asymmetry (FA) in tarsus length. FA refers to small, non-directional differences in the development of the left and right sides of bilateral traits (*12*) and is widely regarded to act as a measure of developmental stability and predictor of stress-mediated changes in fitness (*13*). Individual FA estimates were based on repeated measurements, corrected for body size and obtained from mixed model analysis with Restricted Maximum Likelihood parameter estimation to distinguish FA from directional asymmetry and measurement error (*14*). We previously showed a consistent, positive relationship between current population levels of tarsus FA and the degree of forest deterioration (*15*). We further measured tarsus FA in 133 museum specimens of six study species that were collected before the majority of the Taita Hills forest patches became severely deteriorated several decades ago (*16*). Sensitivity to forest deterioration was calculated as the species-specific deviance from the average increase in tarsus FA between museum samples and current captures in the most degraded of the larger fragments (Chawia), compared to a control patch with most intact indigenous vegetation (Mbololo) (*17*). Previous analyses confirmed that levels of FA increased over time in the degraded but not in the control patch (*15*).

As shown in Fig. 1A, more mobile species showed a significantly higher level of persistence than less mobile species after correction for the effects of change in asymmetry, i.e. they occupied a higher proportion of patches than expected from their estimated stress sensitivity. Highly comparable results (not shown) were obtained when using the estimates of recapture rate and constant dispersal probability described above and listed in Table 1. Change in asymmetry, in turn, significantly explained residual variance in patch occupancy (Fig. 1B), i.e. less sensitive species occupied a higher proportion of patches than predicted from their estimated level of mobility (*18*). Together, dispersal rate and change in asymmetry explained 88% of the observed variation in patch occupancy between species, with each factor contributing equally to the relationship (i.e. 45% of variation explained by probability of dispersal; 43% of variation explained by change in asymmetry). Based on these results, we conclude that individual-level parameters, such as mobility and developmental homeostasis, can be scaled up to predict species-specific patterns at landscape level (i.e. the 'behavioural ecology of ecological landscapes' concept; *19*). In a comparable approach, models have been developed that scale mass-related energy requirements with population density (*20*). The use of simple, accurate and cost-effective biomarkers, such as individual asymmetry, further permits to measure the impact of environmental stress and take appropriate conservation action before species become irreversibly affected (i.e. the 'early warning' concept; *21-22*). Application of such individual-level approach in part of one of the world's most threatened biodiversity hotspots, suggests that conservation tactics may fail unless they include action both within sites, to minimise habitat deterioration, and across landscapes, to maximise dispersal.

