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Drivers of avian diversity on an altitudinal gradient of Mount Cameroon
Faktory ovlivňující rozmanitost ptáků na altitudinálním gradientu Kamerunské hory

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I declare that this thesis has not been submitted for the purpose of obtaining the same or any other academic degree earlier or at another institution. My involvement in the research presented in this thesis is expressed through the authorship order of the included publications and manuscripts. All literature sources I used when writing this thesis have been properly cited.

In Prague, June 30th 2015

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Eric Djomo Nana

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ABSTRACT

Altitudinal gradients constitute a powerful test system for understanding distribution of species around the globe. Tropical mountains are quite rich in species even after controlling for environmental productivity, and are ideally suited for studying patterns of species distributions because they have had sufficient time for species to produce a response to environmental changes that affect their life histories. In this thesis, I investigate basic ecological mechanisms potentially behind avian distribution patterns along an altitudinal gradient in West-Central Africa. I used data collected with four methodological approaches (point counts, mist netting, random walks and artificial nest experiments) along an altitudinal gradient on Mt. Cameroon from October 2011 to September 2013. This work is focused on two interrelated themes: selection pressures on life histories (Chapters 1, 2, 3 & 4), and avian assemblage structures (Chapters 5 & 6). In the General Introduction, I present an overview of the study area with conservation implications of the study and my study objectives. In Chapters 1, 2 & 3, I investigate how selection pressures, i.e., nest predation and parasitism by haematozoa, affect bird assemblages. I used artificial nest experiments to assess nest predation rates in Chapters 1 & 2, and my results show that the structure of the vegetation has a significant influence on success of artificial nests along elevations through its influence on nest position and type. In Chapter 3, I investigate haemosporidian infections, an alternative selection pressure on avian life histories, with molecular analyses on 1044 birds belonging to 76 species and 23 families. My results reveal a low prevalence but high rate of host-parasite reciprocal specializations. Parasites mostly infect abundant bird species foraging at ground level. In Chapter 4, I explore inter-sexual-morphological variation in a monochromatic frugivorous bird species, and show that males in this species are not under intense male-male competition to develop pronounced morphological traits. Similar ecological space use or low sexual selection is presumably behind this. In Chapters 5 & 6, I look at bird assemblage distribution patterns along this altitudinal gradient and compare species richness and abundance patterns of two montane bird assemblages on different mountains. High abundances of montane species are behind a distorted generally observed positive abundance–range size relationship. The mountain with more pristine forest has species with higher abundances while the mountain with more degraded forest has higher species richness. These findings illustrate the influence of the environment on the ecology of birds, and open the path for more stringent investigations on Afrotropical mountains.

ABSTRAKT

Gradients nadmořské výšky tvoří ideální modelový systém pro pochopení rozšíření druhů po celém světě. Tropické hory jsou poměrně bohaté co do počtu druhů, a to i po kontrole na produktivitu prostředí. Jsou proto vhodné pro studium prostorového rozšíření ptačích druhů, které zde měly dostatek času na přizpůsobení se lokálním podmínkám formujících jejich životní strategie. Ve své práci se zabývám základními ekologickými mechanismy potenciálně zodpovědnými za rozšíření ptáků podél výškového gradientu v středozápadní Africe. K výzkumu jsem použil data sesbíraná pomocí čtyř rozdílných metodických přístupů (bodové sčítání, odchyt do nárazových sítí, náhodná procházka a experimenty s umělými hnízdy), které byly aplikovány podél výškového gradientu na Kamerunské hoře od října 2011 do září 2013. Tato práce je zaměřená zejména na dvě provázaná témata: selekční tlaky na životní strategie (kapitoly 1, 2, 3 a 4) a strukturu ptačích společenstev (kapitoly 5 a 6). V obecném úvodu popisuji studovanou oblast s důrazem na její význam v ochraně přírody. V kapitolách 1, 2 a 3 studuji, jak selekční tlaky, tj. hnízdní predace (kapitoly 1 a 2) a parazitace krevními parazity skupiny Haemosporida (kapitola 3), mohou ovlivňovat strukturu ptačích společenstev. Ke zhodnocení míry hnízdní predace jsem aplikoval umělá hnízda a mé výsledky naznačují, že struktura vegetace měnící se podél elevačního gradientu má vliv na predaci umělých hnízd, podobně jako umístění hnízda a jeho typ. V kapitole 3 jsem zkoumal infekce parazity skupiny Haemosporida, což je alternativní selekční tlak ovlivňující životní strategie ptáků, a to molekulární analýzou provedenou na 1044 jedincích 76 druhů z 23 čeledí. Mé výsledky ukázaly celkově nízkou prevalenci, nicméně vysokou míru recipročních specializací mezi hostitelem a parazitem. Paraziti často infikují početné ptačí druhy a ty, kteří vyhledávají potravu blízko země. V kapitole 4 zkoumám mezipohlavní morfologickou variabilitu u monochromatického frugivorního ptačího druhu a zjistil jsem, že samci tohoto druhu nejsou ovlivňováni intenzivní vnitropohlavní kompeticí, která by je nutila vyvinout si výrazné morfologické znaky. Pravděpodobnou příčinou je podobné využívání odlišného ekologického prostoru či nízká intenzita pohlavního výběru. V kapitole 5 a 6 sleduji elevační variabilitu ve struktuře ptačích společenstev, srovnávám druhové bohatství a početnosti společenstev ptáků na dvou různých horách. Vysoké abundance horských druhů vedou k odlišnostem v obecně platném pozitivním vztahu mezi abundancí a geografickým rozšířením. Na hoře s méně narušenými horskými lesy dosahují ptačí druhy vyšších populačních hustot, naproti tomu pro horu s degradovanými lesy je typické vyšší druhové bohatství. Tyto

výsledky ilustrují vliv prostředí na ekologii ptáků a do budoucna otvírají cestu podrobnějším výzkumům v prostředí tropických hor v Africe.

– GENERAL INTRODUCTION

This study is focused on ornithological surveys of forest birds carried out in a continuous forested gradient undisturbed by human activities on Mt. Cameroon in West-Central Africa. In this General Introduction, I start by presenting the background and justification of the study with conservation implications. Next, I present an overview of the chain of mountains that form the Afromontane archipelago in West-Central Africa known as the Cameroon volcanic line. I then present the different avian diversity patterns and underlying mechanisms along altitudinal gradients, with different hypotheses put forward as proposed drivers. I finally give an outline, with objectives and predictions, of my thesis.

I- BACKGROUND AND CONSERVATION IMPLICATIONS OF STUDY

Altitudinal gradients around the world constitute a powerful test system for understanding the distribution of species (McCain, 2009a). These insular habitats are ideal subjects for investigating species distributions because of their isolation, numbers, relative simplicity, and have remained stable over long periods of time which give them a considerable advantage over artificial manipulative experiments.

The structuring of species assemblages along altitudinal gradients continue to present a challenge for understanding basic ecological patterns, as the causes are still not well understood (Lomolino, 2001; Rahbek, 2005; Romdal & Rahbek, 2009). It seems both stochastic and deterministic processes are important in determining the way species assemblages are structured along altitudinal gradients (Ricklefs, 1987). The general rarity of detailed data on tropical species assemblages along altitudinal gradients has slowed progress in our understanding of the factors that structure these assemblages (Robinson *et al.*, 2000).

Explaining altitudinal diversity patterns is one of the great contemporary challenges in ecology, because beyond purely scientific goals and satisfying curiosity, it is essential for applied issues of major concern to mankind, such as the spread of diseases and their vectors, and the likely effects of climate change on the maintenance of biodiversity. Unfortunately, the rate of habitat degradation and biodiversity loss in these areas is also very high, and these ecosystems are believed to be among the most exposed to the negative impacts of future climate change (Sekercioglu *et al.*, 2012). Afrotropical altitudinal gradients, because of their steep slopes and

topographical relief, are still relatively well preserved, and host high abundances of endemic species (Reif *et al.*, 2006). They are quite species rich even after controlling for environmental productivity, because species richness has been shown to be positively correlated to topographical relief (Rahbek and Graves, 2000). These gradients have been recognized as generators of diversity and centers of endemism (Fjelds  *et al.*, 2012), and form part of the global biodiversity hotspots which make them priority areas for conservation (Myers *et al.*, 2000). Most studies on the distribution of species along altitudinal gradients have been done in temperate regions with few in the tropics, and notably in the neotropics. This study is therefore the first of its kind in West-Central Africa despite of the fact that this area presents altitudinal gradients which by virtue of elevational extent, are excellent models for the purpose of such studies. Moreover, data collected in this study will be very helpful to the conservator's office of the Mt. Cameroon National Park, because it will provide information necessary to address pressing conservation issues.

II- GENERAL OVERVIEW OF THE CAMEROON VOLCANIC LINE AND MOUNT CAMEROON

In Africa, the main mountains form clusters at different parts of the continent. Three such clusters can be observed. These are; the mountains of East Africa, i.e. Albertine rift and Ethiopian highlands, the mountains of the southern African region, and the Cameroon mountains also known as the Cameroon volcanic line in West-Central Africa. These mountains have a sufficiently distinct biodiversity that warrant their recognition as a separate phyto-geographic region called the Afromontane archipelago (White, 1981). Concerning birds, though northwestern South America is the world's most species-rich region, Sub-Saharan Africa has the greatest diversity at higher taxonomic levels, and is thus arguably the richest corner of the world for birds (Lotz *et al.*, 2013).

The Cameroon volcanic line in the Gulf of Guinea, is 1600-km long and made of a chain of ten volcanoes that extend from islands in the Gulf of Guinea in the Atlantic ocean to the border region of eastern Nigeria, western Cameroon, and towards lake Chad (Burke, 2001; Smith *et al.*, 2009). Volcanic activity is thought to have started in this area in the Upper Cretaceous around 38 Ma ago (Burke, 2001), but most of the volcanic activity likely occurred during the Pliocene with signs of volcanic activity persisting through the Quaternary to the present (Wright

et al., 1985). This area is a hotspot of biodiversity on a global scale for a wide variety of taxa, and falls within the forest refugia of lower Guinea, thereby representing one of the highest priority sites for biodiversity conservation in Africa (Watts & Akogo, 1994; Brooks & Thompson, 2001; Fishpool & Evans, 2001; Orme *et al.*, 2005). It is home to a number of birds, mammals, amphibians, trees and plant species found nowhere else with 25 endemic bird species, 10 endemic reptiles, and 55 endemic amphibians (Stattersfield *et al.*, 1998; Fishpool & Evans, 2001; Gonwouo *et al.*, 2007). The mainland mountains such as Mt. Cameroon (4°08.67' N 9°07.31' E) are much cooler than the surrounding lowlands.

Data for this study was collected along the south-western slope on Mt. Cameroon because it has a continuous stretch of forest that runs from about 300 m above sea level (a.s.l) to 2250 m. Below 300 m a.s.l. are palm and rubber plantations with human settlements. Three forest types can be observed along this gradient. These are; a lowland rainforest up to about 900 m, a mid-elevation or transitional forest between 900 m and 1600 m a.s.l., and a montane forest found above 1600 m. These forests differ in structural features and microclimate (Proctor *et al.*, 2007) which make Mt. Cameroon a typical wet tropical mountain (*sensu* McCain, 2009a) in this poorly studied region, and therefore, an excellent model for studying species distribution patterns.

III- GENERALITIES ON AVIAN DIVERSITY ALONG ALTITUDINAL GRADIENTS

Bird distribution patterns along altitudinal gradients around the world can be grouped into four distinct categories (Figure 1); (i) diversity decreases monotonically with elevation, (ii) diversity decreases with low-elevation plateau, (iii) diversity shows a broad low-elevation plateau with intermediate peaks, and (iv) diversity decreases with a unimodal mid-elevation peak.

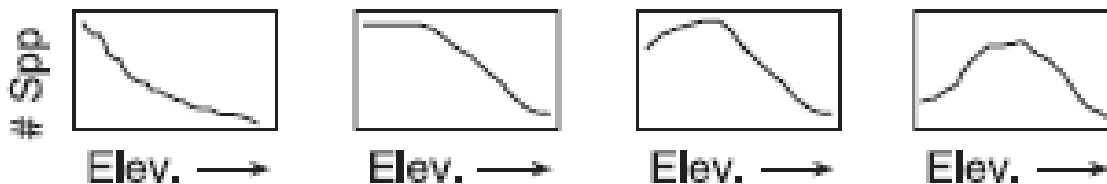


Figure 1. The number of bird studies demonstrating the four elevational richness patterns on montane gradients around the world. Source: McCain, 2009b.

In the tropics, altitudinal gradients can be grouped into two types based on precipitation regimes; wet tropical mountains which usually show low elevation plateaus or a monotonical decrease in

species diversity, and dry tropical mountains which usually show unimodal mid-elevation peaks or a broad low elevation plateau with intermediate peaks (McCain, 2009b). On Mt. Cameroon, we observed that avian diversity decreases with a low-elevation plateau, placing it into the second category above (Figure 2).

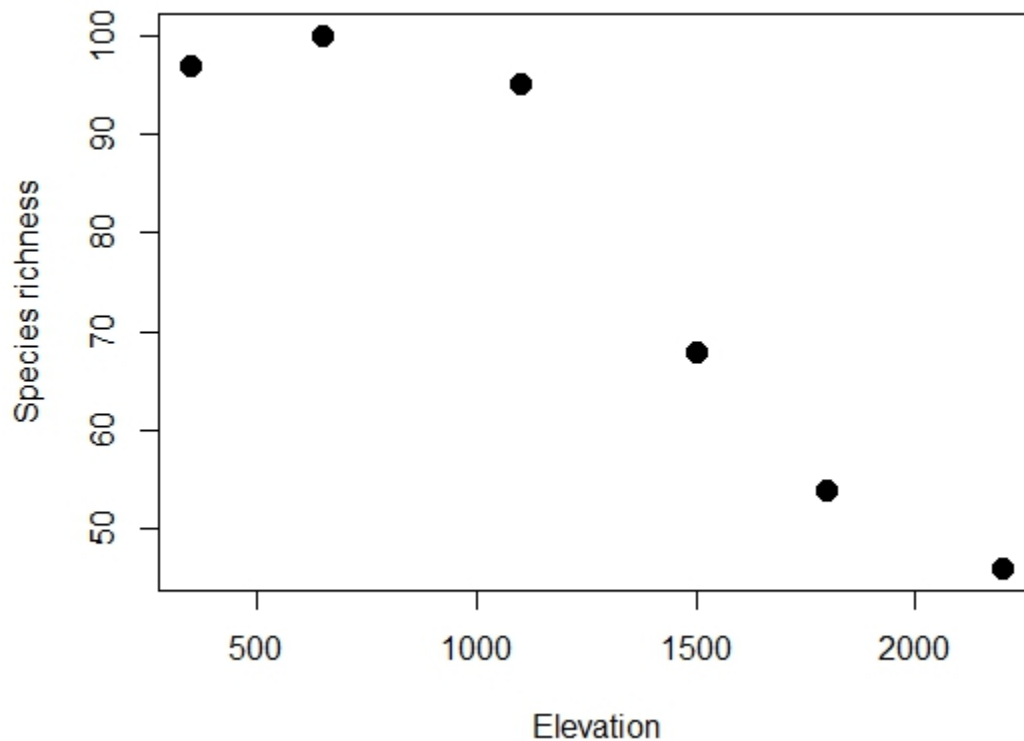


Figure 2. Avian species richness pattern (as estimated by point counts) along an altitudinal gradient on Mt. Cameroon.

Several factors have been suggested to be the drivers of the above observed patterns. The major ones are; temperature, precipitation, water availability, primary productivity, spatial/area, and biotic interactions (Pianka, 1966; Gaston, 2000; McCain, 2009b). It is important to note that many of these factors are dependent on one another, e.g. primary productivity is determined by precipitation regimes, humidity and temperature. Temperature affects physiological tolerance of species at particular elevational bands which then influence biotic interactions such as competition, predation, and parasitism. Area available at particular elevations acts as an

environmental filter by limiting the number of species that can coexist, and therefore has an influence on biotic interactions. Thus, no factor can explain species distributions along elevations singly. Below I will detail each hypothesis specifying its altitudinal application.

a- Temperature

On mountains, temperature decreases monotonically by an average of 0.6 °C per 100-m elevational gain (Barry, 1992), causing the climate to limit the number of species that can inhabit different elevations (Brown, 2001; Hawkins *et al.*, 2003). Few species can physiologically tolerate conditions at high than at low elevations because, high elevations are colder and drier than low elevations (Allen *et al.*, 2002; Sanders *et al.*, 2007). This implies there is a positive relationship between temperature and diversity (Kaspari *et al.*, 2000; Evans *et al.*, 2005). Should temperature be the main determinant of bird diversity, the predominant elevational diversity pattern predicted is decreasing diversity with decreasing temperature and increasing elevation.

b- Water availability

While temperature has been shown to decrease along elevations, water availability seems to follow a more complex association with altitude depending on the local climate (McCain, 2009b). Bird species richness along elevations is predicted to be positively correlated to water availability (van Rensburg *et al.*, 2002). On arid mountains, water availability is highest at intermediate elevations because rainfall and soil water retention are highest at these elevations (McCain, 2009b), but then water availability drops off dramatically towards low elevations because high temperatures and evaporation exceed rainfall inputs, and towards the upper elevations because runoff is high and precipitation more seasonal leading to arid habitats (McCain & Grytnes, 2010). On wet mountains (e.g. Mt. Cameroon), water availability is high across a broad base of lower elevations and only decreases toward the tops of the mountains, again due to higher runoff and low precipitation (McCain & Grytnes, 2010). Thus, there is a mid-elevation peak in bird species richness on arid mountains and decreasing diversity on warm, wet mountains.

c- Primary productivity

It is linked to the species energy hypothesis and suggests that bird diversity is strongly influenced by primary productivity because the amount of available energy sets limits to the

richness of the system (Gaston, 2000; Kaspari *et al.*, 2000; Mittelbach *et al.*, 2001; Evans *et al.*, 2005). Generally on mountains, temperature and precipitation decrease with elevation. On humid mountains like Mt. Cameroon, increased solar energy and precipitation across a broad base of lower elevations cause increased net primary productivity (or photosynthesis) which only decreases toward higher elevations. On dry mountains, precipitation, hence water availability, is highest at intermediate elevations. Water availability drops off dramatically towards low elevations where high temperature and evaporation exceed rainfall, leading to arid habitats (McCain 2009b). Higher net primary productivity means more individuals can be supported at that particular elevation, and more individuals lead to more species (Currie, 1991; Wright *et al.*, 1993) at these particular elevational bands. Bird species richness is predicted to be positively related to the warmest and wettest conditions elevationally, causing mid-elevation peaks in bird species richness on dry mountains and decreasing diversity on warm, wet mountains like Mt. Cameroon. Extinction rates are reduced at elevations with higher populations per species because these are sustained by the greater amount of available energy (Wright *et al.*, 1993). Another factor related to primary productivity is evapotranspiration. This is the process whereby water evaporates from leaves through plant transpiration during photosynthesis. High evapotranspiration promotes increased biodiversity because species richness increases with evapotranspiration (Wilson, 2011). Evapotranspiration is related to factors like temperature and humidity (Moratiel, 2010), such that if the air around the plant is too humid, like in a cloud forest, transpiration and evaporation rates drop. This implies along altitudinal gradients, elevations with high rates of evapotranspiration will also have higher species richness. On wet tropical mountains like Mt. Cameroon, there should therefore exist a decrease in evapotranspiration with elevation because of a decrease in temperature but an increase in humidity from the lowland forest to the montane or cloud forest.

d- Spatial/Area

Also known as species-area relationship, it asserts that the number of biological species in an area of a region is a positive function of the area of that region, because large areas can support more species (Terborgh, 1977; Connor & McCoy, 1979; Rahbek, 1997; Storch *et al.*, 2012). More area at the base of a mountain allows more species to accumulate and to have larger population sizes. Thus, species with large population sizes are likely to have lower extinction rates (Rosenzweig, 1995). It is assumed that at regional and global scales, extinction rates should

decrease and speciation rates should increase with area due to the increased likelihood of allopatric speciation (Rosenzweig, 1995). The combination of lower extinction rates and high rates of speciation leads to high levels of species richness. The elevational diversity patterns on mountains may fall somewhere on the continuum between these two scales and processes. Diversity at different spatial scales is also related to a stochastic phenomenon called the “Mid-Domain Effect” (MDE), which is claimed to be a null model because it excludes any direct environmental or evolutionary influence on species richness (Colwell *et al.*, 2004; 2005). Colwell & Hurtt (1994) pointed out using computer simulations that if species’ ranges were randomly shuffled within the geometric constraints of a bounded biogeographical domain (e.g. the base and top of a mountain), species' ranges would tend to overlap more toward the center of the domain than towards its limits, forcing a mid-domain peak in species richness. On mountains, these simulations predict a unimodal diversity curve with maximum diversity at the mid-point of the mountain (McCain, 2004).

f- Biotic interactions

Due to more species at particular sites, ecological interactions such as competition, predation, mutualism, and parasitism are stronger at these sites (Kircher, 2010). The intensity of species interactions are correlated with the change in species richness. Moreover, these interactions promote species coexistence and specialization, leading to greater species richness (Kircher, 2010). An example is that greater intensity of predation, at lower elevations has contributed to increased diversity of prey, thereby reducing the importance of competition, and permitting greater niche overlap which promotes higher richness of prey.

Apart from the above factors that try to explain bird species diversity along altitudinal gradients, species diversity and assemblage composition of birds are also known to be determined by habitat structure, and these tend to change rapidly along elevations (Terborgh, 1977). Research efforts have not yet fully enabled to elucidate the drivers behind avian diversity along altitudinal gradients. Until recently, studies on avian diversity along elevations have not been a central theme in avian ecology, despite the fact that they can shed more light on the factors behind processes structuring assemblages (Kraft *et al.*, 2011). Fortunately, the last decade

has seen a dramatic increase in the number of studies relating to avian diversity along altitudinal gradients, especially in the tropics (Jankowski *et al.*, 2009; Romdal & Rahbek, 2009; Mallet-Rodrigues *et al.*, 2010; Acharya *et al.*, 2011). Bird assemblages on tropical mountains usually have high abundances, especially towards montane forests (see Chapter 6), and are quite species rich even after controlling for environmental productivity, because species richness has been shown to be positively correlated to topographical relief (Rahbek and Graves, 2000). Our results corroborate the observation that, densely populated montane forests of the Cameroon mountains reveal an unusual ARSR (see Chapter 5, *cf.* Reif *et al.*, 2006). These Afromontane bird assemblages are quite sensitive to changes in their environment, and can therefore serve as good indicators of environmental stress (Chapter 6). I therefore compared in this thesis two montane bird assemblages at the same elevation but different mountains of the same mountain chain, with different histories and positions, and different states of forests, to investigate how these factors affect bird assemblages (see Chapter 6).

Several patterns and mechanisms have been proposed to explain avian diversity and assemblage compositions across different spatial scales. Particularly intriguing is the pattern of sexual dimorphism in which males and females of the same species differ in some trait. Knowledge of sex ratios of birds in field studies is important because it can provide information on population structure and dynamics of species (Wilson & Martin 2012), especially those inhabiting insular habitats like montane forests. Understanding sex-biased movements in wild bird populations in such habitats is relevant to both avian ecology and conservation, as it can enable researchers have detailed information on stress factors. Recently, molecular sexing has successfully been applied to bird species with no apparent sexual dimorphism (Griffiths *et al.* 1998). Despite the reliability of this technique, it is not routinely available to most scientists, especially in tropical Africa, who have access to neither trained staff nor laboratory facilities. As a consequence, information about sex ratios of free living African birds is often lacking. An alternative is a morphometric based field sexing technique. For these reasons, I decided to investigate sexual dimorphism in a montane monochromatic frugivorous passerine species distributed along the entire gradient, because montane environments can affect morphological traits of birds, leading to less intense male-male competition (Chapter 4).

Ecological relationships, e.g predation, affect life histories of birds along environmental gradients such as elevations, and can impose high evolutionary costs (Chapter 3). Elevation has

long been considered a major influence on the evolution of life-history traits. Most elevation-induced variation in life history traits such as clutch size and number of broods, can be attributed to major mechanisms such as: variation in nest predation, food limitation, parasitism, and climate (Cody 1966; Boyce 1979; Krementz and Handford 1984). Nest predation is inversely related to fecundity and more clearly organized by nest sites (Martin, 1995). Species that use nest sites with greater nest predation have repeated nesting attempts, and hence more investment into reproduction (Martin, 1996), which in turn is associated with reduced adult survival. Variation of nest predation, and hence fecundity, along elevations can also be related to phylogeny of birds which determines the type of nest built, because nest type and location significantly affect predation risk (Chapter 1). Hence along elevations, nest predation may increase (Badyaev 1997a) or decrease (Badyaev 1997b) depending on nest type but also on the surrounding vegetation as this parameter has an influence on nest visibility and access of predators to nests (Chapter 2). Thus, this predator-prey interaction is one that is influenced not only by phylogeny of the prey, but also by parameters of the habitat such as vegetation structure.

A similar ecological relationship to the predator-prey interaction is that of parasitism. Parasites are of particular interest in ecological studies because they are known to have caused extinctions of certain bird species (van Riper et al. 1986), and impose high evolutionary costs to their hosts by affecting their distributions and life histories (Hamilton and Zuk, 1982; Lachish et al. 2011). Avian host life history traits and behavior have been associated with host-vector encounter rates (Edman and Kale, 1971), and may be an important filter for transmission of vector-borne pathogens such as malarial parasites (Lutz *et al.*, 2015). Empirically identifying which life history traits have the greatest filtering effects on transmission within vector-borne disease systems will improve our understanding of the fundamental ecological mechanisms underlying prevalence and parasite specificity, as well as host susceptibility across taxa (Lutz *et al.*, 2015). Certain host families across Africa, e.g. Muscicapidae, Nectariniidae, Pycnonotidae and Turdidae, seem to be particularly vulnerable to haemosporidian infections (Loiseau *et al.*, 2012; see Chapter 3), probably because parasites have specialized for these host taxa. The ability for parasites to specialize or generalize and to infect hosts with varying efficiency depend on what factors determine parasite host-specificity, and how the degree of host-specificity impact parasite distribution and diversification (Lauron et al., 2014). Parasites host-specificity and range primarily depend on their compatibility, which is limited by a coevolutionary arms race between

hosts and parasites (Kawecki, 1998). Coevolutionary relationships between avian malaria parasites and their hosts influence the geographical distribution of both hosts (Garamszegi, 2006). Thus, it is crucial to understand the factors that influence host–parasite interactions, which is why Chapter 3 of this thesis is based on host–parasite interactions.

IV- OUTLINE OF RESEARCH

This thesis explores both the concepts and patterns of avian diversity components along elevations. I focus on the first theme, selection pressures on avian life history traits in Chapters 1, 2 and 3 to show how environmentally imposed pressures (nest predation and haemosporidian infections) structure bird assemblages along elevations. I investigate in Chapter 4 how these environmental pressures affect sexual selection in a sexually monochromatic passerine species. I then focus on the second theme, avian assemblage structures, in Chapters 5 and 6 to explore a macroecological rule, the abundance range- size relationship. I investigate if this relationship on Mt. Cameroon is distorted toward higher elevations based on previous observation in the area (Reif *et al.*, 2006), and compare two different bird assemblages found at the same elevation but on different mountains of the same mountain chain.

There is still much to catch up on. Avian diversity along tropical altitudinal gradients is still poorly understood, and we know little about the underlying mechanisms particularly in Africa. My thesis seeks to improve our understanding of this phenomenon, through these two inter-related themes. I explore these themes within the chapters of this thesis and present several related predictions and objectives in the lines that follow.

V- THESIS OBJECTIVES AND HYPOTHESES

My major goal in this study is to investigate the causes of the elevational diversity pattern in the distribution of bird species on Mt. Cameroon. To achieve this goal, I investigate two interrelated themes; selection pressures on life histories and assemblage structures, through the following four principal objectives:

- a- How biotic interactions, nest predation and haemosporidian infections, affect life histories of birds along the gradient;
- b- Test the importance of particular morphological traits for field sexing of a monochromatic montane species;

- c- Investigate structuring of bird assemblages in relation to the ARSR along the gradient on Mt. Cameroon; and
- d- Compare and describe different montane bird assemblages situated at the same elevation but on different mountains in the same mountain chain.

I have the following predictions for each principal objective;

- a-i) Prediction: Nest predation risk decreases with elevation and is influenced by the structure of surrounding vegetation such that, nest position and type affect predation rates.
- a-ii) Prediction: Long term isolation and stability of Mt. Cameroon has made haemosporida to be highly specialized for avian hosts, with prevalence determined by particular avian traits.
- b) Prediction: A combination of morphological traits could be used to discriminate between sexes of a monochromatic species in the field.
- c) Prediction: There is an unusual ARSR along the gradient toward the montane forest because range-restricted species are more abundant than widespread species.
- d) Prediction: Pristine montane forests have more abundant species confined to forest interior while degraded montane forests are generally richer in species due to the presence of non-specialists in forest interior.

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CHAPTER 1

DJOMO, N. E., SEDLÁČEK, O., VOKURKOVÁ, J. & HOŘÁK, D. 2014. Nest position and type affect predation rates of artificial avian nests in the tropical lowland forest on Mount Cameroon. *Ostrich* 85: 93–96.

Short Note

Nest position and type affect predation rates of artificial avian nests in the tropical lowland forest on Mount Cameroon

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Nest predation is the leading cause of reproductive failure in birds and thus it shapes their life history strategies. Intensities of nest predation appear to differ among nest locations and types in both temperate and tropical regions. However, there is limited knowledge of factors influencing susceptibility of avian nests to predation in Africa. The aim of our study was to investigate artificial nest predation rates of different ground and shrub nests located at different heights in the rainforest undergrowth. We placed artificial avian nests within a homogeneous lowland forest interior with sparse forest undergrowth in the Mount Cameroon National Park, Cameroon. We exposed three sets of nests: 50 bare-ground, 50 cup-ground and 50 cup-shrub nests, for 10 d. Predation was higher for cup-ground nests compared to cup-shrub nests, and bare-ground nests were more depredated than cup-ground nests. We concluded that the presence of a cup as well as higher nest position significantly increased probability of artificial nest survival. The results of this study suggest a potential selection pressure on nest type and placement in lowland forest birds for a poorly known tropical region.

Keywords: Africa, artificial nests, Cameroon, nest predation, nest survival, rainforest undergrowth

Nest predation is the leading cause of reproductive failure in birds (Ricklefs 1969; Martin 1988a) and contributes to shaping avian life histories (Robinson et al. 2000; Ghalambor and Martin 2001; Pangau-Adam et al. 2006; Remes et al. 2012). Some studies have indicated that susceptibility of nests to depredation is related to nest characteristics such as location (Maina and Jackson 2003; Sodhi et al. 2003) or nest type (Brawn et al. 2011). Intensities of nest predation appear higher for ground nests compared to shrub nests in temperate zones (Schmidt and Whelan 1999; Burhans et al. 2002; but see Martin 1993) as well as in tropical forests (Söderström 1999; Trujillo and Ahumada 2005; Bobo and Waltert 2011).

Nest predation can have an important influence on population dynamics, therefore understanding patterns of nest predation is an important aspect of species conservation (Martin 1988b). Since nest predation events are difficult to observe in the wild, one indirect way to estimate reproductive success of birds in their habitats is through artificial nest experiments (Major and Kendal 1996; Yahner and Mahan 1996). Although artificial nest experiments are not necessarily a perfect proxy for how well birds are reproducing in their natural habitats, especially if predators perceive artificial nests differently, they can still inform us about relative probabilities of predation for instance between nests at different locations (Vetter et al. 2013).

In Africa, nest predation has been studied mainly in East African forest fragments (Carlson and Hartman 2001; Maina and Jackson 2003; Githiru et al. 2005; Hanson et al. 2007;

Spanhove et al. 2009) where predation was highest at forest edges and for ground nests. In West and Central Africa, there are only few sources of information such as Bobo and Waltert (2011), who found a higher predation rate of ground nests compared to shrub nests along a habitat conversion gradient. There is therefore limited knowledge on predation rates at different nest positions/types of African pristine forests. The aim of our study was to investigate artificial nest depredation rates of different ground and shrub nests located at different heights of rainforest undergrowth.

The study was carried out in the south-western part of the Mt Cameroon National Park, Cameroon (04°05' N, 09°02' E) at an elevation of 350 m above sea level. This area is a biodiversity hotspot with a large number of endemic species (Larsen 1997). We placed artificial nests within a homogeneous lowland forest interior with sparse forest undergrowth and exposed three sets of nests (bare-ground, cup-ground and cup-shrub nests). The bare-ground nest was a small depression in the soil mimicking in placement and type that of a ground nesting bird such as Latham's Francolin *Francolinus lathamii*. The cup-nest was made of cotton material about 3 mm thick and of grey colour. The use of cotton material for the cup-nest might be potentially a flaw in the study design but the texture, softness and thickness of the material mimicked well that of the birds in the area, which frequently utilise plant material, mosses and spider webs to construct their nests (see Appendix). The artificial nests were about 6 cm in diameter by 4 cm in depth and fixed to

herbs. We used one type of cup-nest but we placed them in different positions. The cup-ground nest was made to mimic that of a near-ground nesting passerine such as the Olive-green Camaroptera *Camaroptera chloronota*. The nest was placed so that the upper edge of the cup was at a height up to 10 cm above the ground. The cup-shrub nest mimicking that of a shrub-nesting passerine such as the Red-bellied Paradise Flycatcher *Tersiphone rufiventer* was placed approximately 1 m above the ground. These three species, whose nest locations and general characteristics we mimicked, belong to the common species in this area but differ in real densities (as estimated by point counts; Hořák et al. unpublished data). However, we believe that nest densities artificially created in this study cannot affect relative estimates of predation rates. Nests were placed in triplets containing one nest of each type. Each nest within the triplet was at least 10 m from the closest one. The distance between neighbouring triplets was at least 50 m. To find nests again during subsequent controls, we marked the location of each triplet with a small piece of red tape tied about 10 m away from each triplet and took geographic coordinates using a global positioning system (Garmin GPSMAP 60 CX). The direction and position of the red tape varied from one point to the other.

Nests were exposed for 10 d in March 2012, the beginning of the breeding season for songbirds in the region (Bobo and Waltert 2011). A total of 150 (50 bare-ground, 50 cup-ground and 50 cup-shrub) nests were deployed. In each nest we placed one fresh Common Quail *Coturnix coturnix* egg. We checked the nests after 5 and 10 d. A nest was considered depredated if the egg was absent or broken (Hořák et al. 2011). Predation intensities were estimated as the number of artificial nests preyed upon after 5 and 10 d. We used a χ^2 test to determine if the frequency of predation differed between nest positions and types.

After the 10-day study period, 32% of the nests were depredated. Predation was higher for cup-ground nests (26%) compared to cup-shrub nests (16%), and bare-ground nests were more depredated (56%) than cup-ground nests (26%); see Figure 1. We found significant differences between nest positions; cup-ground and cup-shrub ($\chi^2 = 4.93$, $P < 0.05$) and types, i.e. cup-ground and bare-ground ($\chi^2 = 9.02$, $P < 0.01$).

The results of our study showed that predation rate was higher for cup-ground nests compared to cup-shrub nests and bare-ground nests were even more vulnerable. This indicates that both presence of a cup as well as height above ground influences probability of nest predation. A high level of vulnerability for ground-nesting birds to nest predation has already been reported in previous studies employing artificial avian nests in other tropical environments (Söderström 1999; Trujillo and Ahumada 2005). In the only other study using artificial avian nests in the same region, Bobo and Waltert (2011) placed artificial nests in different habitat types and heights and found predation rates of between 20% (shrub) and 27% (ground) after 8 d of exposure. Our study compared with that of Bobo and Waltert (2011) reveals similar predation rates for cup-ground nests, but we recorded higher predation rates for the bare-ground nests. The difference may be explained, besides two days shorter exposure time in Bobo

and Waltert (2011), by the higher visibility of the nests in the primary forest undergrowth in our study (cf. Carlson and Hartman 2001) or by the fact that Bobo and Waltert (2011) used chicken *Gallus gallus* eggs in their study. Chicken eggs are bigger with a harder shell making them less accessible to small-mouthed predators (DeGraaf and Maier 1996). However, there are some differences in the types of nests used between the studies and our data suggest the importance of nest type.

We found that the presence of a cup significantly increases survival rate in nests located on the ground. This can be attributed to improved concealment of eggs in cup nests making them less visible for visually oriented predators in the area such as small mammals (squirrels) and other bird species. Similarly, Cooper and Francis (1998) suggested the importance of egg visibility and revealed that exposed ground nests were more depredated than covered ground nests. Artificial nest predation rates can be higher (Carlson and Hartman 2001) or lower (Martin 1988b) compared to real nests, but at least visually oriented predators are believed to respond to artificial nests in a similar way as to natural nests (Pangau-Adam et al. 2006). As such, using artificial nests is still a valid approach to providing a basis on which to develop hypotheses on relative predation rate patterns (Carlson and Hartman 2001). However, it is important to point out that nests placed by humans might not properly reflect natural nest locations of birds, which might bias observed predation rates. In addition, differences in predation rates among artificial nests at different heights in our study could be affected by the reaction of different types of predators to human disturbance (presence of human odour). This reaction could be different among the types of predators that are restricted to the ground and those that forage among undergrowth.

We conclude that nest height and the presence of a cup significantly influenced artificial nest survival. As artificial nests employed in this study tried to mimic general characteristics and positions of real nests of lowland forest

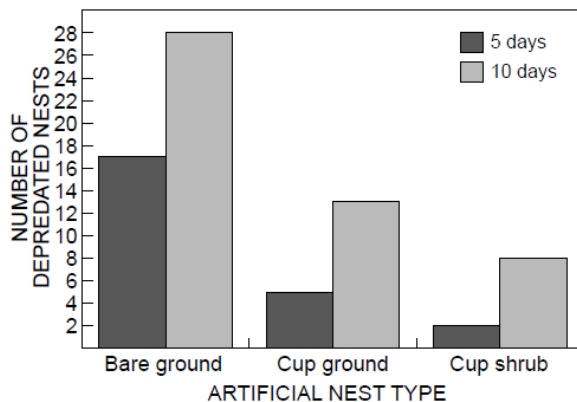


Figure 1: Number of artificial nests that were depredated after 5 and 10 d of exposure. Artificial nests were located at different nest heights: ground nests and shrub nests. For ground nests, we used two nest types: bare-ground and cup-ground nests. All nests were located within the lowland forest interior on Mt Cameroon

birds living on Mt Cameroon, we suggest that ground-nesting birds breeding at the foot of Mt Cameroon face higher nest predation, which might be reflected in their population dynamics and form a selection pressure on their life histories.

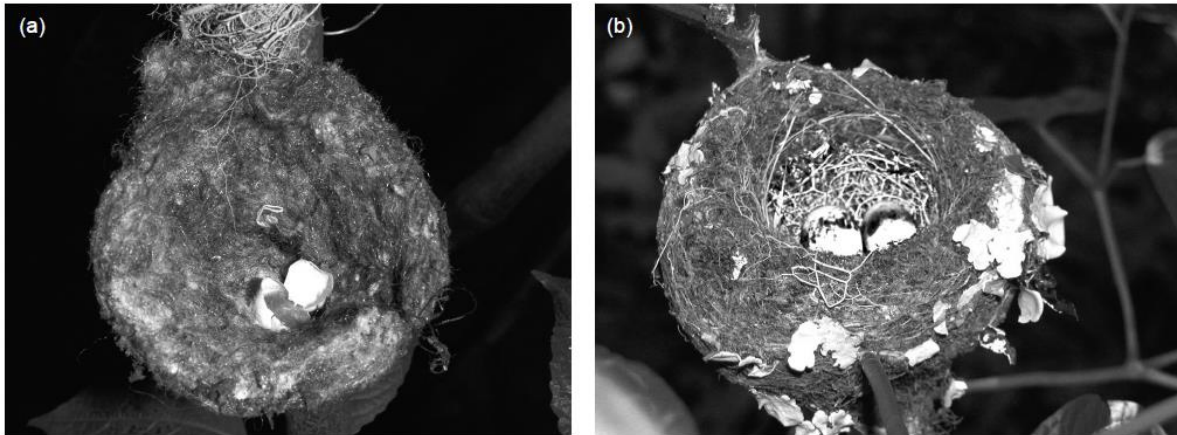
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Appendix

Artificial nest used in the study (a) with shell remnants of a finch egg and (b) a real nest of a passerine bird, *Elminia albiventris*, found in the area at higher elevations. The *Elminia albiventris* nest is quite similar to that of *Terpsiphone rufiventer*, which we mimicked in this study. Both species belong to the Monarchidae family



CHAPTER 2

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Relationship between Survival Rate of Avian Artificial Nests and Forest Vegetation Structure
Along a Tropical Altitudinal Gradient on Mount Cameroon

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ABSTRACT

Nest predation is assumed to be an important factor driving avian life histories. Altitudinal gradients offer valuable study systems to investigate how avian nest predation risk varies between bird populations. In this study, a hypothesis postulating an increase in avian nest survival rate with elevation as a result of decreasing predation pressure was experimentally tested along an altitudinal gradient (300-2250 m) in West-Central Africa. Three types of artificial nests (cup-shrub, cup-ground and bare-ground) were used along the altitudinal gradient. Overall, elevation had no effect on daily survival rate (DSR) of artificial nests. However, there was a significant elevation-nest type interaction. Daily survival rate for cup-shrub nests decreased significantly with elevation, but for cup-ground and bare-ground nests, elevation had no significant effect. We tested the effects of the same vegetation parameters (tree density, herb and shrub layer coverage, and canopy openness) on DSR of different nest types to understand how different vegetation layers or combinations of them affect DSR. Daily survival rate for bare-ground nests significantly decreased with increasing canopy openness, and was positively influenced by coverage of herb layer and tree density. For cup-shrub nests, DSR increased significantly with increasing shrub layer coverage. Finally, for cup-ground nests, we found a positive effect of shrub coverage and canopy openness on DSR. In summary, we found that different forest vegetation layers affect predation risk of different nest types along elevations on Mt. Cameroon.

Keywords: artificial nests, elevations, nest predation, vegetation parameters, West-Central Africa

RÉSUMÉ

La prédation des nids est un facteur important dans l'historique de vie aviaire. Les gradients d'altitudes offrent des systèmes d'étude précieux pour déterminer les variations de prédation entre les populations d'oiseaux. Dans cette étude, une hypothèse postulant une augmentation du taux de survie des nids avec l'altitude en raison d'une diminution de la prédation, fût testée expérimentalement le long d'un gradient d'altitude (300-2250 m) en Afrique ouest-centrale. Trois types de nids artificiels (nid d'arbustes, nid près du sol et nid sur sol nu) furent utilisés. Les résultats montrent que l'altitude n'aurait aucun effet sur le taux de survie quotidienne (TSQ) des nids. Nous avons cependant constaté une interaction significative entre l'altitude et le type de nid. Le TSQ pour les nids d'arbustes diminua de façon significative avec l'altitude, mais pour les nids du sol, l'altitude n'eut aucun effet significatif. Nous avons également testé sur le TSQ, les effets des paramètres de la végétation (densité des arbres, couverture herbacée et arbustive, et ouverture de la canopée) pour comprendre comment la végétation affecte le TSQ. Le TSQ des nids sur sol nu diminuait avec l'ouverture de la canopée, et était positivement influencé par la couverture herbacée et la densité des arbres. Pour les nids d'arbustes, le TSQ augmenta avec la couche d'arbuste. Enfin, pour les nids près du sol, le TSQ fût positivement influencé par la couverture arbustive et par l'ouverture de la canopée. En résumé, nous montrons que la végétation influence la prédation des types de nids aviaires au Mont Cameroun.

Mots clés: nids aviaires artificiels, altitude, prédation, végétation, Afrique ouest-centrale.

Nest predation has a direct influence on avian reproductive success because it is the main cause of nesting failure in birds (Ricklefs 1969, Skutch 1985). Therefore, spatial variation in avian nest predation risk is suggested to be an important factor that drives geographic variation in avian life histories, especially as concerns clutch size variation (Slagsvold 1982, Skutch 1985, Martin 1996, Hořák *et al.* 2011). Elucidating patterns of nest predation risk along various environmental gradients has become an important issue in avian ecology during past decades (Ricklefs 1969, Gering & Blair 1999, Jokimäki & Huhta 2000, Badyaev & Ghalambor 2001) as these may explain spatial variation in avian population structures, as well as functional traits of birds. Special attention has been directed to differences in predation risk between tropical and temperate regions (Ricklefs 1969) with tropical birds reported to suffer from a higher nest predation risk (Skutch 1985, Martin *et al.* 2006, Remeš *et al.* 2012). This is presumed to be the result of a higher diversity and abundance of predators in the tropics (Reidy 2009) and also, longer incubation periods of tropical birds which make them more susceptible to predation (Martin *et al.* 2007).

Ecological patterns along latitudes tend to be similar to those along elevations (Skutch 1985, Stevens 1992, Fleishman *et al.* 1998, Sanders 2002). Thus, investigating altitudinal patterns (especially those from tropical mountains) might provide a deeper insight into the latitudinal variation of nest predation in birds. Surprisingly, only few field studies investigating avian nest predation rates along altitudinal gradients have been done (but see Boyle 2008, Seibold *et al.* 2013). In the temperate zone, Seibold *et al.* (2013) found no clear altitudinal pattern in predation rate of avian artificial ground nests. However, they revealed a strong influence of near ground vegetation and tree cover on estimated predation rate. Predation rate declined with increasing near ground vegetation but increased with increasing tree cover. Boyle

(2008) who studied predation rate of avian artificial shrub nests in a neotropical old growth forest, found that predation decreased with elevation with low intermediate elevation peaks. It is impossible to make any general conclusions based on the studies mentioned above, but it is likely that changes in vegetation structure along elevations are important determinants of nest predation risk. Vegetation parameters such as coverage of herb layer, density of trees, as well as the degree of canopy openness, vary altitudinally between habitats (Doležal *et al.* 2012, Russo *et al.* 2012, Djuikouo *et al.* 2014). Vegetation tends to influence predation of bird nests by affecting both access of predators and visibility of nests (Chalfoun & Martin 2009, Klug *et al.* 2010). Nests located in areas with dense vegetation are difficult to find, especially for visually oriented predators, while nests located higher in vegetation are inaccessible to ground foraging predators. Parameters of vegetation likely have effects at both macro- and microhabitat scales. Thus, access of predators to bird nests depends on overall habitat type and nest position (Reidy & Thompson 2012). Indeed, nest type and location appear to significantly influence predation rate, which is usually higher for ground nests in primary tropical lowland rainforests (Colombelli-Negrel & Kleindorfer 2009, Bobo & Waltert 2011, Djomo *et al.* 2014a).