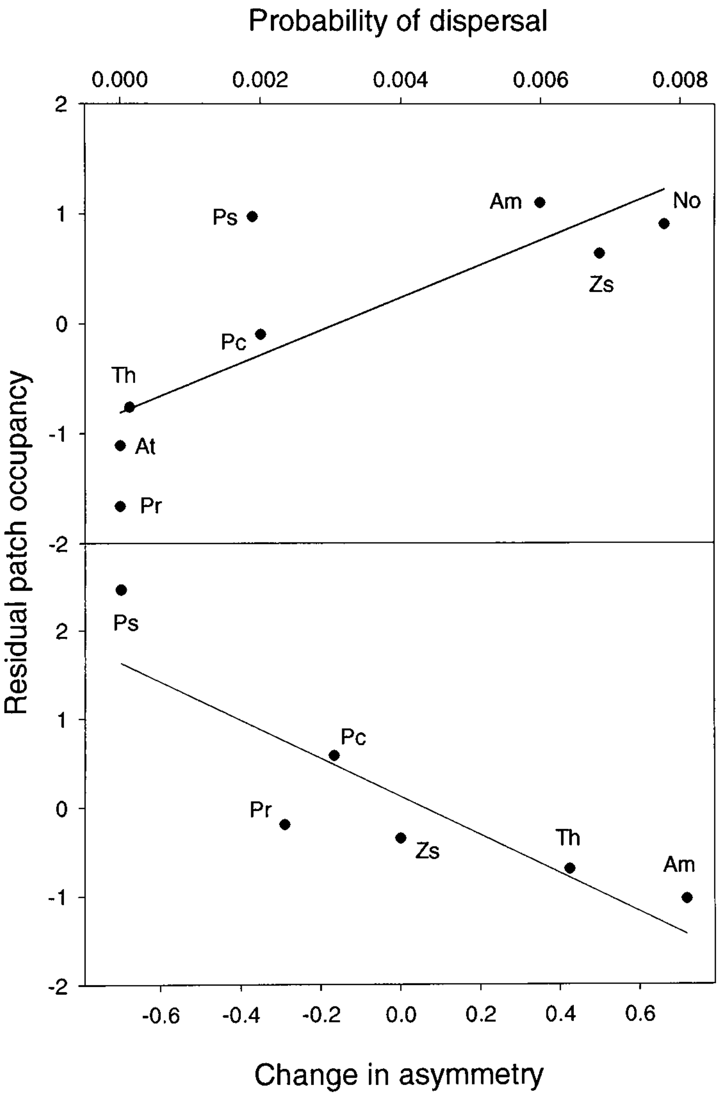

Fig. 1. Relationship between persistence, species-specific levels of mobility (panel A) and stress tolerance (panel B). Y-axes represent residual values of patch occupancy after correcting for the effects of change in asymmetry (A) and dispersal rate (B). Am = ***Andropadus milanjensis*** (3), At = ***Apalis thoracica*** (1), No = ***Nectarinia olivacea*** (7), Pc = ***Phyllastrephus cabanisi*** (4), Pr = ***Phylloscopus ruficapillus*** (0), Ps = ***Pogonocichla stellata*** (8), Th = ***Turdus helleri*** (1), Zs = ***Zosterops silvanus*** (5) (number of small forest fragments occupied between brackets, $n_{tot} = 9$). Patch occupancy was positively related to dispersal rate (par. estim. 301 ± 111, 95% CI 94 –532) and negatively to change in asymmetry (par. estim. -1.87 ± 0.74, 95% CI -3.39 – -0.50). Parameter estimates of the two variables were not statistically correlated (P = 0.3) and remained unaffected after including variable body size in the model.

Table 1. Species-specific dispersal probabilities as estimated with recapture rates and multi-strata models fitted in MARK. * Calculated as the proportion of all recaptured birds that moved between the three large fragments. † Model symbols are defined in the text. ‡ For *Phyllastrephus cabanisi*, two models were equally parsimonious. The Ψ estimated from the model with the lowest AIC value was selected for further analysis. § Multi-strata models that estimate dispersal probabilities between pairs of fragments irrespective of the direction of dispersal. ‖ Species-specific probability of dispersal controlling for dispersal distance (see text for details). These estimates were used for further modelling

Species	Recapture rate *	Model †	Dispersal probability, Ψ	Model †,§	Dispersal probability, Ψ ‖
A. milanjensis	0.083	$\Phi_g p_c \Psi_c$	0.002535	$\Phi_g p_c \Psi_g$	0.005994
N. olivacea	0.114	$\Phi_g p_c \Psi_c$	0.003958	$\Phi_g p_c \Psi_g$	0.007775
P. cabanisi	0.077	$\Phi_g p_c \Psi_c$ $\Phi_g p_g \Psi_c$	0.002161 ‡ 0.002102	$\Phi_g p_g \Psi_g$	0.001998
P. ruficapillus	0.000	$\Phi_g p_c \Psi_c$	0.000000	$\Phi_g p_c \Psi_g$	0.000000
P. stellata	0.024	$\Phi_g p_g \Psi_c$	0.000761	$\Phi_g p_g \Psi_g$	0.001881
T. helleri	0.006	$\Phi_g p_g \Psi_c$	0.000184	$\Phi_g p_c \Psi_g$	0.000132
Z. silvanus	0.079	$\Phi_c p_c \Psi_c$	0.003080	$\Phi_g p_c \Psi_g$	0.006849

References and Notes

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(5) A selection of maps of the study area, illustrating its global position, elevational structure and spatial relationships of the forest fragments can be found at http://bio-www.uia.ac.be/bio/deco/topics.html#study areas.

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(7) Occupancy was calculated as the proportion of small forest fragments ($n_{tot} = 9$) with confirmed breeding activity during one or more breeding seasons between 1996-2001.

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(9) Individual recapture histories were generated using time intervals of one month. Such a short time interval was necessitated by the fact that over longer intervals (e.g. three, six, or twelve months) a number of individuals were recaptured in different forest fragments within a single interval. A total of 889 individuals were captured-recaptured in two or more months, and among these, 47 individuals were captured-recaptured in two or more fragments.

(10) We used Akaike's Information Criteria (AIC) to determine the most parsimonious model among a candidate set, and computed species-specific dispersal probabilities for further analysis from this model. Recapture data were too sparse to include fully time-dependent models of survival and recapture probabilities in the candidate set of models, and sample size did not allow us to calculate complex multi-strata models for *Apalis thoracica*. For this species, no single individual was captured in more than one fragment, hence Ψ was estimated as 0. There is no formal goodness-of-fit test for multi-strata models, yet our results were robust for a range of 1 - 1.5 in the overdispersion parameter $\hat{c}$.

(11) More complex dispersal models could not be fitted to all species in MARK because models were overparameterised. For the more mobile species with adequate numbers of recaptures after dispersal between fragments, a model assuming direction-dependent dispersal rates between fragment pairs fitted the recapture data significantly better than the model described in Table 1 (note 4) for two species, but equally well for two others (nested models compared using likelihood ratio tests).

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(16) The validity of this relationship depends on the assumption that tarsi develop in the patch where they are measured. Violation of this assumption, however, can only bias results against the hypothesis tested in this paper.

(17) No museum samples were available for *Apalis thoracica* (rare species) and *Nectarinia olivacea* (abundant species yet not collected in the Taita Hills).

(19) Estimates were obtained from the random species*time interaction (χ^2_1=4.1, p<0.05) in a three-way mixed ANOVA with unsigned FA as dependent variable, fragment as fixed factor, and species, time and all relevant two- and three-way interaction terms as random factors (model specifications in *(15)*).

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(20) Logistic regression analysis performed in WINBUGS ver1.3 to allow for missing values and use of all available data. The occupancy-dispersal association was based on eight species, the occupancy-asymmetry association on six species. An extra dispersion variance parameter (par. estim. 0.22 ± 0.71, 95% CI 0.001 – 1.63) was added to correct for overdispersion (25).

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