In this study, we focused on a tropical forested altitudinal gradient on Mt. Cameroon in West-Central Africa with the aim to test a hypothesis that there is an increase in avian nest survival rate with elevation as a result of decreasing predation pressure. For the purpose of this hypothesis, we investigated altitudinal variations in vegetation structure and linked this to daily survival rates of artificial avian nests. We tested for differences in daily survival rates of artificial nests between elevations, and placed three sets of nests; cup-shrub (henceforth shrub nest), cup-ground and bare-ground to test for interactions between elevation and nest placement. Artificial nest experiments have their limitations and are therefore not necessarily a perfect proxy for how

well birds are reproducing in their natural habitats. These limitations may be due to the fact that predators perceive artificial nests differently probably due to the attractiveness of egg type and human odour on nests which can act as a deterrence to certain olfactory predators such as mammals or snakes (Thompson & Burhans 2004). These experiments can however still inform us about relative probabilities of predation which is very difficult to obtain by alternative approaches in tropical rainforests, as finding real nests is difficult under harsh tropical conditions.

MATERIALS AND METHODS

STUDY SITE. –This study was carried out on the south-western slope of the Mt. Cameroon National Park (4°10'2" N, 9°05'3" E), along a forested gradient relatively undisturbed by human activities. Mt. Cameroon is located on the Atlantic coast in the Gulf of Guinea in the Southwest region of Cameroon. It is part of an extensive volcanic chain of mountains called the Cameroon volcanic line (DeLancey & DeLancey 2000). Due to volcanic activity, the tree line in the montane forest on Mt. Cameroon, is at 2250 m asl instead of *ca.* 3000 m as on other mountains in the same mountain chain. This volcanic line has been recognized for its biological uniqueness, and is considered a ‘hotspot’ of biodiversity and endemism on a continental scale for a wide variety of taxa (Brooks & Thompson 2001, Fishpool & Evans 2001). Mount Cameroon is a typical tropical wet mountain (*sensu* McCain 2009) in a poorly studied region, and therefore, an excellent model for the purpose of this study.

We carried out our experimental study along this tropical altitudinal gradient spanning three forest types (lowland, mid-elevation and montane) in March 2012, November 2012, and February 2013. These periods correspond to the breeding seasons for most passerine birds in the region (Serle 1981). These forests differ in structural features and microclimate (Proctor *et al.*

2007). We found the pristine part of the lowland forest to start from 300 m asl, and this forest extends up to approximately 900 m asl. The forest here has a closed canopy, and understory is sparse. Average and maximum tree height are 16.8 m and 48 m, respectively. The mid elevation forest (or transition forest) between 900 m and 1600 m asl is quite degraded and patchy because of the intense activities of the African forest elephants (*Loxodonta cyclotis*). The herbaceous understory is quite dense because it receives more solar radiation. Average and maximum tree height are 11.8 m and 43 m, respectively. The montane forest is found above 1600 m asl, and has an extensive cloud cover, and frequent mists. Its understory is rather dense compared to the lowland forest with a relatively open canopy. Average and maximum tree height are 13.3 m and 45 m, respectively. Mature forest here is interspersed with forest in various stages of regeneration due to periodic lava flows. Above the tree line at 2250 m asl is a montane grassland dominated by the grass *Loudetia simplex*.

NEST PLACEMENT. –

We placed artificial nests at six different elevations spanning all forest types along the gradient. These elevations were: 350 m (data on nest predation at this elevation has already been published in Djomo *et al.* 2014a), 700 m, 1100 m, 1500 m, 1800 m and 2200 m asl respectively.

These artificial nests mimicked those of locally nesting species on Mt. Cameroon, and we placed three sets of them. We distinguished between shrub nests (about 1 m above ground), cup-ground nests (about 10 cm above ground), and bare-ground nests (0 cm above the ground). Apart from height of placement, the nests differed in presence of a cup. The cup was made of cotton material about 3 mm thick and of grey colour. The use of cotton material for the cup-nest might be potentially a flaw in the study design but the texture, softness and thickness of the material mimicked well that of birds in the area (see Djomo *et al.* 2014a), which frequently utilise plant

material, mosses and spider webs to construct their nests. Each artificial cup-nest was about 6 cm in diameter by 4 cm in depth and fixed to the vegetation. The bare-ground nest was a small depression in the soil mimicking in placement and type that of ground nesting birds, *e.g.*, Mount Cameroon Francolin *Francolinus camerunensis*.

At each point along each elevation, we placed a triplet of nests. We placed nests in different directions at each point changing the direction of nests from one point to the other (see Fig. S1 in Supplementary material). Each nest within the triplet was at least 10 m from the closest one. The distance between neighbouring triplets was at least 50 m. We placed in total 50 triplets of nests at each elevation making 150 artificial nests along a transect ~2.5 km long, except at 1800 m where we placed 126 nests due to logistic reasons. In total, we placed 876 artificial nests along the gradient. We found no indication of spatial dependence in nest fate among experimental nests. To find nests again during subsequent controls, we used a global positioning system (*Garmin GPSMAP 60 CX*). In each nest, we placed one fresh common quail (*Coturnix coturnix*) egg, and monitored nests after five and ten days. We considered a nest was depredated if the egg was absent or broken.

VEGETATION STRUCTURAL CHARACTERISTICS. – We collected stand structural data for the same six elevations and along the same transects on which artificial nests experiments were carried out (Figure S1 in Supplementary material; note, that botanical transects were slightly shorter if compared to those with experimental nests). Each elevation had a transect of 16 plots (circle with 40 m in diameter) 150 m apart. In total, there were 96 plots with a total area of 12.06 ha. We identified all trees (live and dead) with diameter at breast height (DBH, at 1.3 m) >10 cm and recorded their height within each plot. In total, we measured 5729 trees >10 cm DBH. To assess shading potential of the canopy, light transmitted through the canopy from hemispherical

186 photographs were taken at 1.8 m above ground at five fixed points within each plot (one in plot
187 centre and four in cardinal direction points 10 m apart from the centre, in total 480 photographs)
188 and quantified. The Nikon F9 digital camera with Nikkor fisheye lens was used. The obtained
189 photographs were converted to black and white bitmaps using automatic thresholding
190 implemented in SideLook 1.1 (Nobis & Hunziker 2005). Transmitted direct, diffuse, total solar
191 radiation, and canopy openness were calculated in the Gap Light Analyzer software (Frazer *et al.*
192 1999). The cover of herb and shrub layers was visually estimated over the entire plot area by the
193 same observer (M. Dančák) at all sites. We defined herbs as all non-woody plants rooted in the
194 soil and shrubs as all woody plants not exceeding the height of 4 m and with DBH < 10 cm
195 rooted in the soil and not classified as climbers. We then tested the relationship of tree density,
196 herb and shrub layer to the altitudinal gradient.

197 DATA ANALYSIS. – We estimated survival of nests as the proportion of artificial bare-ground,
198 cup-ground and shrub nests not depredated. Proportions of depredated nests after five and ten
199 days were used to calculate daily survival rates (DSR, Mayfield 1975). We used analysis of
200 covariance (ANCOVA) to test the effect of elevation on DSR within each nest type. We built a
201 model in which DSR was the response variable with elevation as a continuous explanatory
202 variable and nest type as factor. We used one-way analysis of variance (ANOVA) to test the
203 relationship of structural parameters of vegetation to the altitudinal gradient, with elevation as
204 categorical predictor variable and canopy openness, tree density, shrub layer, and herb layer
205 coverage as response variables. We used average values of structural parameters of vegetation
206 for different elevational bands to assess their effects on DSR of avian artificial nests across
207 elevations. We performed analyses separately for each nest type. In all cases, we built a maximal
208 model containing DSR of particular nest type as response variable and all four vegetation

parameters as explanatory variables. We then reduced the models using backward elimination of the term with maximum p-value. Each step of elimination procedure was justified by comparing change of deviance between the models by *anova* function. We provide results of minimum adequate models. Analyses were done using the R software version 3.1.1 (R Development Core Team 2014).

RESULTS

DAILY SURVIVAL RATE ALONG THE GRADIENT. – Out of 876 artificial nests deployed, 646 (73.7%) survived along the altitudinal gradient (for details see Table 1). The *ANCOVA* analysis revealed no overall effect of elevation on DSR ($F_{1,12} = 0.03$, $p = 0.861$). However, the model revealed a significant elevation-nest type interaction ($F_{2,12} = 5.61$, $p = 0.019$). Therefore, we tested the effect of elevation on DSR for each nest type separately, using regression analyses. We found no significant effect of elevation on DSR on bare-ground ($t = 1.56$, $p = 0.194$, $r^2 = 0.38$), and cup-ground nests ($t = 0.76$, $p = 0.492$, $r^2 = 0.13$; Fig. 1). However, the effect of elevation was significant and negative on shrub nests ($t = -4.36$, $p = 0.012$, $r^2 = 0.83$; Fig. 1). In addition, survival rate differed among nest types ($F_{2,12} = 23.76$, $p < 0.001$), see Fig 2. The *post-hoc* analysis (*Tukey HSD test*) revealed significant differences between bare-ground and shrub nests ($p = 0.006$) as well as between bare-ground and cup-ground nests ($p < 0.001$), however we found no difference between cup-ground and shrub nests ($p = 0.237$).

VEGETATION STRUCTURAL PARAMETERS ALONG ELEVATIONS. – The forests on Mt. Cameroon differ in stand structure, canopy openness and light availability (Fig. 3). Herb layer density ($F_{5,90} = 24.8$, $p < 0.001$), and canopy openness ($F_{5,471} = 66.9$, $p < 0.001$), were lowest at lower elevations in the lowland forest, increasing with elevation, and then declined towards the

treeline at 2250 m asl. The highest value for canopy openness was in the mid elevation forest at 1500 m because of elephant disturbance. Shrub layer coverage ($F_{5,90} = 17.76, p < 0.001$) and tree density ($F_{5,84} = 5.45, p < 0.001$) on the other hand, were highest at lower elevations, decreasing with elevation, with the lowest values for shrub layer and tree density at 1500 m and 1800 m asl respectively.

EFFECT OF ENVIRONMENTAL VARIABLES ON DSR. –

Bare-ground nests. – The minimum adequate model explained almost all variance (99.9%), $F_{3,2} = 5266, p < 0.001$ and contained herb layer, canopy openness, tree density. We found that DSR of bare-ground nests was significantly and positively influenced by coverage of herb layer ($t = 124.48, p < 0.001$) and tree density ($t = 32.66, p < 0.001$). In addition, DSR significantly decreased with increasing canopy openness ($t = -57.11, p < 0.001$).

Cup-ground nests. – The minimum adequate model explained 79.8 percent of variance ($F_{2,3} = 5.91, p = 0.091$) and contained canopy openness and shrub layer coverage. Both of them were positively related to DSR. We found a significant effect of canopy openness ($t = 3.44, p = 0.041$) and marginally non-significant effect of shrub layer ($t = 2.88, p = 0.064$) on DSR.

Shrub nests. – The minimum adequate model explained 81.5 percent of variance and contained only shrub layer ($F_{1,4} = 17.65, p = 0.014$). DSR of shrub nests increased significantly with increasing shrub layer coverage ($t = 4.20, p = 0.014$). Univariate correlations between DSR and particular environmental variables are provided in Table S1 in Supplementary material.

DISCUSSION

In this study, we compared survival of different artificial nest types relative to the same vegetation parameters, and found that overall daily survival rate of nests was quite high unlike in other tropical environments (Pangau-Adam *et al.* 2006, Boyle 2008, Sedláček *et al.* 2014).

However, Bobo & Waltert (2011) using artificial nests also found a high nest survival (80%) in the same region as Mt. Cameroon. It seems birds have a high nesting success in this region or this might be attributed to the use of artificial nests, as quail eggs used in our study and chicken eggs used in Bobo & Waltert (2011) are bigger than common passerine eggs in the region, and therefore not accessible to small mouthed predators (Degraaf & Maier 1996, Oliveira *et al.* 2013). Also, artificial nests don't smell like real nests to predators, which might lower their attractiveness to predators (Whelan *et al.* 1994, Clark & Wobeser 1997, Rangen *et al.* 2000). Other factors such as different predator communities could also be a possible reason for intra-tropical differences in predation rates. These differences can also be as a result of different predominance of visual and olfactory predators such as birds and snakes but to better understand predation by olfactory predators like snakes, real nests should be used. Unfortunately, we were not able to estimate composition of predator communities in the field, and finding real nests in landscape-scale studies in the tropics is impractical (Villard & Pärt 2004).

Detailed information on nest predators in African forests is still scarce. Studies on avian nest predation rate in other tropical forests (Boyle 2008, Reidy 2009), and notably in the same region as Mt. Cameroon (Bobo & Waltert 2011), found small and medium-sized predators belonging to mammals, reptiles and other birds, to be the most common nest predators. Small and medium-sized predators of these three categories that can be found on Mt. Cameroon include rodents, *e.g.*, *Hybomys badius*, *Myosciurus pumilio*, *Cricetomys gambianus*, *Atherurus africanus* (Bobo & Waltert 2011, Kingdon *et al.* 2013), reptiles, *e.g.*, *Varanus ornatus*, *Lamprophis virgatus* (Gonwouo *et al.* 2007), and bird species with high abundances whose diet comprise larger invertebrates and small vertebrates, *e.g.*, *Lanarius* spp. (Djomo *et al.* 2014b). Thus, we assume that these species were likely active predators of our nests too.

We found no effect of elevation on daily survival rates of ground nests (both bare-ground and cup-ground). There was however a significant and negative effect of elevation on the survival of shrub nests, which revealed that elevational patterns in nest survival differed among nest types on Mt. Cameroon. Bare-ground nests had the lowest survival rate along the gradient but showed a positive relationship with elevation even though this was not significant. This positive trend was mostly due to the fact that survival rate of bare-ground nests was greatest at the highest elevation, 2250 m asl, which corresponds to the forest edge. Interestingly, at this elevation, the survival rate of shrub nests significantly decreased, and was even lower than for bare-ground nests. It has been shown that nest loss can be higher at habitat edges *e.g.*, due to more frequent animal movements, with shrub nests more depredated than ground nests (Gibbs 1991, Pangau-Adam *et al.* 2006). Such an edge effect might play a role also in our study as the uppermost location of our gradient is situated at the border between the montane forest and savannah (*cf.* Sedláček *et al.* 2014). The tree line apparently affects the structure of vegetation, and composition of predator community is likely influenced by migration from forest to savannah and back along the edge. Unfortunately, at this point, data on nest predators is not available for our study area, and thus we can only speculate about the causes.

The decreasing survival rate of shrub nests – the most common nest type among members of the avian communities along the gradient (see Fig. S2 in Supplementary material) – might be attributed to generally high abundances of such species in the montane forest (see Djomo *et al.* 2014b). Indeed, higher densities of particular species can make their nests an attractive target for predators (Reitsma 1992, Oro *et al.* 2006). In addition, low survival rate of shrub nests can be attributed to decreasing shrub cover with elevation making the nest more exposed. On the other

hand, bare-ground nests can be less visible in edge habitats as those are frequently rich in dense undergrowth vegetation.

As visibility and accessibility of bird nests are influenced by vegetation layers, we investigated the altitudinal variation of vegetation layers and how this affects artificial nest survival. The dense herb layer coverage and tree density related to increased daily survival rate of ground nests, while increased shrub layer coverage related to increased survival rate for shrub nests along the gradient. These observations suggest that different vegetation layers or combinations of them affected survival of different nest types tested in our study. Particularly, that always the layer in which the nest was placed was the most important (the importance of tree density can be attributed to its effect on lower layers). It implies that elevational changes in vegetation structure affect probability of nest success at particular nest locations presumably via changes in nest visibility and accessibility, which are indeed important factors affecting survival of bird nests (Martin & Joron 2003, Seibold *et al.* 2013). This highlights the importance of differential nest placement for breeding success of birds. Further investigation is therefore necessary to find out if the distribution of both visually oriented and olfactory predators (*e.g.*, birds and snakes) relates to vegetation layers.

When we compare patterns of artificial nest survival on Mt. Cameroon with those of other studies in other forests, only bare-ground nests on Mt. Cameroon showed a similar trend to that for bare-ground nests in the temperate zone (Seibold *et al.* 2013), where bare-ground nests survived less in areas with decreased near ground vegetation and increased tree cover. For artificial shrub nests on the other hand, nest survival rate on Mt. Cameroon was higher than that of the only other study that endeavoured to estimate predation risk of artificial avian nest along elevations in the neotropics (Boyle 2008). Boyle (2008) revealed a linear increase in nest

survival with elevation, with lowest values at low-intermediate elevations. Besides differences in egg type between Boyle (2008, canary egg) and this study (quail egg), differences in the extent and types of forests on both altitudinal gradients, can probably explain the observed differences in survival of similar nests (*i.e.*, our shrub nests and Boyle's nests) on both tropical mountains. Quail eggs are larger than canary eggs and have a thicker shell. These put their contents out of reach for small-mouthed predators (Degraaf & Maier 1996, Oliveira *et al.* 2013). Also, the longer forest gradient (30 m asl to 2906 m) in Boyle (2008) compared to Mt. Cameroon (300 m asl to 2250 m) with possibly different vegetation structures, could lead to differences in predator communities which affected nest survival differently.

In conclusion, our results cannot support an overall increase in artificial nest survival rates along the elevation on Mt. Cameroon. Such an expectation was based on two points: (i) generally decreasing complexity of vegetation along tropical elevations and (ii) generally decreasing diversity of animal taxa (of which predators) with elevation. Instead, our results show that different vegetation layers or combinations of them affected different nest types. Shrub nests on Mt. Cameroon have a high survival rate at low elevations with increased shrub layer coverage, while ground nests have a high survival rate at the uppermost elevation with a high herb layer coverage. These observed differences in survival of different nest types relative to the same vegetation parameters might be attributed to elevational variation of forest layers which affect visibility of nests. This study is a significant step forward in our understanding of spatial variation in breeding success of birds in tropical forests. A replication of nest predation risk studies on other Afrotropical altitudinal gradients is required to further our understanding of mechanisms underlying selection pressures on bird populations.

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530 TABLE 1. *Proportion of artificial avian nests depredated at different locations after five and ten*
 531 *days along an altitudinal gradient on Mt. Cameroon.*

Elevation (m)	Day	Nest location		
		Bare-ground	Cup-ground	Shrub
350	5	0.34	0.1	0.04
	10	0.56	0.26	0.16
700	5	0.24	0	0.02
	10	0.48	0.04	0.08
1100	5	0.22	0.1	0.14
	10	0.46	0.22	0.24
1500	5	0.4	0.04	0.12
	10	0.46	0.1	0.34
1800	5	0.38	0	0.07
	10	0.44	0.05	0.1
2200	5	0.16	0.08	0.08
	10	0.24	0.16	0.38

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535 FIGURE 1. Elevational changes in daily survival rate among types of artificial avian nests on
536 Mt. Cameroon. Bare-ground nests are indicated by open squares (\square), cup-ground nests by open
537 circles (\circ) and shrub nests by filled circles (\bullet). Only shrub nests showed a significant pattern (p
538 = 0.012) as indicated by a regression line.

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540 FIGURE 2. Differences in daily survival rate among types of artificial avian nests on Mt.
541 Cameroon. Only Bare-ground nest survival differed significantly ($p < 0.001$) from the two
542 remaining nest types.

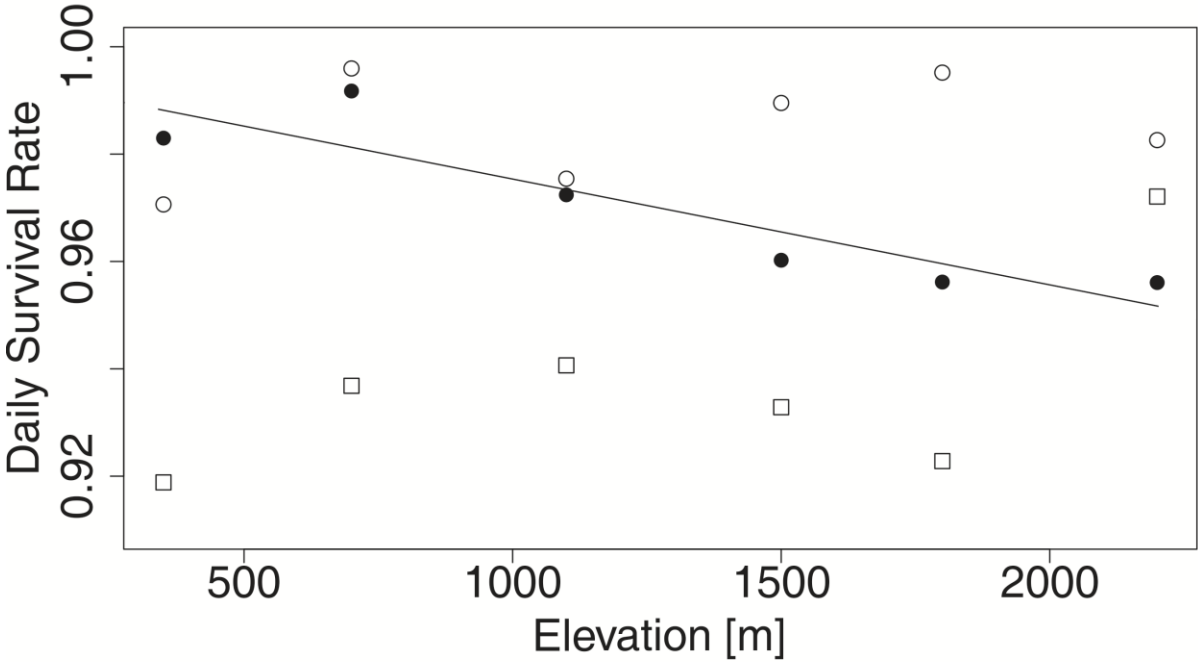
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544 FIGURE 3. Comparison of canopy openness, herb layer, shrub layer and tree density between six
545 elevations on Mt. Cameroon. Boxes represent 25–75 percent of values, points near the middle of
546 the box are the medians, boxes indicate the 1.5 interquartile range, and dots are outliers.

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548 FIGURE 1.

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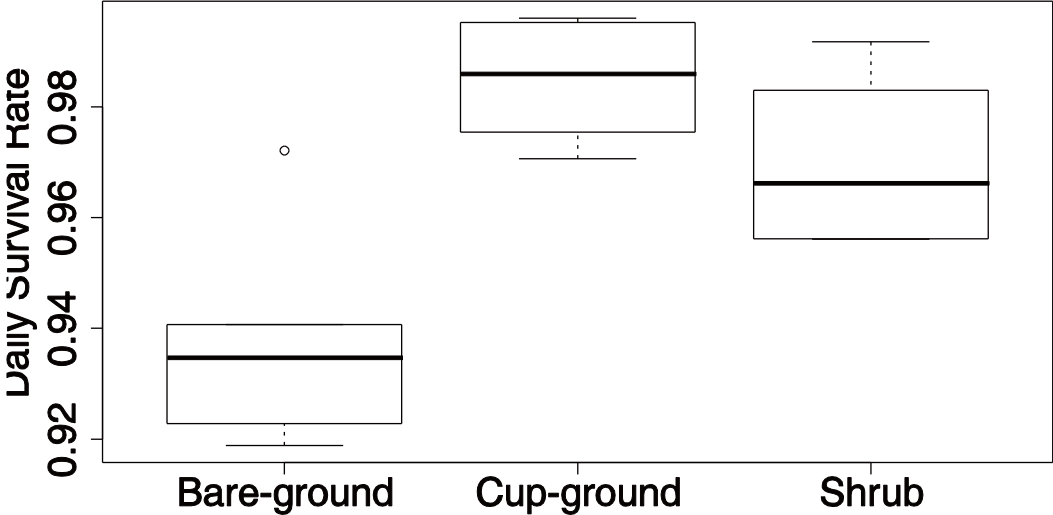
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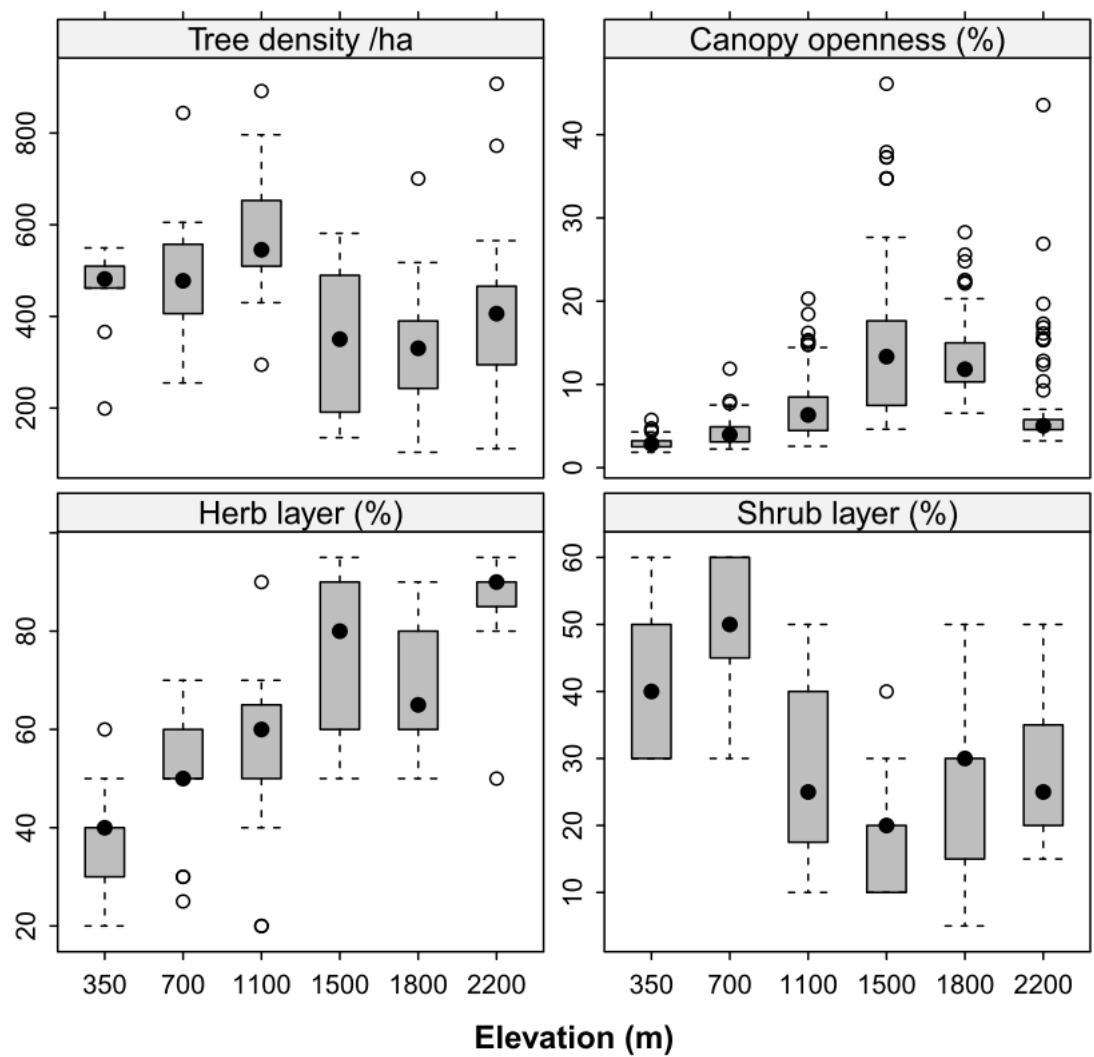
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569 Table S1. Correlation coefficients (r) between daily survival rate of artificial nests and particular
 570 vegetation parameters on Mt. Cameroon. Significant values are given in bold and the level of
 571 significance is indicated with an asterisk. Bare-grd = Bare-ground, Cup-grd = Cup-ground.

	Shrub layer	Canopy openness	Herb layer	Tree density
Bare-grd nests	-0.22	0.06	0.78*	-0.07
Cup-grd nests	0.001	0.35	0.38	-0.52
Shrub nests	0.91**	-0.72	-0.82*	0.59

572 * p< 0.05, ** p< 0.01

573

APPENDIX

FIGURE S1

Study design showing artificial nest layout and vegetation sampling along a transect at each elevation on Mt. Cameroon. Nests varied systematically in placement from one point to another. Bare-ground nests are indicated by open squares (\square), cup-ground nests by open circles (\circ) and shrub nests by filled circles (\bullet).

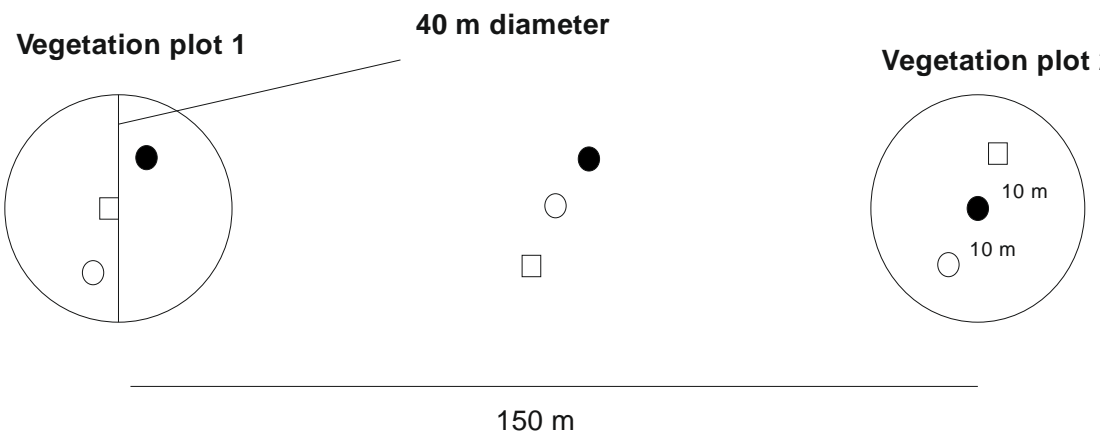
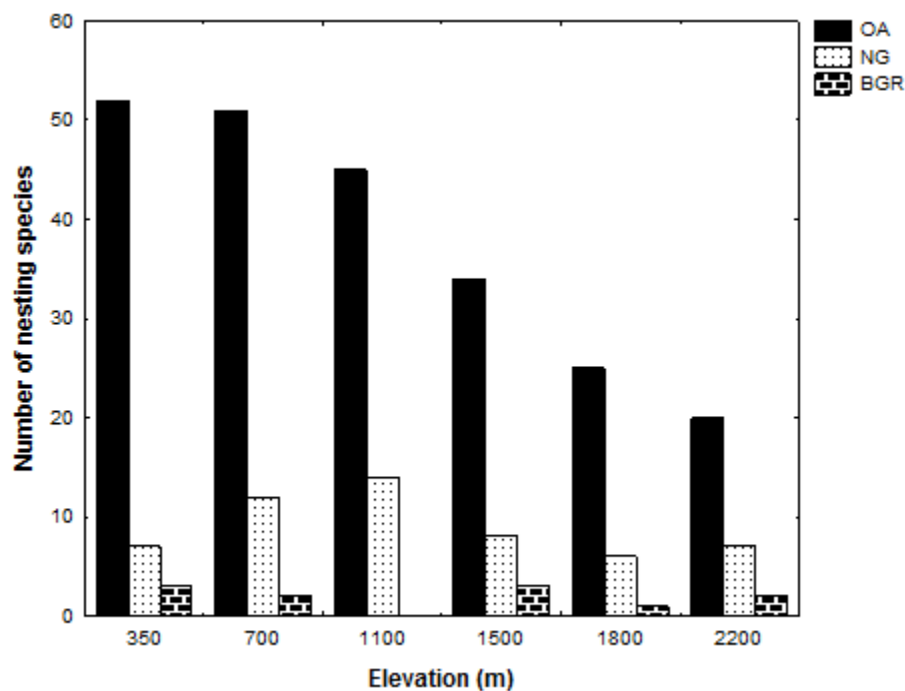


FIGURE S2. Number of bird species according to nest types along an altitudinal gradient on Mt. Cameroon. Nest types were classified according to (Fry & Keith 1986/2002) and assemblage compositions at particular elevations were based on field checklists (Hořák et al. unpublished data). OA stands for Open arboreal nesters (represented by shrub artificial nests); NG stands for Near ground nesters (represented by cup-ground artificial nests); BGR stands for bare-ground nesters (represented by bare-ground artificial nests).



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CHAPTER 3

Djomo N. E., Munclinger, P., Synek, P., Sedláček, O., Albrecht, T., Ferenc, M. & Hořák, D. 2015. Haemosporidian diversity, host trait importance, and high host-parasite specificity in an avian assemblage of a tropical forest on Mount Cameroon. *Manuscript*.

Hemosporid diversity, host trait importance and high host-parasite specificity in an avian
assemblage of a tropical forest on Mount Cameroon

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ABSTRACT

Vector-borne pathogens such as haematozoan parasites impose high evolutionary costs on their avian hosts, and can adversely affect host distribution and life history traits. In this study, we focused on rates of parasitism within an avian assemblage on Mount Cameroon in tropical Africa to achieve four main objectives: (i) describe diversity and phylogenetic relationships between Haemosporid avian parasites, (ii) estimate prevalence of parasites between members of a bird assemblage, (iii) determine the influence of host-specific traits (nest height, foraging strata, body size and host abundance) on observed prevalence and parasite richness in the hosts, and (iv) describe host-parasite reciprocal specializations in the assemblage. We used bipartite network analysis to estimate the level of specialization between parasite lineages and their avian hosts. We identified 36 mitochondrial cyt b lineages, and found a low level of prevalence (16.4 %). We found that host abundance and preference for ground foraging stratum significantly influenced prevalence and parasite richness. We found a highly specialized network-wide assemblage, with parasites and their hosts highly specialized for each other. We argue that the low prevalence on Mt. Cameroon can be attributed to the scarcity of ornithophilic vectors, which prefer feeding at ground level and on densely populated hosts. The highly specialized host-parasite assemblage on Mt. Cameroon may be due to the isolated nature of the habitat, and great phylogenetic distances between bird hosts which does not favour host shifts.

Keywords: host-parasite interactions, prevalence, host traits, reciprocal specializations, Mt. Cameroon.

INTRODUCTION

Avian parasites constitute a potent selective force which affects the distribution and evolution of their hosts (Freed et al. 2005, Schemske et al. 2009). Avian haemosporida are of particular interest because they are known to have caused extinctions of certain bird species (van Riper et al. 1986), and impose high evolutionary costs to their hosts by affecting their life histories (Hamilton and Zuk 1982, Lachish et al. 2011). Thus, understanding transmission dynamics and evolutionary relationships of these parasites with their hosts is of particular importance to avian ecology and conservation.

Ecological and evolutionary processes that affect host populations also affect their parasites, and these lead to a complex host-parasite system in which each component evolves strategies to outcompete the other (Horwitz and Wilcox 2005). Hosts evolve complex immune proteins to resist parasite infections and improve their fitness (Schmid-Hempel 2009, Lachish et al. 2011), while parasites on the other hand evolve immune evasion proteins such as glycoconjugates that enable them evade the host's immune defences in order to survive (Cummings and Turco 2009). This evolutionary arms race is one that leads to different levels of host specificity of parasites. Evolution should then select for host life history traits that increase host fitness or lifespan (Poulin and Mouillot 2003).

Previous studies have shown that host traits such as, foraging strata, host abundance, nest location and body size, influence prevalence of haemosporida in birds differently (Garvin and Remsen 1997, Fecchio et al. 2011, Gonzalez et al. 2014, Lutz et al. 2015). This suggests there is a spatial variation in feeding preferences of dipteran vectors which transmit these haemosporida, with some preferring to feed at a higher spatial level on nests located toward canopy or on host species that forage toward the canopy while others prefer feeding at ground level (Bennett and

Fallis 1960, Černý et al. 2010). Also, host species with large bodies or high abundances usually suffer from higher infections (Brown, et al. 2001) probably because they attract more dipteran vectors by producing more CO₂ and olfactory cues such as kairomones known to attract vectors (Anderson and May 1981, Logan et al. 2010) or that high abundances lead to increased encounter rates with vectors.

Vector transmission and spatial feeding preferences can also be attributed to their sensitivity to environmental conditions because they require a source of water for their development (Njabo et al. 2009, Valkiūnas 2005). Thus, haemosporidian prevalence in host populations is related to rainfall patterns or availability of water sources (Wood et al. 2007) which differ spatially, especially between tropical environments (Malhi and Wright 2004). Similarly, tropical environments also differ in host breadth which implies different host specificity patterns, with specialist parasites usually more prevalent than generalists (Medeiros and Ellis 2014). Understanding therefore host-parasite interactions, and effects of host traits on prevalence in different tropical environments is crucial but still under explored. Of particular importance are studies in insular tropical habitats such as those on tropical mountains. These insular tropical habitats provide relatively stable and closed systems which shed light on mechanisms by which parasites structure host assemblages. So far, only few studies have explored host-parasite interactions, and effects of host traits on prevalence in insular tropical habitats (Apanius et al. 2000, Loiseau et al. 2012, Zamora-Vilchis et al. 2012), especially in Africa (Lutz et al. 2015). Such habitats, however, present unique ecological conditions (e.g. long term stability and isolation), which can lead to highly specific associations (Apanius et al. 2000). In this study, we focused on rates of parasitism within an avian assemblage on Mt. Cameroon in tropical Africa. To our knowledge, this is one of the first on an Afrotropical mountain (but see

Beadell et al. 2009). Our general goals were to: (i) describe diversity and phylogenetic relationships between Hemosporid avian parasites, (ii) estimate prevalence of parasites between members of a bird assemblage, (iii) determine the influence of host-specific traits (nest height, foraging strata, body size and host abundance) in relation to probability of infection, and (iv) describe host-parasite reciprocal specializations in the assemblage.

MATERIALS AND METHODS

Field work and bird traits

This study was carried out in the Mt. Cameroon National Park (4° 08 N 9° 07 E), in West-Central Africa. Data were collected during four field sessions in November 2011, March 2012, November 2012 and August 2013. We used mist netting to sample birds and established a transect 200 m long along which we mounted 16 mist nets (12 m, 16 x 16 mm mesh; Ecotone, Poland). We opened the nets at 06:00 am and closed them at 18:00 pm for three days. All birds caught were identified, sampled and released. We estimated body mass of all individuals using a spring scale to the nearest 0.5 g. A small amount of blood (50 – 100µl) was taken from the brachial vein of all birds for laboratory analysis. The blood was preserved in 96% ethanol.

For all caught species, we collected information on specific traits (body size, nest height, foraging strata and host abundance). We estimated body size of each species by averaging the masses of all individuals within a species. For foraging strata, we estimated from the Hand book of Birds of Africa series (Fry and Keith 1986-2004) the proportion of time each species spent foraging at particular spatial levels and used time spent on ground as variable for foraging height. From the same source, we obtained information on nest height for each species. We determined the abundance of each host species as the total number of individuals caught during mist netting.

Parasite detection

All blood samples were dried in the laboratory and DNA was extracted using DNeasy® Tissue Kit (Qiagen). Parasites were detected following the nested PCR protocol (Hellgren et al. 2004), which enables to distinguish *Plasmodium* or *Haemoproteus* infections from *Leucocytozoon* ones using genera-specific nested primers which amplify the mitochondrial cytochrome b gene. Only samples that were positive after two nested PCR runs were sequenced using primers HaemF designed for *Plasmodium* or *Haemoproteus* or HaemFL designed for *Leucocytozoon* (Hellgren et al. 2004). Parasite lineages were identified and classified according to Genbank and Malavi databases (see Table S1 in supplementary material). All new lineages differing by one or more substitutions from the sequences deposited in GenBank were sequenced also from the 3'-end with primers HaemR2 designed for *Plasmodium* or *Haemoproteus*, and HaemR2L designed for *Leucocytozoon* (Hellgren et al. 2004). We named new lineages starting with two letters; the first from the avian host genus, and the second from the avian host species. These letters were followed by numbers. Sequences of new lineages were deposited in GenBank and Malavi databases. See supplementary material for accession numbers.

Phylogenetic analyses of parasites

We used the Maximum Likelihood method to construct the phylogenetic tree of parasite lineages on Mt. Cameroon. The evolutionary history was inferred by using the Tamura-Nei+G model in which the tree with the highest log likelihood (i.e. lowest AIC) is chosen. The initial trees for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. A discrete Gamma distribution was used to model evolutionary rate differences among sites. The analysis involved

all 36 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All positions containing gaps and missing data were eliminated. There were a total of 440 positions in the final dataset. Phylogenetic analyses of parasites were conducted in MEGA 6 software.

STATISTICAL ANALYSES

Parasite prevalence influenced by host life history traits

To avoid bias in detecting prevalence in host species with different abundances, Jovani and Tella (2006) suggest using host species with a minimum sample size of about 15 individuals. Due to limitations of our dataset, we chose 13 as minimum sample size and believe this to be enough. We also compared prevalence between well represented host families, i.e., host families with at least 20 individuals sampled. We tested the influence of all four host traits collected on prevalence and parasite lineage richness. To control for phylogenetic non-independence in trait values, we tested for the effect of the taxonomic family membership of species as a part of the analyses. We performed ANOVA with family as an explanatory factor. Then we used residuals from this analysis for further calculations. We then built maximal models with residual values of traits as continuous explanatory variables with prevalence and parasite lineage richness as response variables. We generated minimum adequate models (MAMs) by backward elimination of the non-significant terms. Each step of elimination procedure was justified by comparing change of deviance between models by *anova* function. We provide results for the MAMs. Analyses were done using the R software version 3.1.1 (R Development Core Team 2014).

Parasite-host reciprocal specializations

To estimate the level of specialization between parasite lineages and their avian hosts, we used bipartite network analysis in the R package “bipartite” (Bluthgen et al. 2006, Svensson-Coelho et al. 2014). Bipartite network analysis focuses on webs consisting of only two levels such as host-

154 parasite webs. Nodes in such networks represent species, and links connect hosts with parasites if
155 they interact. The fewer links that emerge from a particular parasite, the more specialized it is
156 with respect to host breadth. The width of each link is proportional to the abundance of each
157 interaction, and the width of each node is proportional to the abundance of the host species and
158 parasite lineage (Svensson-Coelho et al. 2014).

159 We used two indices as network descriptors; network-wide specialization (H_2') and
160 species level specialization (d'). Indices summarize different aspects of ecological patterns
161 (Dormann et al. 2014). The network-wide specialization H_2' is the standardized two-dimensional
162 Shannon index of entropy, and estimates specialization of an entire assemblage. It is used for
163 comparing consumer-resource networks of different sizes, dimensions, and evenness of
164 interactions because it is robust to changes in these potentially confounding factors (Bluthgen et
165 al. 2008; Dormann et al. 2008). It ranges from 0 (all species interact to equal degrees) to 1 (all
166 interactions are cases of perfect reciprocal specialization). However, on its own, it gives no
167 insight into knowing whether parasite lineages tend to use fewer host species on average or
168 whether host species tend to harbor fewer parasite lineages. This information is given by the
169 species level specialization index d' , which is the standardized Kullback-Leibler index of
170 entropy. It gives a measure of specialization for each species within an assemblage (Bluthgen et
171 al. 2006). It ranges from 0 (generalist) to 1 (specialist).

172 As we intended to compare our results with those of the only other study that used
173 bipartite network analysis to determine avian host-parasite specialization in a tropical forest
174 (Svensson-Coelho et al. 2014), we ran two separate analyses. First, for a proper comparison with
175 Svensson-Coelho et al (2014), we made a network analysis with only *Haemoproteus* and
176 *Plasmodium* lineages because the authors studied only these two genera. We later on used all

three parasite genera (*Haemoproteus*, *Plasmodium* and *Leucocytozoon*). We considered our haplotypes as evolutionary lineages because they fulfilled the criteria for the definition of evolutionary lineages according to Svensson-Coelho et al. (2013), i.e., haplotypes that were separated from each other by four mutations or less (~0.6%) were abundant and segregated onto different host species (see Figure S1 in Supplementary material).

Assemblages that differ in diversity may not be directly comparable in a bipartite analysis without generating null models which create random matrices with the same diversity and connectance as the original matrix to estimate the expected pattern under random interactions, and to calculate standardized effect sizes (SES) for mean comparisons (Gotelli and Graves 1996, Vazquez et al. 2007, Svensson-Coelho et al 2014). We created 10,000 null matrices in the R package “bipartite”. Network-wide specialization and d' for each of these 10,000 matrices was estimated yielding a null distribution of index values. The SES gives a measure of the strength (number and intensity of interactions) of the host-parasite associations in the assemblage under study (Cohen 1977). Therefore, the higher the value of SES, the greater the number of host-parasite interactions in an assemblage. By comparing observed values to null models within our assemblage, we determined whether interactions were significantly structured with respect to host and parasite specificity.

RESULTS

Phylogenetic analysis of parasites

We screened a total of 1044 birds representing 76 species and 23 families. We identified 36 mitochondrial cyt b lineages of which 20 were new. The phylogenetic analysis of the haemosporidian cyt-b sequences revealed three highly supported genera which could each be

subdivided into two clades with *Haemoproteus* and *Plasmodium* being phylogenetically closer compared to *Leucocytozoon* (Figure 1).

Parasite diversity and prevalence in relation to host traits

One hundred and fifty eight birds comprising 21 species and 11 families were infected (16.4%) with blood parasites of either *Plasmodium*, *Haemoproteus* or *Leucocytozoon*. *Haemoproteus* (7.3%) was the richness parasite genus with 14 lineages of which 7 new, while *Leucocytozoon* (6.2%) had 13 lineages of which 11 new, and *Plasmodium* (2.9%) had 9 lineages of which one new. Prevalence between well-represented avian host families was significantly different ($\chi^2 = 50.01$, $df = 10$, $p < 0.001$), with Turdidae, Nectarinidae and Pycnonotidae being most infected while Cisticolidae, Estrilidae and Sylviidae had no infections (Table 1). This revealed a strong effect of taxonomic family membership of species. Data for each host species examined is summarized in Supplementary Table S2. The minimum adequate models contained host abundance ($Z = 3.68$, $P < 0.001$), and time spent foraging on ground ($Z = -3.05$, $P = 0.002$) as explanatory variables which significantly influenced prevalence, while parasite lineage richness was significantly influenced by only host abundance ($Z = 3.73$, $P < 0.001$).

Parasite-host reciprocal specialization

Bipartite network analysis revealed a highly specialized assemblage on Mt. Cameroon with few cases (five *Haemoproteus* and one *Plasmodium*) of perfect reciprocal specialization (Figure 2a). When we included *Leucocytozoon* into the network, the number of cases of perfect reciprocal specialization did not change, revealing that *Leucocytozoon* lineages shared more host species than *Plasmodium* and *Haemoproteus* lineages (i.e. the 13 *Leucocytozoon* lineages shared six host species while the nine *Plasmodium* lineages shared eight host species and the 14 *Haemoproteus* lineages shared 16 host species, Figure 2b). Overall, parasites infected few host species while

birds were good hosts harbouring many parasite lineages. Network-wide specialization (H_2') was significantly higher than expected by chance ($p=0$) implying parasites and their hosts do not interact at random on Mt. Cameroon. Models generated from 10,000 null matrices predicted a high index value for H_2' based on its range from 0 to 1 ($H_{2null}' = 0.69 \pm 0.07$), and this corroborated the observed values for H_2' ($H_2' = 0.927$, Figure 3a). The standardized effect size for H_2' also revealed a strong network-wide specialization ($SES_{H_2'} = 3.16$). Species-level specialization (d') based on its range from 0 to 1 revealed that, hosts were more specialized than parasites (host $d' = 0.84$, parasite $d' = 0.79$, Figure 3b), but the number and intensity of interactions at species level given by Cohen's d' was higher for hosts (3.83) than parasites (3.72) showing that on average, host species interacted with more individuals of parasite lineages than parasites lineages with individuals of host species. Mean comparisons between the null and observed values for d' with 95% confidence intervals using t -tests significantly differed for both parasites ($t = 14.92$, $df = 21$, $P < 0.001$) and hosts ($t = 16.01$, $df = 19$, $P < 0.001$).

DISCUSSION

The majority of lineages identified in our study were novel parasite lineages indicating that the area should be of special interest to researchers studying vector-borne parasitic infections. No parasite lineage within any of the three genera studied occurred in high frequency suggesting high host fidelity or host constraint, presumably as a result of low host-switching of parasites over recent evolutionary history. Beadell et al. (2009) who studied host-parasite associations and evolutionary relationships from several sites in West Africa, found that certain parasite lineages were constrained to few host families over recent evolutionary history. This host constraint on

Mt. Cameroon can also be because competent vectors of these novel lineages are quite scarce in on Mt. Cameroon.

Our results also show that the overall prevalence of avian Hemosporid parasites on Mt. Cameroon is over 16%, which is rather low if compared to other tropical environments (Lacorte et al. 2013, Svensson-Coelho et al. 2013, Lutz et al. 2015). Such a low prevalence can be attributed to the scarcity of ornithophilic vectors on Mt. Cameroon, which is surprisingly relatively dry despite the fact that it is situated in the wettest region of Africa (Debundscha), and receives over 10,000 mm of rainfall annually (Cable & Cheek 1998). This water scarcity is mostly because the soil is dominated by porous andisols derived from volcanic ash (Proctor et al. 2007), and tends to absorb rain water immediately after rainfall, leaving almost no water sources, in which dipteran vectors can breed. Thus, these vectors are forced to breed in small pools found in temporary streams and trees. We suggest that the low availability of permanent water pools on Mt. Cameroon affects the ecology of ornithophilic vectors thereby influencing transmission dynamics of haemosporida.

Our results show that transmission and richness of haemosporida on Mt. Cameroon were significantly influenced by two life history traits of hosts; host abundance and preference for foraging at ground level. Other studies in the tropics have shown that foraging strata of birds has a significant influence on parasitism, with prevalence either increasing (Lutz et al. 2015) or decreasing (Svensson-Coelho et al. 2013) with height of foraging strata. Differences in prevalence with foraging strata can be attributed to different feeding preferences of vectors, with some ornithophilic vectors preferring ground level habitats while others prefer the canopy (Černý et al. 2010). It seems therefore on Mt. Cameroon, ornithophilic vectors mostly prefer ground

level habitats. However, further investigation into the feeding preferences of ornithophilic vectors on Mt. Cameroon is required.

Parasitism also increased with host abundance showing that host population density is critical for the maintenance of parasite lineage richness. Host species living in high densities usually present high parasite lineage diversity (Morand 2015). This is probably because CO₂ and olfactory cues such as kairomones are produced more intensely in areas with dense host populations as host density is often positively correlated with parasite prevalence and richness (Anderson and May 1981, Brown et al. 2001). The effects of host abundance on parasite prevalence can also be explained by the fact that parasite transmission is frequency-dependent (Keesing et al. 2006). Abundant hosts lead to high host-to-vector transmission rates as a result of higher encounter rates (Brown et al. 2001). The higher the number of individuals of a particular host, the higher the risk of infection through “amplification effects” (Keesing et al. 2006). The higher encounter rates of host with vectors also lead to higher encounter rates of parasites with hosts thereby affecting host specialization (Medeiros and Ellis 2014). This observation of increased parasite lineage richness with host abundance in our sample could probably be the result of sampling bias because the most highly infected avian species were also the most abundant, but given that we determined prevalence and richness of parasite lineages in only well sampled host species, we believe this bias was minimized.

Reciprocal specialization between parasites and their hosts as revealed by bipartite network analysis showed that both hosts and their parasites on Mt. Cameroon are highly specialized. This might imply the few infected birds on Mt. Cameroon recently speciated and have higher probabilities of infection because of still adapting immune systems to parasites. As an example, when we consider the 12 greenbul species (Pycnonotidae) sampled in our study,

only two were infected with haemosporida, *Andropadus tephrolaemus* and *Phyllastrephus icterinus*, with the former being a montane species having prevalence of 50%, while the latter a lowland species with prevalence of 7%. Fjeldsa° et al. (2007) showed that these two species recently speciated compared to other greenbul species, with speciation of *P. icterinus* anterior to that of *A. tephrolaemus*. With time, the ranges of recently diversified montane species gradually shifts toward the more productive lowland forest as they adapt. That is probably why the prevalence of *P. icterinus* was much lower than that of *A. tephrolaemus* and only these two greenbuls were infected, but it should also be noted that the higher prevalence of *A. tephrolaemus* reflects a broader altitudinal range (see Djomo et al. 2014) which makes it encounter a greater diversity of vectors.

When we compared our study with that of Svensson-Coelho et al. (2014) who also determined parasite-host reciprocal specialization in a tropical forest in Ecuador, both the observed ($H'_2 = 0.927$) and null values ($H_{2null}' = 0.69 \pm 0.07$) of network-wide specialization (estimates of specialization of the entire assemblage) on Mt. Cameroon, were higher than in Ecuador, observed $H'_2 = 0.54$, and null models $H_{2null}' = 0.32 \pm 0.024$, with SES on Mt. Cameroon ($SES_{H'_2} = 3.16$) much lower than in Ecuador ($SES_{H'_2} = 9.4$). On the other hand, species-level specialization (d') revealed that both hosts and parasites on Mt. Cameroon (host $d' = 0.84$, parasite $d' = 0.79$) were more specialized than in Ecuador (host $d' = 0.44$, parasite $d' = 0.60$), whereas the number of interactions, Cohen's d' , in Ecuador were higher for parasites (Cohen's $d' = 4.93$) but lower for bird hosts (Cohen's $d' = 2.44$) than on Mt. Cameroon (host Cohen's $d' = 3.83$, parasite Cohen's $d' = 3.72$). These showed that specialization both at the level of the entire assemblage and at species level was greater on Mt. Cameroon with parasites interacting less, but bird hosts interacted more probably because these birds were infected with

more individuals of the same parasite lineages. The lower parasite lineages richness with high abundances on Mt. Cameroon, an insular habitat with limited dispersal options, compared to Ecuador is probably a result of an adaption to reduce extinction risk (Johnson 1998). One possible explanation for this observation is that phylogenetic distances between the birds in Ecuador are shorter (i.e. they are more closely related) than those in Africa (Jetz et al. 2012), and this has facilitated host shifts. Another explanation is that the multi-host parasites in Ecuador with broader host ranges have developed greater immune compatibilities with the phylogenetically more closely related hosts they encounter. Host range of haemosporida has been reported to be the main determinant of compatibility of haemosporida with hosts (Medeiros et al. 2013).

Another point worth mentioning here is the fact that richness of vectors most certainly differed between these two tropical forests. The water scarce environment on Mt. Cameroon is unfavourable for breeding of dipteran vectors while the water rich forest in Tiputini, Ecuador (Cisneros-Heredia 2006), is more favourable for the proliferation of vectors. A greater diversity of vectors most certainly implies an increased transmission of parasite lineages to vertebrate hosts because the higher the diversity of vectors, the higher the diversity of parasite lineages they can transmit (Nunn et al. 2005). Moreover, invertebrate host shifts in vector-parasite interactions are quite frequent in tropical forests (Njabo et al. 2010), meaning a small number of vectors are able to transmit a large number of parasite lineages. We should therefore expect to find that avian hosts living in an area with more vectors should also be infected with a greater number of parasite lineages.

In conclusion, we report new avian malaria data from host-parasite interactions on Mt. Cameroon, a relatively understudied region. We found highly specific parasite lineages with a

low level of prevalence probably due to the scarcity of water. Prevalence was influenced by host abundance and foraging at ground level, implying a spatial feeding preference of vectors for ground level and for abundant hosts. Our results suggest that host-parasite interactions on Mt. Cameroon are stronger and more specialized compared to the neotropics but also that tropical mountains are areas of high specificity, endemism and diversity of haemosporida. The low prevalence but high specificity of haemosporida and their hosts indicate that Mt. Cameroon is a suitable model region for research on vector-borne pathogens. To fully understand host-parasite interactions and the mechanisms underlying such associations on Mt. Cameroon, future studies should focus on exploring coevolutionary relationships, vector distribution, as well as the extent to which parasite prevalence is affected by elevation, sexual dichromatism, age, and immune defences of hosts.

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512

513 Table 1. Prevalence of haematozoan parasites across well-represented (≥ 20 individuals) bird host
514 families on Mt. Cameroon.

Host family	Species (N)	Individuals (n)	Haemproteus		Plasmodium		Leucocytozoon	
			Infected	(%)	Infected	(%)	Infected	(%)
Cisticolidae	5	71	0	0	0	0	0	0
Estrildidae	5	31	0	0	0	0	0	0
Sylviidae	7	45	0	0	0	0	0	0
Fringillidae	1	34	1	2.94	1	2.94	0	0
Monarchidae	3	29	7	24.14	0	0	0	0
Muscicapidae	4	68	1	1.47	1	1.47	0	0
Ploceidae	4	45	2	4.44	0	0	0	0
Timaliidae	4	70	2	2.86	2	2.86	1	1.43
Turdidae	5	139	19	13.67	17	12.23	18	12.95
Nectariniidae	8	202	32	15.84	4	1.98	4	1.98
Pycnonotidae	12	227	4	1.76	5	2.2	34	14.98

Figure 1. Molecular Phylogenetic analysis of haemosporidian cyt-b lineages by Maximum Likelihood method. The evolutionary history was inferred based on the Tamura-Nei + G model. Numbers located near of the branches indicate Bayesian probability values. The analysis involved 36 nucleotide sequences.

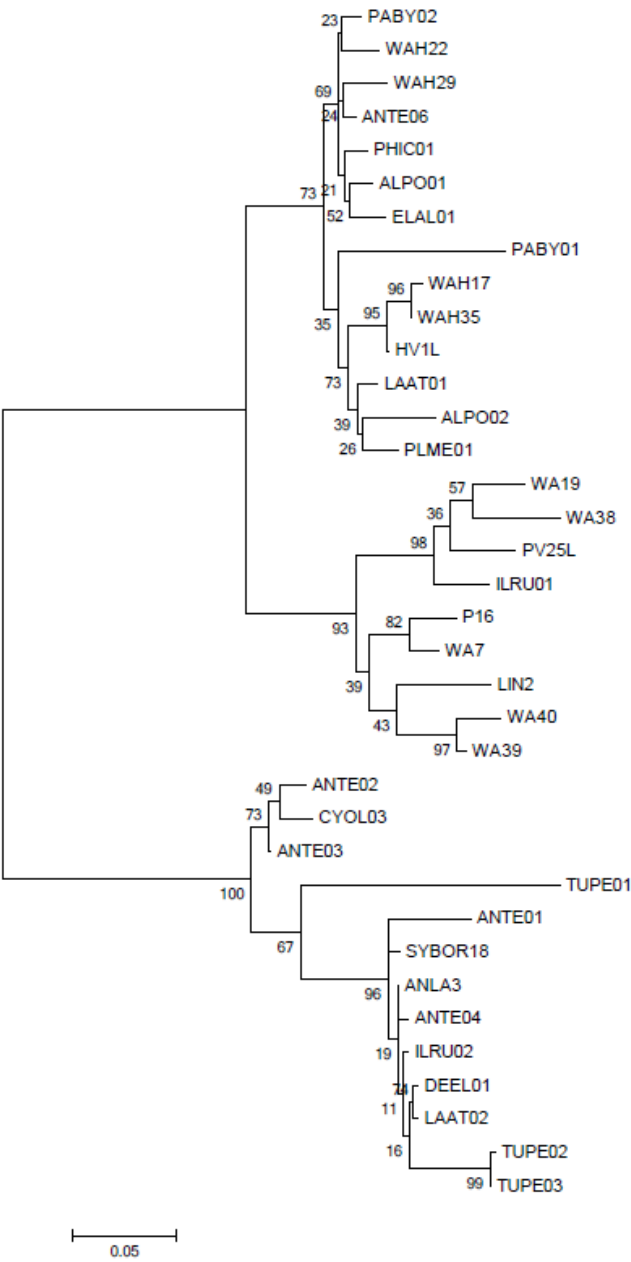
Figure 2. The bipartite network of interactions of parasite lineages and bird hosts on Mt Cameroon. The nodes (black) are species. The links (gray) connect parasites and host if they interact. The width of each link is proportional to the abundance of each interaction, and the width of each node is proportional to the abundance of species. (a) network analysis of *Haemoproteus* and *Plasmodium* lineages at top with bird hosts bottom (b) network analysis of *Haemoproteus*, *Plasmodium* and *Leucocytozoon* lineages at top with bird hosts at bottom.

Figure 3 (a) Null distribution of network-wide specialization H'_2 estimates of 10,000 randomized matrices compared to the observed estimate (dashed vertical line) on Mt. Cameroon. The H'_2 values range from 0.0 (generalist) to 1.0 (specialist). The value on Mt. Cameroon shows a highly specialized host-parasite assemblage. (b) Species-level specialization d' comparisons using t -tests between null distributions (curves) and observed means (vertical dash lines) with 95% confidence intervals (grey vertical lines) for parasites and avian hosts on Mt. Cameroon. The value of Cohen's d is used to estimate the effect size between the observed mean and the null model. The higher the value of Cohen's d , the greater the number of interactions.

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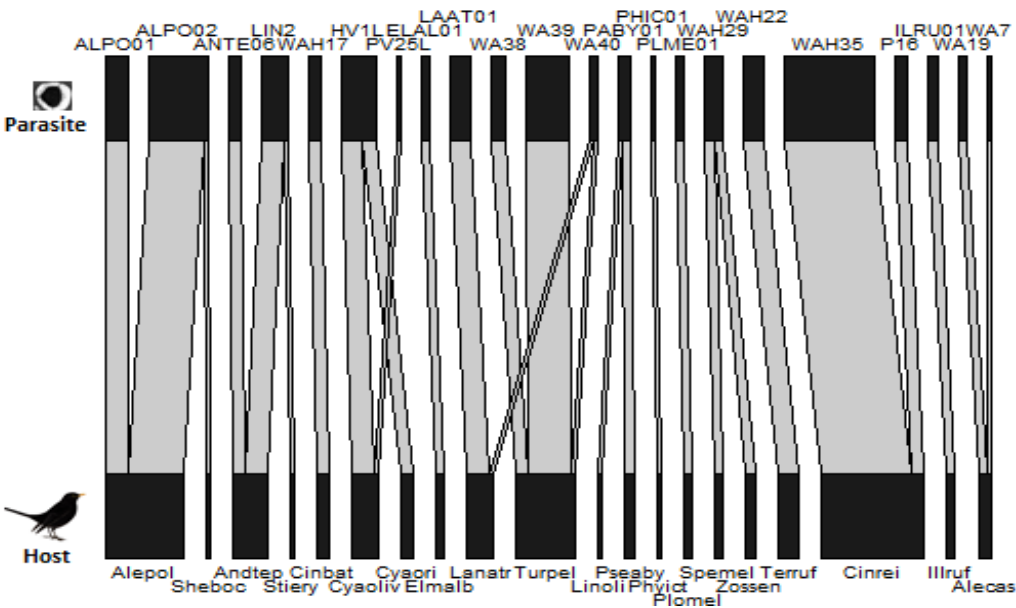
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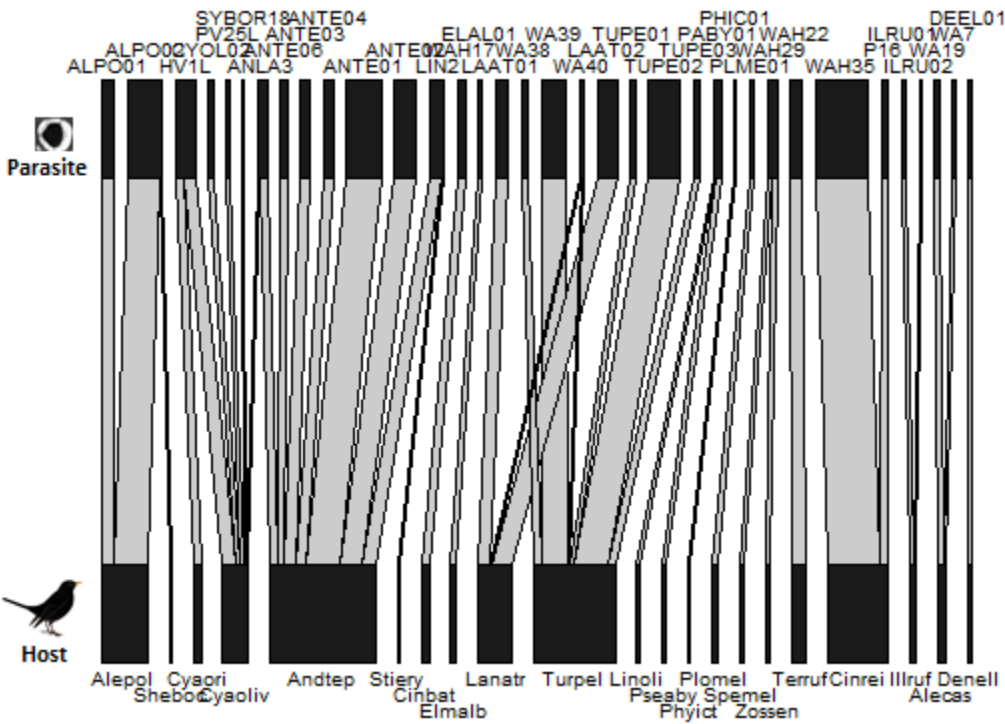


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Figure 2a.



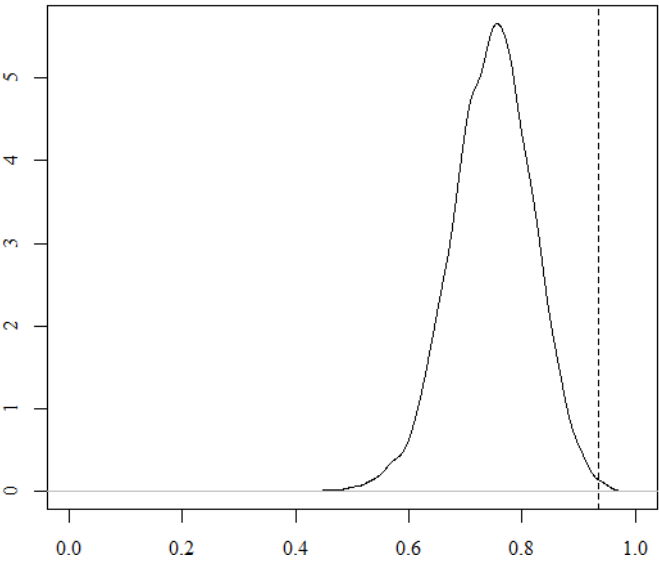
546 Figure 2b



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549 Figure 3a

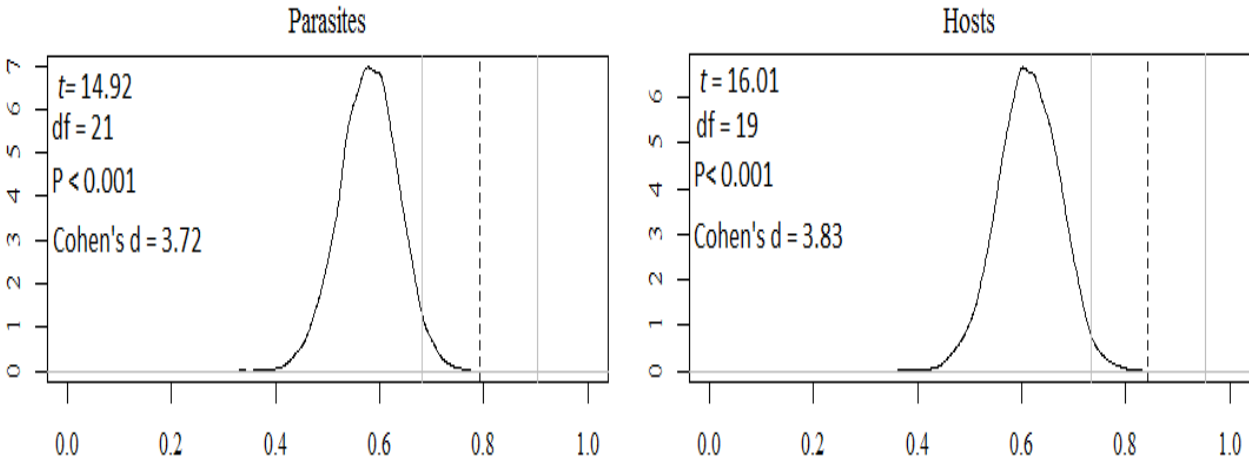


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553 Figure 3b



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Table S1. Parasite lineages on Mt. Cameroon identified and classified according to Genebank and Malavi databases. The Genebank name is given with its alternative name in Malavi database.

MalAvi name	Genebank name	New	Bird species Mt Cameroon	Species/genus/family - other studies	Authors other studies
/	/	ALPO01	Alethe poliocephala	/	/
/	/	ALPO02	Alethe poliocephala, Sheppardia bocagei	/	/
ANSEI01	WAH17	/	Cinnyris batesi	Nectarinidae	Beadell et al 2009
PABY02	PABY02	/	Linurgus olivaceus	Muscicapa	Perez-Tris et al. 2007
/	/	PHIC01	Phyllastrephus icterinus	/	/
/	/	PLME01	Ploceus melanogaster	/	/
/	/	ELAL01	Elminia albiventris	/	/
ZOSSTE01	WAH29	/	Speirops melanocephala, Zosterops senegalensis	Zosterops	Ishtiaq et al 2010
/	PABY01	/	Pseudoalcippe abyssinica	Muscicapa	Perez-Tris et al. 2007
CINPRE01	WAH35	WAH35	Cinnyris reichenowi	Nectarinidae	Beadell et al 2009
TERUF01	WAH22	/	Terpsiphone rufiventer	Monarchidae	Beadell et al 2009
ANLAT12	ANLA3	/	Andropadus tephrolaemus	Andropadus latirostris	Valkiunas et al. 2009
/	/	ANTE01	Andropadus tephrolaemus	/	/
/	/	ANTE02	Andropadus tephrolaemus	/	/
/	/	ANTE03	Andropadus tephrolaemus	/	/
/	/	ANTE04	Andropadus tephrolaemus	/	/
/	/	ANTE05	Andropadus tephrolaemus	/	/
/	/	DEEL01	Dendropicus ellioti	/	/
/	/	ILRU02	Illadopsis rufipenis	/	/
/	/	LAAT01	Lanarius atroflavius	/	/
/	/	LAAT02	Lanarius atroflavius	/	/
/	/	TUPE01	Turdus pelios	/	/
/	/	TUPE02	Turdus pelios	/	/
/	/	TUPE03	Turdus pelios	/	/
CYAOLI03/HV5L	HV1L	/	Cyanomitra olivacea	Cyanomitra olivacea	Chaser et al 2009
/	/	CYOL03	Cyanomitra olivacea	/	/
/	/	ILRU01	Illadopsis rufipenis	/	/

GRW06	LIN2	/	Andropadus tephrolaemus	New Zealand (Anthornis melanura)	Baillie & Brunton 2011
RBQ22	P16	/	Cinnyris reichenowi	Passer domesticus, Acrocephalus arundinaceus	Beadell et al. 2006
RECOB4	PV25L	/	Cyanomitra olivacea	Cyanomitra olivacea	Chaser et al 2009
ALEDIA02	WA19	/	Alethe castenea	Turdidae	Beadell et al 2009
AFTRU08	WA38	/	Turdus pelios	Turdidae	Beadell et al 2009
SYBOR27	SYBOR18	/	Cyanomitra olivacea	?	Hellgren et al. unpubl.
AFTRU5	WA39	/	Turdus pelios	Turdidae	Beadell et al 2009
AFTRU09	WA40	/	Lanarius atroflavius	Turdidae	Beadell et al 2009
ALEDIA01	WA7	/	Alethe castenea	Turdidae	Beadell et al 2009

Table S2. Number of individuals sampled per bird species (n) and prevalence (%) for each host species with at least 13 individuals sampled as assessed by nested PCR on Mt. Cameroon.

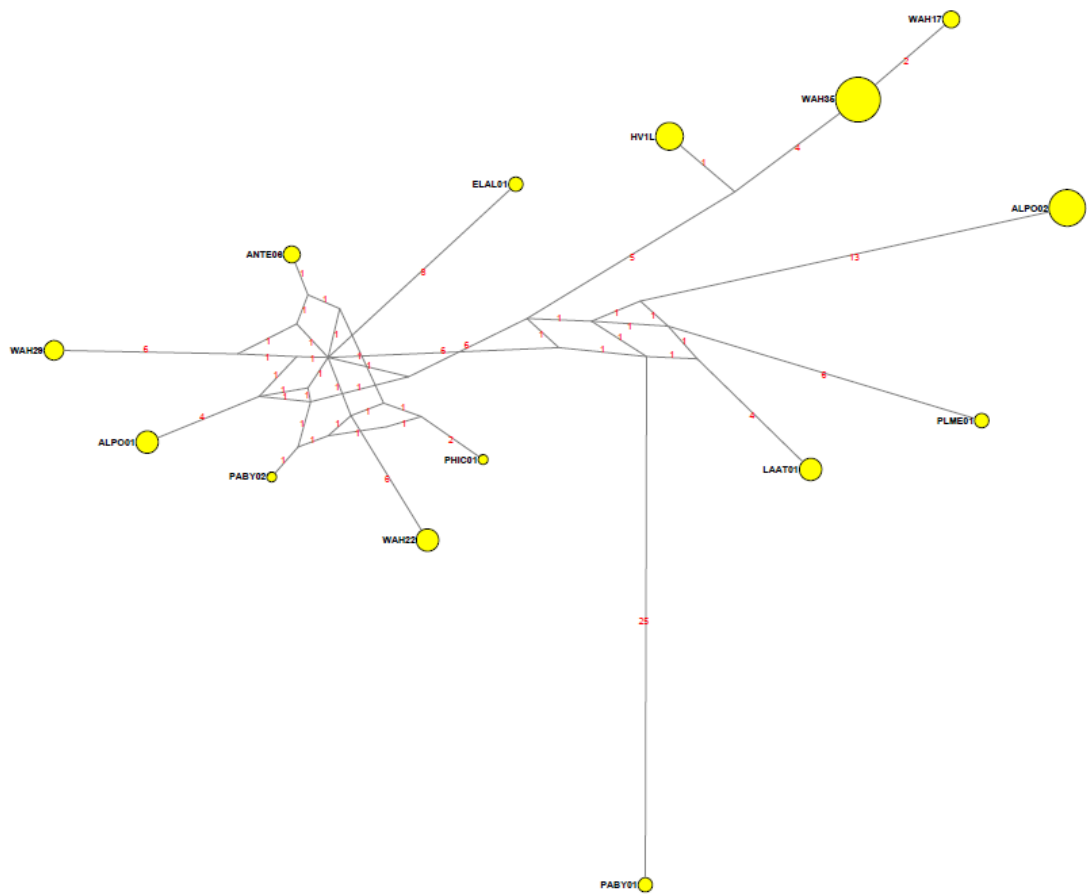
Host species	n	Prevalence (%)						
		Overall (%)	P ¹	H ²	L ³	P+L	L+H	P+H+L
<i>Andropadus tephrolaemus</i>	94	49.99	5.32	3.19	37.23	3.19	1.06	0
<i>Andropadus curvirostris</i>	3							
<i>Andropadus latirostris</i>	57	0	0	0	0	0	0	0
<i>Andropadus virens</i>	17	0	0	0	0	0	0	0
<i>Andropadus ansorgei</i>	1							
<i>Phyllastrephus icterinus</i>	14	7.14	0	7.14	0	0	0	0
<i>Phyllastrephus poensis</i>	13	0	0	0	0	0	0	0
<i>Phyllastrephus poliocephala</i>	3							
<i>Nicator chloris</i>	1							
<i>Criniger chloronotus</i>	10							
<i>Bleda notata</i>	13	0	0	0	0	0	0	0
<i>Bleda syndactylus</i>	1							
<i>Pseudoalcippe abyssinica</i>	24	12.5	0	12.5	0	0	0	0
<i>Kakamega poliothorax</i>	19	0	0	0	0	0	0	0
<i>Illadopsis cleaveri</i>	8							
<i>Illadopsis rufipennis</i>	19	15.79	10.53	0	0	0	5.26	0
<i>Alethe castanea</i>	16	25.0	18.75	6.25	0	0	0	0
<i>Alethe poliocephala</i>	57	29.82	0	29.82	0	0	0	0
<i>Turdus pelios</i>	57	47.37	15.79	0	24.56	7.02	0	0
<i>Zoothera crossleyi</i>	3							
<i>Neocossyphus poensis</i>	6							
<i>Bradypterus lopezi</i>	16	0	0	0	0	0	0	0
<i>Phylloscopus herberti</i>	2							
<i>Nigritta fusconotus</i>	2							
<i>Alcedo leucogaster</i>	2							
<i>Poliolais lopezi</i>	18	0	0	0	0	0	0	0
<i>Hylia prasina</i>	3							
<i>Macrosphenus concolor</i>	2							
<i>Macrosphenus flavicans</i>	3							
<i>Psilidoprocne fuliginosa</i>	5							
<i>Lanarius atroflavus</i>	19	42.10	0	5.26	5.26	0	26.32	5.26
<i>Dendropicus ellioti</i>	7	28.57	0	0	28.57	0	0	0
<i>Indicator maculatus</i>	2							
<i>Trochocercus nitens</i>	4							
<i>Elminia albiventris</i>	13	15.38	0	15.38	0	0	0	0
<i>Terpsiphone rufiventer</i>	13	30.77	0	30.77	0	0	0	0
<i>Dicrurus atripennis</i>	1							
<i>Prinia bairdii</i>	4							
<i>Cisticola chubbi</i>	17	0	0	0	0	0	0	0
<i>Urolais epichlorus</i>	27	0	0	0	0	0	0	0
<i>Camaroptera chloronota</i>	7							
<i>Apalis cinerea</i>	4							
<i>Pogoniulus bilineatus</i>	3							
<i>Pogoniulus scolopaceus</i>	2							
<i>Buccanodon duchaillui</i>	1							
<i>Speirops melanocephalus</i>	6							
<i>Zosterops senegalensis</i>	6							
<i>Halcyon badia</i>	2							

<i>Cossypha isabellae</i>	44	0	0	0	0	0	0	0
<i>Stiphrornis erythrothorax</i>	18	11.11	11.11	0	0	0	0	0
<i>Sheppardia bocagei</i>	2							
<i>Muscicapa adusta</i>	4							
<i>Smithornis sharpei</i>	1							
<i>Turtur tympanistria</i>	4							
<i>Turtur brehmeri</i>	2							
<i>Aplopelia larvata</i>	1							
<i>Campephaga petiti</i>	2							
<i>Nigrita fusconotus</i>	2							
<i>Cryptospiza reichenovii</i>	24	0	0	0	0	0	0	0
<i>Parmoptila woodhousei</i>	5							
<i>Spermophaga haematina</i>	3							
<i>Estrilda nonula</i>	1							
<i>Cinnyris reichenowi</i>	70	34.29	4.29	30.0	0	0	0	0
<i>Cyanomitra oritis</i>	61	3.28	0	3.28	0	0	0	0
<i>Cyanomitra olivaceus</i>	60	23.33	10.0	5.0	8.33	0	0	0
<i>Cinnyris ursulae</i>	1							
<i>Cinnyris batesi</i>	5							
<i>Hedydipna collaris</i>	1							
<i>Deleornis fraseri</i>	3							
<i>Ploceus melanogaster</i>	28	7.14	0	7.14	0	0	0	0
<i>Ploceus insignis</i>	4							
<i>Ploceus bicolor</i>	2							
<i>Euplectes capensis</i>	11							
<i>Platysteira cyanea</i>	5							
<i>Dyaphorophia castanea</i>	6							
<i>Linurgus olivaceus</i>	35	2.86	0	2.86	0	0	0	0

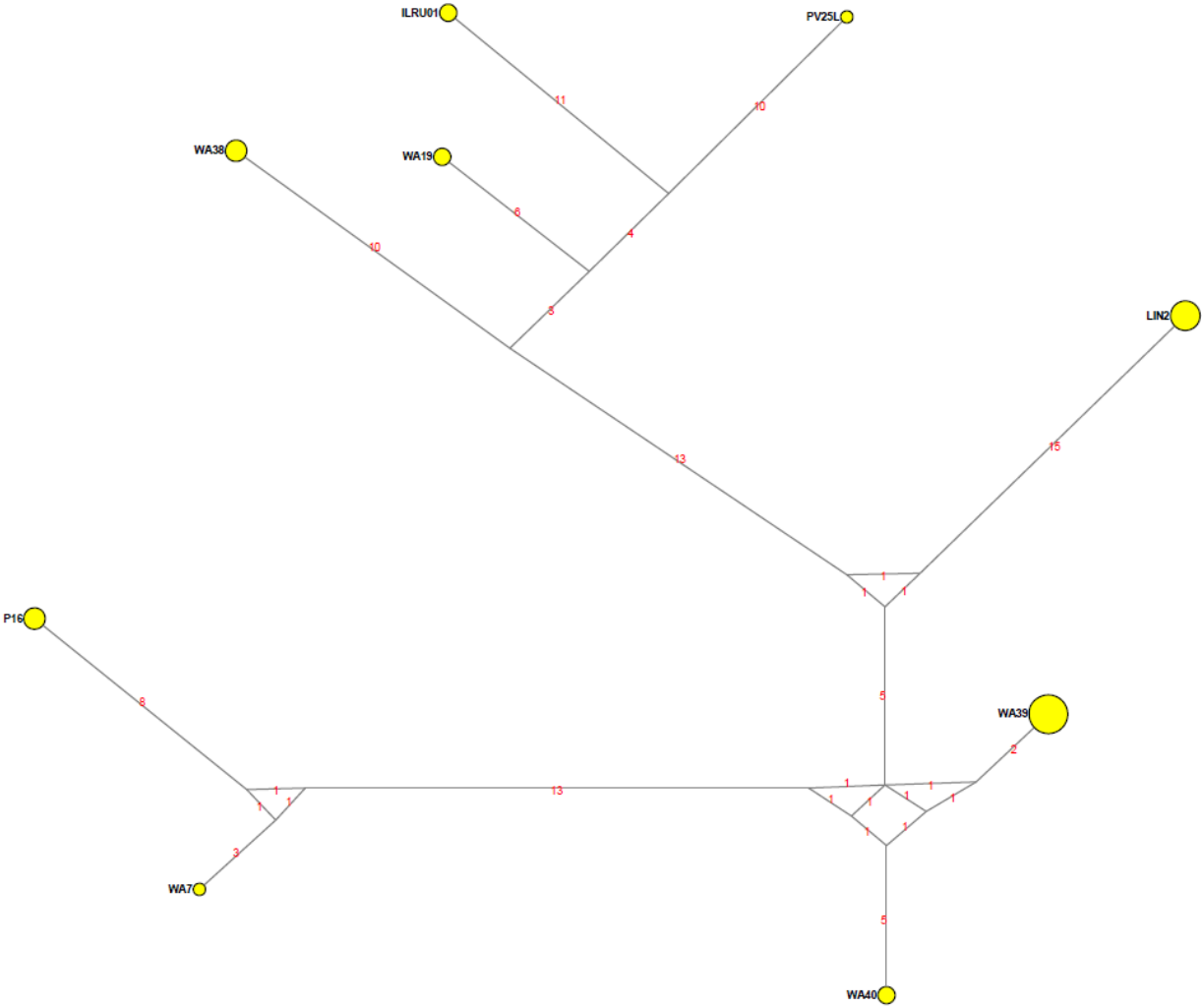
P¹=*Plasmodium* spp; H²=*Haemoproteus* spp; L³=*Leucocytozoon* spp

Figure S1. networks of (A) haemoproteus, (B) plasmodium and (C) leucocytozoon showing divergence between haplotypes. The numbers represent number of mutations between haplotypes and circles are actual haplotypes with their names. The larger the circle the more individuals of that haplotype that were sampled.

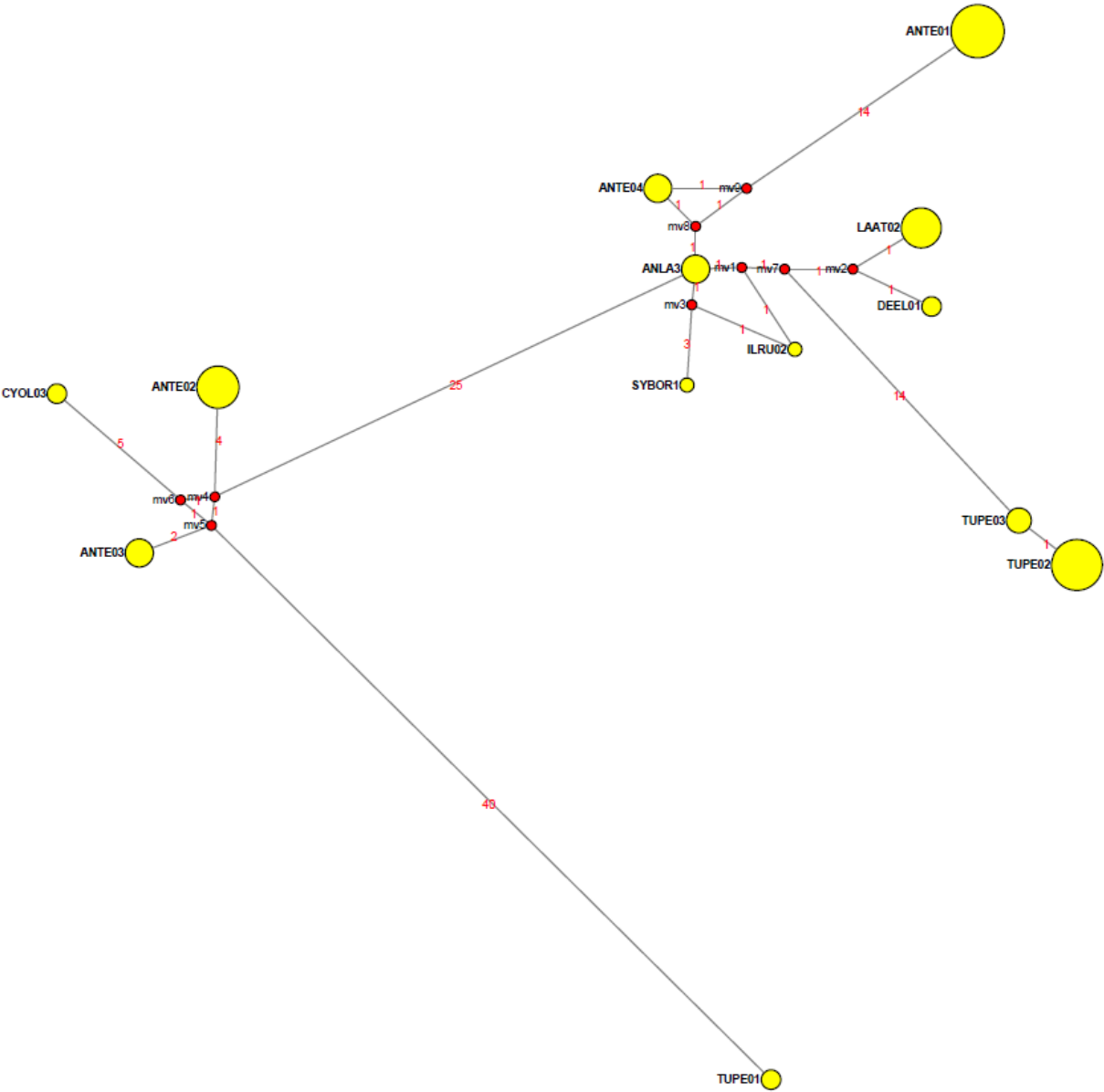
A. *Haemoproteus* haplotypes



B. *Plasmodium* haplotypes



C. *Leucocytozoon* haplotypes



CHAPTER 4

Djomo, N. E., Munclinger, P., Ferenc, M., Sedláček, O., Albrecht, T., & Hořák, D. 2014. Sexing monomorphic western mountain greenbuls on Mount Cameroon using morphometric measurements. *African Zoology* 49(2): 247–252.

Sexing monomorphic western mountain greenbuls on Mount Cameroon using morphometric measurements

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The western mountain greenbul, *Andropadus tephrolaemus*, is a poorly-known monomorphic forest greenbul. We investigated whether morphological measurements could be used to discriminate between sexes of this species, with a sample of birds captured in two forest types on Mt Cameroon. We used discriminant function analysis based on a combination of traits to develop models to discriminate between sexes. The sex of birds predicted from these models was compared with molecular sexing of the same individuals. Discriminant analysis revealed that a discriminant function incorporating wing length, tail length and bill height allowed 74% of western mountain greenbuls to be sexed correctly based on morphometric measurements alone. Sex ratios varied between montane and lowland forests, with the former having a higher proportion of males (70.5 and 54.6%, respectively), but the difference was not statistically significant. Cloacal sizes did not differ between males and females, and males do not develop large cloacal protuberances while breeding. This is in agreement with low predicted levels of sperm competition in this species. We show that sexing based on morphology has its limitations, but can still provide some insight if DNA analysis is not available.

Key words: morphology, *Andropadus tephrolaemus*, sex ratio, discriminant function analysis, tropical Africa.

INTRODUCTION

The ability to identify sexes of birds in the field is important for studying many aspects of avian ecology, including studies of life history and population structure and dynamics (Stahl & Oli 2006; Wilson & Martin 2012). Knowledge of how bird sex ratios vary across space and time is important because it enables researchers to investigate how stress factors (e.g. environmental stress) modulate sex ratios (Nager *et al.* 2000; Freed *et al.* 2009), as well as the conservation implications of sex-biased movements in wild bird populations (Clout *et al.* 2002; Donald 2007). In sexually dimorphic bird species, there are marked differences in plumage traits. However, in species with no clear sexual dimorphism in appearance, distinguishing male from female individuals is often a problem in the field and to overcome this, ornithologists use a variety of morphological characteristics. Sexing based on morphometrics is often the choice for quick and efficient sex identification (Dechaume-

Moncharmont *et al.* 2011) as significant, albeit small, differences in morphological measurements often exist between males and females (Murphy 2007; Cardoni *et al.* 2009).

Recently, molecular sexing has successfully been applied to bird species with no apparent sexual dimorphism (Griffiths *et al.* 1998; Reynolds *et al.* 2008; Berkunsky *et al.* 2009). Despite the reliability of this technique, it is not routinely available to most scientists, especially in tropical Africa, who do not have access to trained staff or laboratory facilities. As a consequence, information about sex ratios of free-living African birds is often lacking. An alternative is a morphometric based field sexing technique. Bird species to which such a technique could be applied are the greenbuls of the bulbul family Pycnonotidae. These are birds that form an important part of the rainforest bird community in Africa and show no obvious plumage differences between sexes. However, some sexual dimorphism in size, typically with males being larger than females, has been reported (Stuart *et al.* 1986; Keith

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et al. 1992). The aim of this study was explicitly to test the importance of particular morphological traits for field sexing of a sample of the western mountain greenbul, *Andropadus tephrolaemus*, a montane species restricted to the Cameroon volcanic line, but quite abundant in this area (Reif *et al.* 2006; Hořák *et al.* 2010; Djomo *et al.* 2014). We took a series of measurements from birds captured in the field, including details of cloacal size (trait widely used to sex adult breeding birds in northern temperate zone), and compared the morphometric data with the known sex of the birds based on molecular sexing methods. In addition, we provide information on sex ratios for two forest types.

MATERIALS & METHODS

Study site and species

The study was carried out in the rainforests of the Mount Cameroon National Park; Cameroon (4°08'N, 9°07'E). The study species, the western mountain greenbul, is monogamous and territorial and inhabits montane forest of all types mostly at elevations above 1600 m above sea level (a.s.l.). It forages at all levels from understorey to canopy and is mainly a frugivore (Dowsett & Dowsett-Lemaire 1984). Individuals of this species usually occur singly or in pairs, but also in small parties when juveniles are usually present and in large flocks on certain fruiting trees, notably figs (Stuart *et al.* 1986). Two subspecies are recognized in the Afromontane region of the Gulf of Guinea: *Andropadus tephrolaemus tephrolaemus*, occurring on Mt Cameroon and the island of Bioko, and *Andropadus tephrolaemus bamendae*, a darker race found from Mt Kupe to Mt Tchabal Mbabo (Louette 1981).

Data collection

We used mist netting to sample birds in the montane (2250 m a.s.l.) and lowland forests (350 m a.s.l.) and established a transect 200 m long where we mounted 16 mist nets (12 m, 16 × 16 mm mesh; Ecotone, Poland). Field work was carried out in November 2011, March 2012 and November 2012. These periods correspond to the breeding seasons for most passerine birds in the region (Serle 1981), including *A. tephrolaemus*. We opened the nets at 06:00 am and closed them at 06:00 pm for three days. Cloacal size, bill length (measured to the feathers), bill height (measured at the distal end of nostrils), bill width (measured at the distal end of nostrils), and tarsus length were measured using

dial callipers while wing chord and tail length were measured with a ruler and body mass was recorded using a 100 g Pesola spring balance (to the nearest 0.5 g). All measurements were taken by the same person (D.H.).

To confirm that birds were breeding during these periods, we collected sperm samples from males following the methods outlined in Albrecht *et al.* (2013). A drop of blood (50–100 µl) was taken from the brachial vein of all birds for molecular sexing and preserved in 96% ethanol. Ethanol was evaporated from the blood, and DNA was extracted using a DNeasy 96 Blood & Tissue kit (Qiagen) according to the manufacturer's instructions. We used P2/P8 primers (Griffiths *et al.* 1998) to amplify a size-different intron within the highly conserved Chromo-helicase-DNA-binding (CHD) gene located on the sex chromosomes of birds (Griffiths *et al.* 1998). The amplification protocol consisted of an initial 94°C for 90 s followed by 40 cycles of 56°C for 45 s, 72°C for 45 s, 94°C for 30 s, with a final 48°C for 60 s and 72°C for 5 min. Polymerase chain reaction (PCR) products were separated on a 2% agarose gel stained with ethidium bromide and visualized under ultraviolet light. The presence of one band indicated males (ZZ), whereas two bands indicated females (ZW).

Data analysis

Many studies have used discriminant analysis to determine sex in size-dimorphic species that are monomorphic in plumage characteristics (Reynolds *et al.* 2008; Berkunsky *et al.* 2009; Dechaume-Moncharmont *et al.* 2011; Wojczulanis-Jakubas & Jakubas 2011). The principal of discriminant function analysis (DFA) is to provide equations based on morphological measurements which could be used to predict the sex of birds. The equations are calibrated on individuals of known sex from molecular sexing. We used a forward stepwise logistic regression to construct models from a combination of traits to determine the best traits to sex these greenbuls. Our first model was built from the three traits that showed significant differences between males and females. The others were built from a combination of other traits. We compared the sexes of predicted individuals from our models with molecular sexing and assessed the effectiveness of each model as the percentage of birds that was correctly sexed. The logistic regression produces estimates for a constant (k) and a regression coefficient (x) for all (n) characters (m), in the regression model. The discriminant function

(D) from which birds were sexed takes the form:

$$D = x_1m_1 + x_2m_2 + \dots + x_nm_n + k. \quad (1)$$

We then calculated discriminant scores (hereafter DS) from our chosen model to determine the cut-off point in the frequency distribution of DS of individual greenbuls. This was done by dropping k and dividing each coefficient x by x_1 (van Franeker & ter Braak 1993; Weidinger & van Franeker 1998; Reynolds *et al.* 2008). The equation for calculating the discriminant scores is now:

$$DS = m_1 + (x_2/x_1)m_2 + \dots + (x_n/x_1)m_n. \quad (2)$$

The cut-off point was the midpoint between the mean DS of males and females. When the focal bird's DS fell below or above the cut-off point, it was classified as either a female or male, respectively. We further assessed the reliability of the chosen discriminant function used to sex individual greenbuls by a jackknife cross-validation. The jackknife validation is a process in which each bird is classified using a function obtained from the total sample, excluding the individual bird to be classified. This process was repeated for the entire dataset of birds, and the percentage of birds correctly sexed was calculated.

The effectiveness of discriminant analysis depends in part on the constancy of traits used in the function. For this reason, we excluded body mass from the variables used in our discriminant function analysis because of the possible temporal vari-

ation in this trait especially in frugivores (Levey & Karasov 1989). In order to apply a discriminant function to a particular species, it is important to recognize the extent to which geographical and seasonal variations, as well as age, influence size and shape (Phillips & Furness 1997). We used a t -test to compare cloacal sizes of males and females, and chi-square test to compare sex ratios between montane and lowland forests. Data analyses were done in R 2.15.2. software (R Development Core Team 2012).

RESULTS

In total, we sampled 103 individuals in the field and molecular analysis using P2/P8 primers enabled sexing of 92 of these individuals. Sixty-six of these were identified as adults in the field (43 males and 23 females), and these were used to investigate whether sex could be determined solely on the basis of their external morphological measurements. Of the measurements taken in our sample of western mountain greenbuls, wing length, bill height and tail length differed significantly between sexes, males being on average bigger than females (Table 1). Cloacal sizes of males did not differ significantly from those of females (Table 1). Although the proportion of males caught varied from 70.5% in montane forest to 54.6% in lowland forest, this difference was not significant; $\chi^2 = 1.21$, d.f. = 1, $P = 0.3$.

We constructed three discriminant models (see

Table 1. Means, standard deviations (SD) and ranges of eight morphometric measurements of 43 male (M) and 23 female (F) western mountain greenbuls (*Andropadus tephrolaemus*) on Mount Cameroon. Statistically significant differences are given in bold.

Measurement	Sex	Mean	S.D.	Range	<i>P</i>	<i>t</i> -value
Wing length (mm)	M	86.3	3.2	80–98	<0.001	-4.1
	F	82.9	3.1	76–88		
Tail length (mm)	M	77.8	4.3	70–87	0.05	-2.1
	F	75.7	4	67–86		
Tarsus (mm)	M	24.9	5	22.1–26.2	0.19	-1.31
	F	23.6	1.2	21.0–25.7		
Bill length (mm)	M	15	0.7	14.1–16.3	0.99	-0.01
	F	14.9	0.5	14.1–15.8		
Body mass (g)	M	36.9	5.3	26.4–57.8	0.35	-0.92
	F	35.7	5.3	26.0–54.2		
Bill height (mm)	M	5	0.6	4.1–6.1	<0.04	-2.1
	F	4.8	0.4	4.0–5.6		
Bill width (mm)	M	6.6	0.7	5.9–7.9	0.61	-0.51
	F	6.5	0.8	4.3–7.8		
Cloacal size (mm)	M	4.8	1.1	3.1–7.1	0.23	-0.44
	F	4.6	0.8	3.2–6.4		

Table 2. Formulae for the calculation of discriminant scores for western mountain greenbuls (*Andropadus tephro-laemus*) on Mount Cameroon. A discriminant score is calculated for each bird and if it falls above or below the cut-off point, the bird is classified as a male or a female, respectively.

Model number	Discriminant model formula	Cut-off point
1	Wing + (0.09 × tail) + (1.05 × bill height)	96.71
2	Wing + (0.08 × tail) + (1.05 × bill height) + (0.06 × tarsus) + (0.11 × bill length)	99.01
3	Wing + (0.09 × tail) + (1.19 × bill height) + (0.04 × tarsus) + (0.10 × bill length) – (0.17 × bill width)	98.74

Table 2) using forward stepwise logistic regression. The first analysis was conducted with three morphometric measurements and resulted in one discriminant model that included wing length, tail length and bill height as discriminatory variables and it correctly sexed 74% of the individuals. It was the best model and misclassified only five males and 12 females (Fig. 1). The analyses using five and six morphometric variables resulted in discriminant models that correctly sexed 72% and 71% of the adult western mountain greenbuls, respectively. The jackknife validation for the best function (first model) gave similar results, predicting the sex correctly in 73% of individuals.

DISCUSSION

Our results show that for the western mountain greenbul, males are larger than females on average in three of the six traits considered – wing length, tail length and bill height. Although the discriminatory power of the best discriminant model is not very high – this shows morphological sexing has some limitations – it still provides some insight if molecular analysis is not available. The observed discriminatory power seems to be comparable to other studied bird species (Jakubas & Wojczulanis 2007; Reynolds *et al.* 2008) but generally discriminant function should be used with caution in species having a high degree of overlap in morphometrics

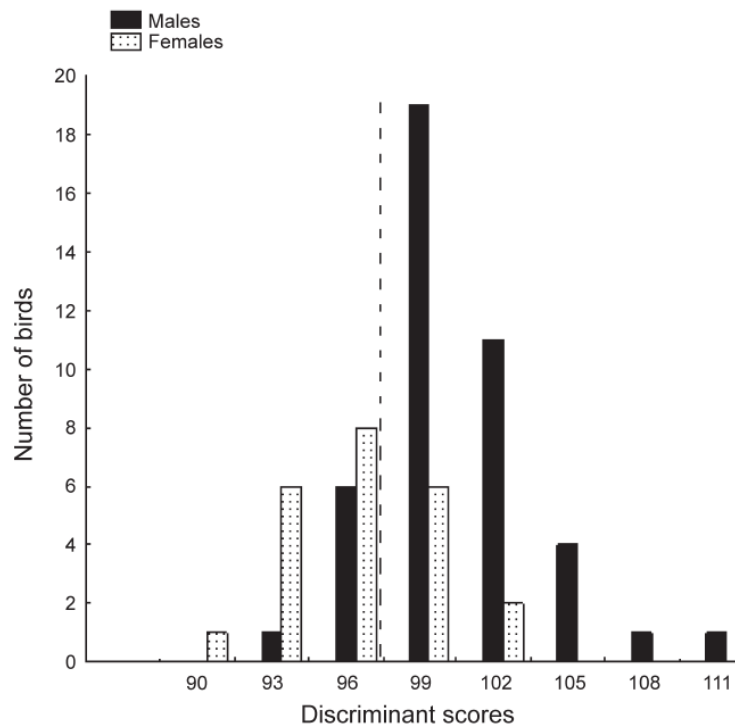


Fig. 1. Frequency distribution of discriminant scores (DS) of western mountain greenbuls (*Andropadus tephro-laemus*) based on the following equation: $DS = \text{wing} + (0.09 \times \text{tail}) + (1.05 \times \text{bill height})$. The vertical dashed line represents the cut-off point. Individuals on the left side are classified as females and on the right as males. Birds were correctly classified as male or female in 74% of cases.

between the sexes. From an ecological point of view, our results indicate that males in *Andropadus tephrolaemus* are not under intense selection pressure (e.g. male–male competition) to develop pronounced traits in the montane forest on Mt Cameroon.

In temperate regions, males usually develop cloacal protuberances during breeding (Ralph *et al.* 1993; Ralph 2001) because they are under intense competition for sperm production (Pitcher *et al.* 2005; Albrecht *et al.* 2013). Ornithologists then use these cloacal protuberances to discriminate between breeding individuals in the field. The similarity of cloacal sizes of males and females in *A. tephrolaemus* during the breeding season indicates that the development of a large cloaca, which is an indication of sperm competition in males (Pitcher *et al.* 2005), may not be a major factor in the breeding biology of this species. This is supported by Albrecht *et al.* (2013) who showed that for *A. tephrolaemus*, the predicted level of sperm competition is very low and as such, a low-sperm production is expected as well as a low level of sexual dimorphism in cloacal sizes.

In conclusion, our results suggest that sexes of *A. tephrolaemus* on Mt Cameroon on average show morphometric differences for at least three traits, but also that these differences are not very pronounced – wing length seems to be the trait with the greatest difference between sexes. Our results also support a previous finding that male–male competition in this tropical species is probably not as intense as those for males in temperate regions. Future studies should focus on intra- and interspecific competition in *A. tephrolaemus* to understand the morphological variation between sexes. For rapid, inexpensive field sexing of the western mountain greenbul, a combination of tail length, wing length and bill height is the most reliable. However, ornithologists should not rely on cloacal protuberances of males in this species to sex individuals.

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CHAPTER 5

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**Abundance-area relationships in bird assemblages along an Afrotropical elevational
gradient: montane forest species compensate for less space available**

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ABSTRACT

The positive inter-specific relationship between range size and abundance of local populations is a remarkably pervasive ecological pattern, however some notable exceptions exist. Afrotropical montane areas could be an example as the range-restricted bird species are unusually abundant there. Here we aimed to describe abundance-area relationships in passerine assemblages along a tropical elevational gradient of Mt. Cameroon, West-Central Africa. We tested how the area occupied locally by a species and its geographical range size relate to local abundances and how the relationships change with elevation. Data on bird assemblage structure were collected at six forested elevations (350m, 650m, 1100m, 1500m, 1850m, 2200m a.s.l.). Birds were recorded at 16 locations at each elevation using a standardised point count method. Data on elevational ranges of passerines were compiled from primary published sources to calculate the area occupied locally and to estimate their total population sizes on the mountain. Species' geographic range sizes were determined as the occupancy of 1° x 1° grid cells. We found a negative relationship between local abundance and geographic range size within the entire passerine assemblage on Mt. Cameroon, which disagrees with the most frequently observed pattern. However, we found that the patterns differ between elevations so that the positive lowland trend changes to a negative one towards higher elevations. Interestingly, we found that the total assemblage abundances do not differ among elevations and population size estimates of species occupying different parts of the gradient remain relatively constant. These patterns are caused mostly by relatively high abundances of montane species, which might be a result of long-term ecological specialization and/or competitive release in species poor montane locations and possibly can be facilitated by an extinction filter. Our data suggest that species inhabiting mountain tops might compensate for less area available locally by being abundant.

Introduction

Macroecological studies have revealed a pervasive positive inter-specific correlation between range sizes and abundance in local populations (Brown 1984, 1995; Gaston et al. 2000; Gaston and Blackburn 2000). Several hypotheses have been proposed to explain this pattern. Besides methodological issues such as incomplete sampling (Bock and Ricklefs 1983; Komonen et al. 2009), mechanistic explanations include (i) resource use and availability – species utilizing wider range or more abundant resources becoming most abundant and widely distributed (Brown 1984; Hanski et al. 1993); (ii) vital rates - high population growth rate leading to high abundance and more occupied sites (Holt et al. 1997); or (iii) dispersal – intensive dispersal among sub-populations of individual species producing a positive inter-specific abundance-range size relationship (O’connor 1987; Hanski et al. 1993; Venier and Fahring 1998); for review see Gaston et al. (2000) and Borregaard and Rahbek (2010).

The majority of positive abundance range-size relationships (hereafter ARSR) have been demonstrated on datasets from temperate regions and relatively few datasets on local abundances are available from tropical regions (but see Gaston 1996; Blackburn et al. 2006), where the majority of the world’s biodiversity concentrates (Willig et al. 2003). Before more comprehensive data on local abundances from tropical regions are available, some caution is warranted with respect to the shape of the inter-specific ARSR (*cf.* Chown et al. 2004; Orme et al. 2006). Recently, it has been found to be systematically violated in avian assemblages in tropical montane forest environments (Reif et al. 2006; Djomo et al. 2014), where range restricted species were generally abundant (Fjeldså 1999; Ryan et al. 1999; Owionji et al. 2005; Sekercioglu and Riley 2005; Hořák et al. 2010; Fjeldså et al. 2010, 2012). Factors underlying high abundances of montane forest endemics remain unknown, but several mutually non-exclusive hypotheses have been proposed: (i) long-term eco-climatic stability (especially on the mountains near thermally stable ocean currents) facilitates ecological

specialization, which consequently results in high local abundances of montane species (Fjeldså et al. 2012); (ii) high abundances of montane forest species are a result of density compensation in species poor communities at high altitudes (MacArthur 1972); (iii) locally abundant tropical montane species compensate for their small range sizes, whereas those not abundant enough are systematically removed by an extinction filter (Johnson 1998; Williams et al. 2009). Joint influence of the above mentioned mechanisms appears to be likely. Indeed, a high degree of ecological specialization together with less intensive inter-specific competition due to low species richness might support high population numbers in montane species and consequently help them to circumvent the extinction filter.

It is difficult to disentangle the role of individual mechanisms, because ecological processes may operate at large as well as local spatial scales. However, in the first step, investigations of relationships between abundances of avian populations and area occupied by a species locally and regionally have a potential to elucidate the pattern. For this purpose, a complete elevational gradient in the tropics seems to be an ideal model system. Given the fact that most species prefer a specific elevational band (Dowsett 1986; Romdal 2001; Päckert et al. 2012; Price et al. 2014), the area occupied by particular species will, in general, decrease towards the highest elevations. Similarly, range sizes of species reflect their positions along the elevational gradient, with less widespread species being found at higher elevations (Fjeldså et al. 2012). Thus, by comparing area effects on local abundances of birds we can shed some light on mechanisms behind the distorted ARSR in tropical mountains (Reif et al. 2006; Djomo et al. 2014). To be more specific, if the extinction risk hypothesis holds, probability of extinction is expected to be higher in island-like conditions of montane areas where the communication among populations in different parts of their range is limited (Dowsett 1986; Fjeldså and Bowie 2008; Fjeldså et al. 2010; Voelker et al. 2010). Consequently, different shapes of ARSR within individual bird communities located along an

elevational gradient might arise. This hypothesis also predicts that population sizes of individual species should be more strongly related to locally occupied area than to geographical range size, because the former directly influences the extinction risk of local population (Shaffer 1981; Lande 1988).

In this study, we focused on passerine assemblages along the elevational gradient of Mt. Cameroon in West-Central Africa. The specific goals of the present study are (i) to describe changes in abundances of species occupying different parts of the elevational gradient; (ii) to reveal how such changes affect ARSR at different elevations and across the whole elevational gradient, which has not been investigated so far; (iii) to examine the effects of local and regional area available for particular species on their local abundances to determine if patterns are in accordance with the extinction risk hypothesis; and (iv) to estimate population sizes on Mt. Cameroon to test to what extent montane bird species compensate by higher local abundances for smaller area available.

Material and methods

This study was performed along the SW slope of Mt. Cameroon (Cameroon, West Africa), belonging to the Cameroon Volcanic Line stretching 1600 km in the NE-SW direction (Favalli et al. 2012). It is a 4095 m high active volcano lying at the sea coast of the Gulf of Guinea with perhumid climate with a distinct rainy season from late March to the beginning of November (peaking in July/September), and persistent cloud cover (Payton 1993; Fonge et al. 2005). Its south-western slopes are to a large extent covered by pristine tropical forest, which is structurally rather different from the habitats of the surrounding lowlands (Cheek et al. 1996). However, the primary lowland forest below 350 m a.s.l. has been replaced by plantations or secondary forests, whereas the montane forest is compressed from above, as ongoing volcanic activity generates an abrupt treeline at ca. 2200 - 2300 m a.s.l. The mid-elevation forest is interspersed by extensive clearings due to disturbances caused by forest

elephants. For more detailed description of elevational variation in forest structure see Bussmann (2006) and Proctor et al. (2007). Due to its high degree of spatial isolation, it represents a clearly defined geographical unit with specific avian assemblages with two strictly endemic species and 10 endemic subspecies (Gill and Donsker 2014).

Bird communities were sampled in 2011-2013 during the dry season (November - December) at six forested elevations (350 m, 650 m, 1100 m, 1500 m, 1850 m, 2200 m a.s.l.) using a standardised point count method (Bibby et al. 2000). Birds were recorded in the morning (6 am – 10 am) at 16 points at each elevation. The sample sites had a radius of 50 m, and were located at least 150 m apart to diminish the probability of multiple counting of individuals while remaining logistically tractable for the study. Each point was visited on three different days, the order of points was changed during each visit to avoid biases due to daytime, and birds were recorded in three consecutive 5 min intervals during each visit. The maximum number of individuals of a species recorded at any of these 5 min intervals was recorded as its abundance at the given point, and the sum across all 16 points as its abundance at the given elevation (hereafter “elevational abundance”). Subsequently, the mean elevational abundance across occupied elevations was recorded for each species (hereafter “mean abundance”) and used for further analyses, except for the analyses of actual bird communities occurring at individual elevations, where their elevational abundances were used. The aggregate abundances of birds in assemblages at a given elevation (hereafter “total abundance”) were calculated as the sum of abundances of all species present. Only passerine bird species were considered in this study to minimize potential confounding effects of taxonomy and/or e.g. body mass on the studied patterns. Furthermore, visitor migrants and aerial feeders (Willow Warbler - *Phylloscopus trochilus*; Wood Warbler - *Phylloscopus sibilatrix*; Barn Swallow - *Hirundo rustica*; Mountain Saw-Wing - *Psalidoprocne fuliginosa*)

were also excluded from this study. The taxonomy used in this study followed the IOC World Bird List version 4.2 (Gill and Donsker 2014).

A distance sampling protocol was used, with birds recorded in five 10 m wide radial distance bands (Buckland et al. 2001). We utilized the Distance v6.2 software (Thomas et al. 2010) to account for differences in species detectability and to estimate the number of unobserved individuals based on fitted detection functions (Buckland et al. 2001). However, we used the observed abundance estimates instead of the distance sampling-based estimates in further analyses for the following reasons: (i) There were too few records for rare species (out of 108 species 49 had less than 10 detections) for detection functions to be fitted and reliable abundance estimates to be retrieved. These naturally scarce species, however, cannot be simply omitted from our analyses. (ii) Our estimates derived from distance sampling were highly correlated with the observed abundance estimates ($r = 0.63$, $n = 59$, $p < 0.001$; Supplementary material Appendix 1, Fig. A1.1). (iii) Exceptions exist for which abundance estimates based on detection functions are unrealistically high (see Appendix 1 in Supplementary material for further details). (iv) To verify that our results are not sensitive to the type of abundance estimates used, we run additional analyses for a subset of species (with at least 10 observations, although generally at least 60-80 observations are recommended (Buckland et al. 2001)). We found similar main results (see Supplementary material Appendix 1): a negative ARSR (Spearman's $\rho = -0.25$, $p < 0.05$, Fig. A1.2) and species having their elevational midpoint in the montane forest had the highest mean abundances (Kruskal-Wallis chi-square: 18.00, $df = 2$, $p < 0.001$, Fig. A1.3).

Data on elevational ranges of passerines were compiled from primary published sources containing exact elevational observations or altitudinal limits recorded for each bird species on Mt. Cameroon (Bayly and Motombe 2004; Stuart 1986; Serle 1950, 1964; Young 1946; Boulton and Rand 1952; Eisentraut 1973; Bannerman 1915; this study). Elevational midpoint

was calculated from lower and upper altitudinal limit of a species distribution on Mt. Cameroon. Species were divided into three exclusive groups according to the position of their elevational midpoint as follows: (i) species having their elevational midpoint in lower third of the elevational gradient (up to 800 m a.s.l.) were included in the "lowland" group; (ii) species with midpoints between 800 m a.s.l. and 1600 m a.s.l. comprised the "middle" group; and (iii) birds with midpoint in the upper third of the gradient (above 1600 m a.s.l.) represented the "montane" species group. The classification approximately reflects basic altitudinal zonation of the forest on Mt. Cameroon.

The global species' range sizes were determined as the occupancy of $1^\circ \times 1^\circ$ grid cells where a species breeds or is resident (Rahbek et al. 2012). Mt. Cameroon was sliced to 100 m elevational bands and their area was calculated using the GMTED2010 dataset provided by the U.S. Geological Survey (<http://earthexplorer.usgs.gov/>). The local area on Mt. Cameroon potentially occupied by individual species was calculated as the summed area of elevational bands that each species occupies. Subsequently, the extrapolated population size of each species on the mountain was calculated as the product of its recorded mean density on Mt. Cameroon and local area occupied.

Non-parametric Spearman-rank correlation analysis was utilized to describe the relationship between local abundance and range size or local area occupied by a species. Differences in abundances, range sizes, local area occupied and extrapolated population sizes of species having their midpoints in lowland, mid-elevations or montane environment were analysed by means of a non-parametric Kruskal-Wallis test.

Results

Altogether 108 passerine species were recorded in the study area (excluding visitor migrants and aerial feeders; see Methods for further details). The mean abundance of individual species

across elevations ranged from 1 to 48.33 (mean = 8.82, sd = 8.16) and increased with the midpoint of their elevational distribution (Spearman's $\rho = 0.38$, $p < 0.001$). The global range sizes spanned from one $1^\circ \times 1^\circ$ grid cell to 1081 grid cells (mean = 186.50, sd = 184.24) and decreased with the species' elevational midpoint ($\rho = -0.44$, $n = 108$, $p < 0.001$). The local area potentially occupied by each species on Mt. Cameroon also decreased with its elevational midpoint ($\rho = -0.40$, $n = 108$, $p < 0.001$). Species having their elevational midpoint in the montane forest (above 1600 m a.s.l.) had the highest mean abundances (Fig. 1a; Kruskal-Wallis chi-square: 15.11, $df = 2$, $p < 0.001$), but the lowest range sizes (Fig. 1b; Kruskal-Wallis chi-square: 30.19, $df = 2$, $p < 0.001$) and occupied the least area locally on the mountain (Fig. 1c; Kruskal-Wallis chi-square: 30.81, $df = 2$, $p < 0.001$).

The total abundances of birds in focal assemblages along the elevational gradient were relatively similar, reaching values of ca. 430 to 470 individuals at 16 sampling points. Exceptions were the lowest elevation of 350m a.s.l. harboring only 320 individuals, and the elevation of 1100m a.s.l. with the most abundant bird community having a little less than 600 individuals (Fig. 2, dark bars). The number of individuals per species increased continually with altitude, with approximately three times as many individuals per species at the highest elevation as in the lowland (Fig. 2, light bars).

The ARSR across all species of the entire forested elevational gradient of Mt. Cameroon showed a negative trend ($\rho = -0.16$, $n = 108$, $p < 0.1$; Fig. 3a). The signature of an extinction filter, if it operates, should be most pronounced in endemic species and subspecies (highlighted as grey triangles in Fig. 3) as they have no or limited possibilities of recolonization from other areas. Unfortunately, their low sample size does not allow for proper statistical testing. In contrast with the ARSR of all species along the entire elevational gradient, the ARSR of the three species groups with different elevational midpoints showed a variable pattern, as it changed from a positive trend in the "lowland" group ($\rho = 0.40$, $n =$

56, $p < 0.01$; Fig. 4a) to a negative trend for “middle” species ($\rho = -0.40$, $n = 33$, $p < 0.1$; Fig. 4b), and no trend for “montane” species ($\rho = -0.03$, $n = 19$, $p = 0.91$; Fig. 4c). A similar pattern was found for passerine assemblages at different elevations as it changed from a positive trend in the lowland (350m a.s.l.: $\rho = 0.39$, $n = 53$, $p < 0.01$; 650m a.s.l.: $\rho = 0.26$, $n = 61$, $p < 0.05$; Fig 5a, b) to a negative or no trend at higher elevations (1100m a.s.l.: $\rho = -0.20$, $n = 52$, $p = 0.15$; 1500m a.s.l.: $r = -0.40$, $n = 34$, $p < 0.05$; 1850m a.s.l.: $\rho = -0.37$, $n = 32$, $p < 0.05$; 2200m a.s.l.: $\rho = -0.14$, $n = 21$, $p = 0.54$; Fig. 5c, d, e, f). On the contrary, no trend in abundance-local area relationship was revealed across the entire elevational gradient ($\rho = -0.10$, $n = 108$, $p = 0.31$; Fig. 3b). The trend was positive in “lowland” species ($\rho = 0.26$, $n = 56$, $p < 0.1$) and “montane” species ($r = 0.64$, $n = 19$, $p < 0.01$), whereas no trend was detected in “middle” species ($\rho = -0.02$, $n = 33$, $p = 0.90$). Within assemblages at individual elevations a positive trend was detected at the lowermost elevation (350 m a.s.l.: $\rho = 0.36$, $n = 53$, $p < 0.01$) but was insignificant elsewhere (650 m a.s.l.: $\rho = 0.17$, $n = 61$, $p = 0.18$; 1100 m a.s.l.: $\rho = -0.07$, $n = 52$, $p = 0.65$; 1500 m a.s.l.: $\rho = -0.13$, $n = 34$, $p = 0.45$; 1850 m a.s.l.: $\rho = 0.10$, $n = 32$, $p = 0.59$; 2200 m a.s.l.: $\rho = 0.12$, $n = 21$, $p = 0.60$). The extrapolated population sizes for individual passerines on Mt. Cameroon did not differ among the three groups of species classified according to the position of their elevational midpoint (Kruskal-Wallis chi-square: 0.66, $df = 2$, $p = 0.72$; Fig. 6).

Discussion

In this study, we tested the abundance-area relationship in passerine assemblages along a perhumid tropical elevational gradient, which has never been done before. We found a negative relationship between local abundance and range size at the scale of the whole mountain, which contradicts a positive trend frequently observed in temperate regions (Gaston and Blackburn 2000, 2003). Deviation from a positive ARSR is obviously caused by

a combination of decreasing range sizes and increasing abundances of birds towards high elevations, as the montane range-restricted species turned out to be the most abundant ones, in agreement with several previous studies (Fjeldså 1999; Ryan et al. 1999; Owiunji et al. 2005; Sekercioğlu and Riley 2005; Reif et al. 2006; Fjeldså et al. 2010, 2012; Djomo et al. 2014).

Avian species richness declines monotonically with elevation on Mt. Cameroon (Hořák et al. unpublished data), which is a typical pattern for wet-based mountains (McCain 2009), and we show here that the number of individuals per species increases with elevation. Such an observation fits to predictions of density compensation hypothesis, which suggests that in species poor assemblages individual species may increase their abundances to fill the available free ecological space (MacArthur 1972). Our data suggest “an exact compensation” as the total abundances of bird assemblages in montane elevations were similar to those of lower ones. Only the lowest (350 m a.s.l.) and mid-elevation (1100 m a.s.l.) deviated notably from the typical values. This is an interesting fact considering that overall environmental productivity (McCain 2009) and food availability as estimated by abundance of insects or fruits seems to decrease with altitude (Janzen 1973; Janzen et al. 1976; Loiselle and Blake 1991). Thus, one would expect elevational decrease in total abundances, too. However, the food limitation issue remains poorly studied along tropical elevational gradients and abundance patterns observed here could be obscured for instance by seasonal variation in food supply (Ashmole 1963), patterns of which remain vastly unexplored. Uniform abundance pattern could also be explained by fine specializations of montane species to habitats at high elevations, allowing them to reach total abundances comparable to those of more diverse communities (Diamond 1970; MacArthur 1972; Wright 1980). Nevertheless, the extent to which competitive release and density compensation can account for high abundances of montane species remains to be evaluated within guilds of competing species (Wright 1980).

In addition, we found differences in ARSR between elevations. For the lowland forest assemblage (350 m and 650 m a.s.l.) the ARSR was positive, while it was negative at mid-elevations (1500 m and 1850 m a.s.l.), and we revealed a negative but insignificant trend at 1100 m a.s.l. and in the upper montane forest (2200 m a.s.l.). The same qualitative patterns emerged for groups of species defined according to the position of their elevational midpoint, with positive ARSR in the "lowland" group, negative trend of ARSR in "middle" group and no trend in the "montane" species. This finding implies two important points. First, the overall negative trend of ARSR across all species occurring on the elevational gradient of Mt. Cameroon is not a single relationship, but is composed of multiple forms of ARSR occurring along this steep environmental gradient (*cf.* Gaston 1996; Blackburn et al. 2006). Second, it suggests that the inverse ARSR, as reported for some tropical environments, may be an idiosyncrasy of montane (or other insular) environments rather than a general feature of tropical bird assemblages, because lowland patterns follow the expectations based on the most frequently observed patterns. The density compensation hypothesis alone is unable to fully account for the diversity of ARSRs detected, as it does not make any predictions about differential effects of range sizes within individual elevational assemblages. We propose that interactions of several factors are responsible. Specifically, a combination of missing range restricted species in lowland areas, and increased densities (facilitated by ecological specialization and/or density compensation) in species of upper elevations coupled with their small ranges creates the observed elevational changes in ARSR.

Basically, by maintaining high local abundances, Afromontane bird species might compensate for small range sizes and thus lower the risks of extinction, as has been suggested for marsupials in Australia (Johnson 1998), birds of Australian wet tropics (Williams et al. 2009) or butterflies in Finland (Komonen et al. 2009). Such a hypothesis ultimately assumes that extinction filter removes small ranged species that have scarce local populations. This

mechanism could account for elevational differences in ARSR described here, as its effect should be more pronounced towards higher elevations, where factors influencing probability of extinction, i.e. the area occupied locally and range sizes (Shaffer 1981; Lande 1988) tend to decrease. The extinction risk hypothesis further predicts relatively stronger effect of local area on abundances, if compared to range size, because of its more direct effect on local populations. Contrary to our expectations, we observed none and positive relationships between area occupied locally and abundance in passerine assemblages on Mt. Cameroon. Moreover, a non-significant pattern observed in the uppermost bird assemblages, where the effect of extinction filter should be the strongest, does not fit to the extinction risk hypothesis. Nevertheless, the extinction hypothesis should not be discarded, as the estimated population sizes of individual bird species on Mt. Cameroon did not change with their elevational midpoint. It suggests that high abundances of species living at upper elevations compensate for area reduction towards higher altitudes, so that overall population sizes of montane birds remain on average similar to population sizes of species at low elevations (Fig. 6). Small populations of montane species would presumably raise their extinction risk significantly (Lande 1988; Purvis et al. 2000).

In conclusion, we found that the distorted ARSR in an avian assemblage on Mt. Cameroon is mostly a result of relatively high local abundances of species at high elevations. At the same time it is not a single relationship, but bird assemblages inhabiting different elevations show contrasting shapes of ARSR. Our data imply that high abundances of montane passerines might be a compensation for small area available at high elevations, and as a result they can maintain population sizes comparable to their lowland-forest counterparts. This pattern might partly be an output of an extinction filter which favours tropical montane forest species that are able to attain high local abundances by means of specialization or by taking advantage of local environments with less intensive competition.

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467 Supplementary material (Appendix .XXXXX at <www...journal.org/readers/appendix>).

468 Appendix 1.

469

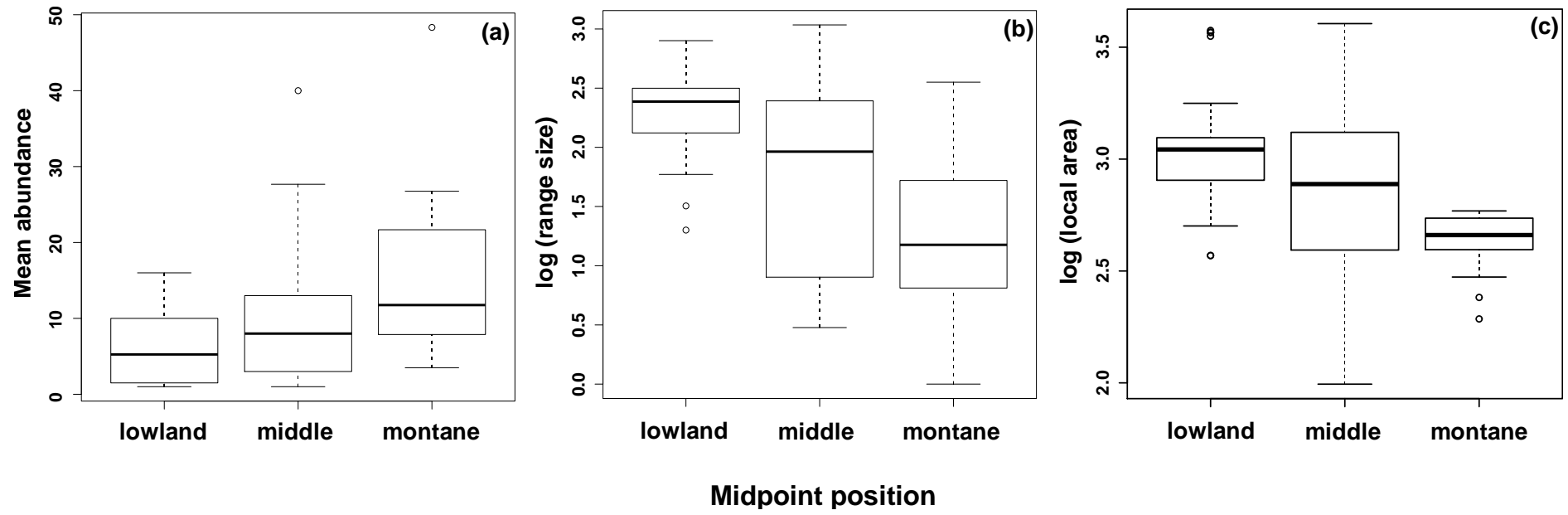
470 **Fig. 1:** Passerine species divided into three groups based on the position of their midpoint of elevational distribution on Mt. Cameroon (see
 471 Methods): **a)** mean abundance of individual species across elevations (Kruskal-Wallis chi-square: 15.11, $df = 2$, $p < 0.001$); **b)** log-transformed
 472 range size (Kruskal-Wallis chi-square: 30.19, $df = 2$, $p < 0.001$); **c)** log-transformed local area occupied on Mt. Cameroon (Kruskal-Wallis chi-
 473 square: 30.81, $df = 2$, $p < 0.001$).

474 **Fig. 2:** Total abundances and number of individuals per species for particular bird assemblages along the elevational gradient on Mt. Cameroon.

475 **Fig. 3:** **a)** Abundance-range size relationship of passerine species occurring along the elevational gradient of Mt. Cameroon (Spearman's $\rho = -$
 476 0.16, $n = 108$, $p < 0.1$). **b)** Abundance-local area relationship ($\rho = -0.10$, $n = 108$, $p = 0.31$).

477 **Fig. 4:** Abundance-range size relationships of three groups of passerine bird species: **a)** species with midpoints below 800 m a.s.l. (Spearman's
 478 $\rho = 0.40$, $n = 56$, $p < 0.01$); **b)** species with midpoints between 800 m a.s.l. and 1600 m a.s.l. ($\rho = -0.40$, $n = 33$, $p < 0.1$); **c)** species with
 479 midpoints above 1600 m a.s.l. ($\rho = -0.03$, $n = 19$, $p = 0.91$). **Fig. 5:** Abundance-range size relationships of individual passerine bird assemblages
 480 along the elevational gradient of Mt. Cameroon. **a)** 350m a.s.l.: Spearman's $\rho = 0.39$, $n = 53$, $p < 0.01$; **b)** 650m a.s.l.: $\rho = 0.26$, $df = 61$, $p <$
 481 0.05; **c)** 1100m a.s.l.: $\rho = -0.20$, $df = 50$, $p = 0.15$; **d)** 1500m a.s.l.: $\rho = -0.40$, $n = 34$, $p < 0.05$; **e)** 1850m a.s.l.: $\rho = -0.37$, $n = 32$, $p < 0.05$; **f)**
 482 2200m a.s.l.: $\rho = -0.14$, $n = 21$, $p = 0.54$.

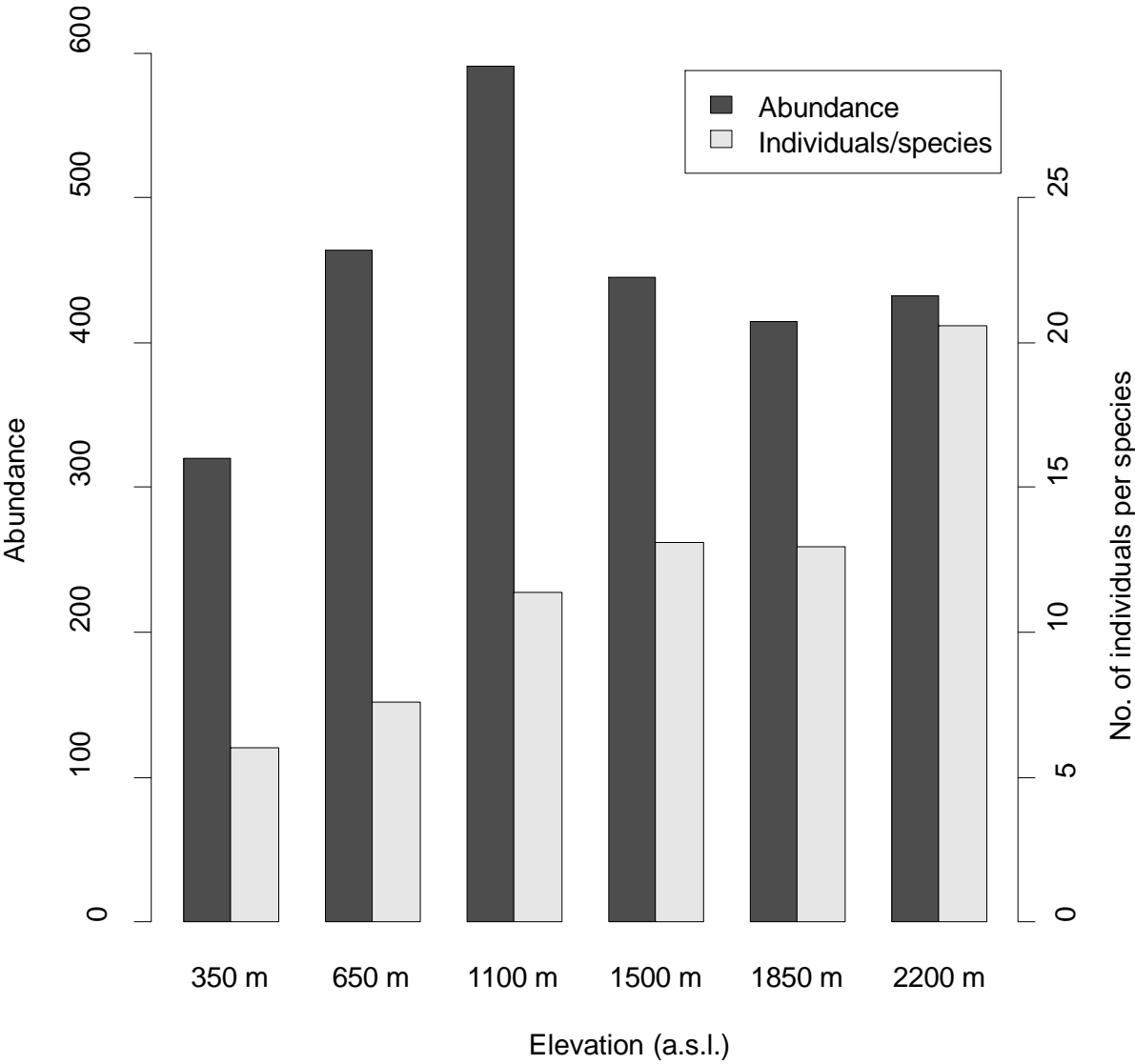
483 **Fig. 6:** Extrapolated population sizes (mean abundance x area occupied locally) of detected passerine bird species on Mt. Cameroon (Kruskal-
 484 Wallis chi-square: 0.66, $df = 2$, $p = 0.72$).

485 **Fig. 1**

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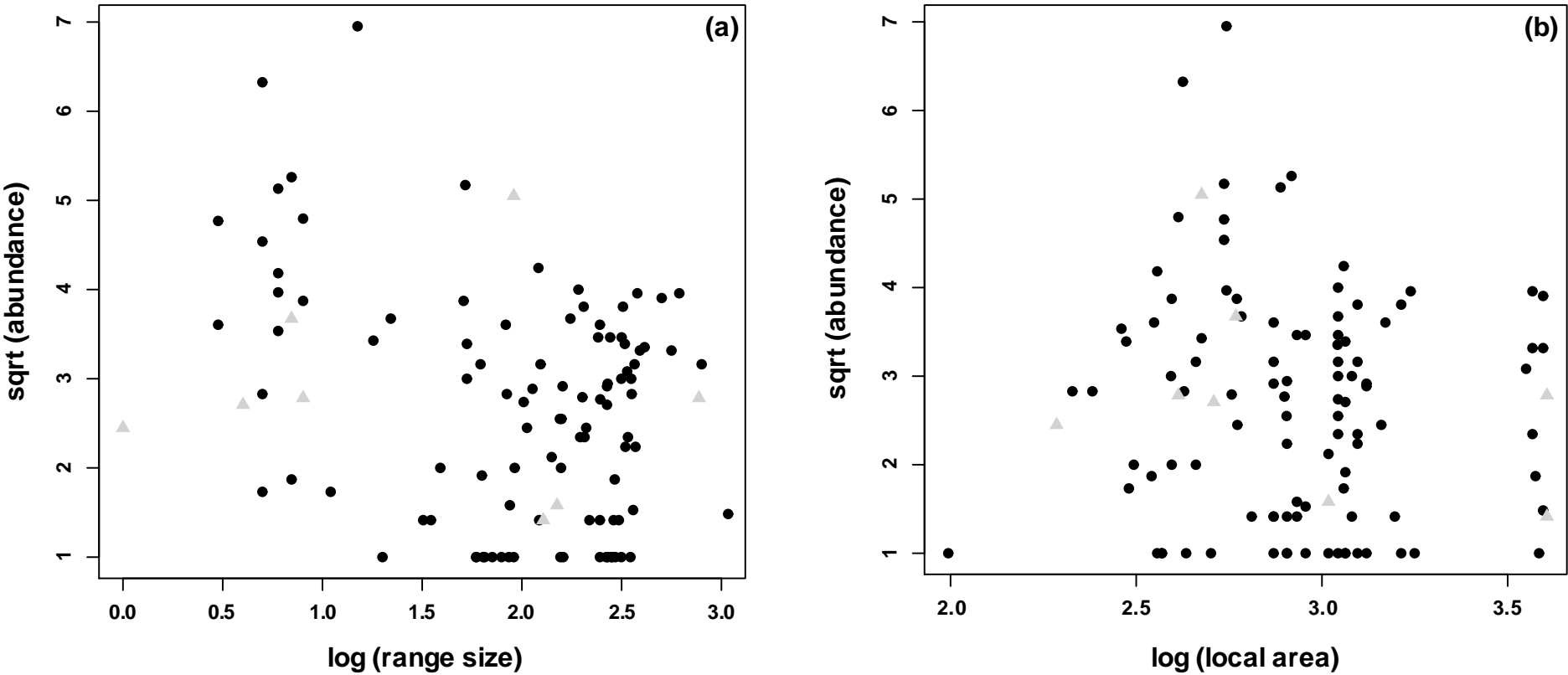
488 **Fig. 2**



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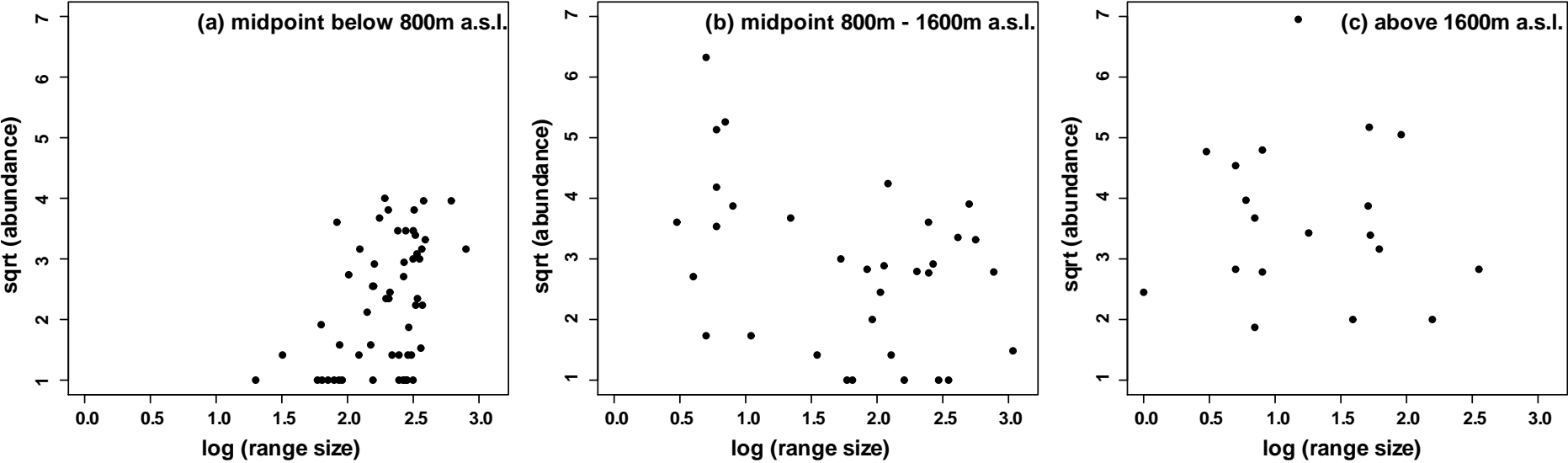
491 **Fig. 3**



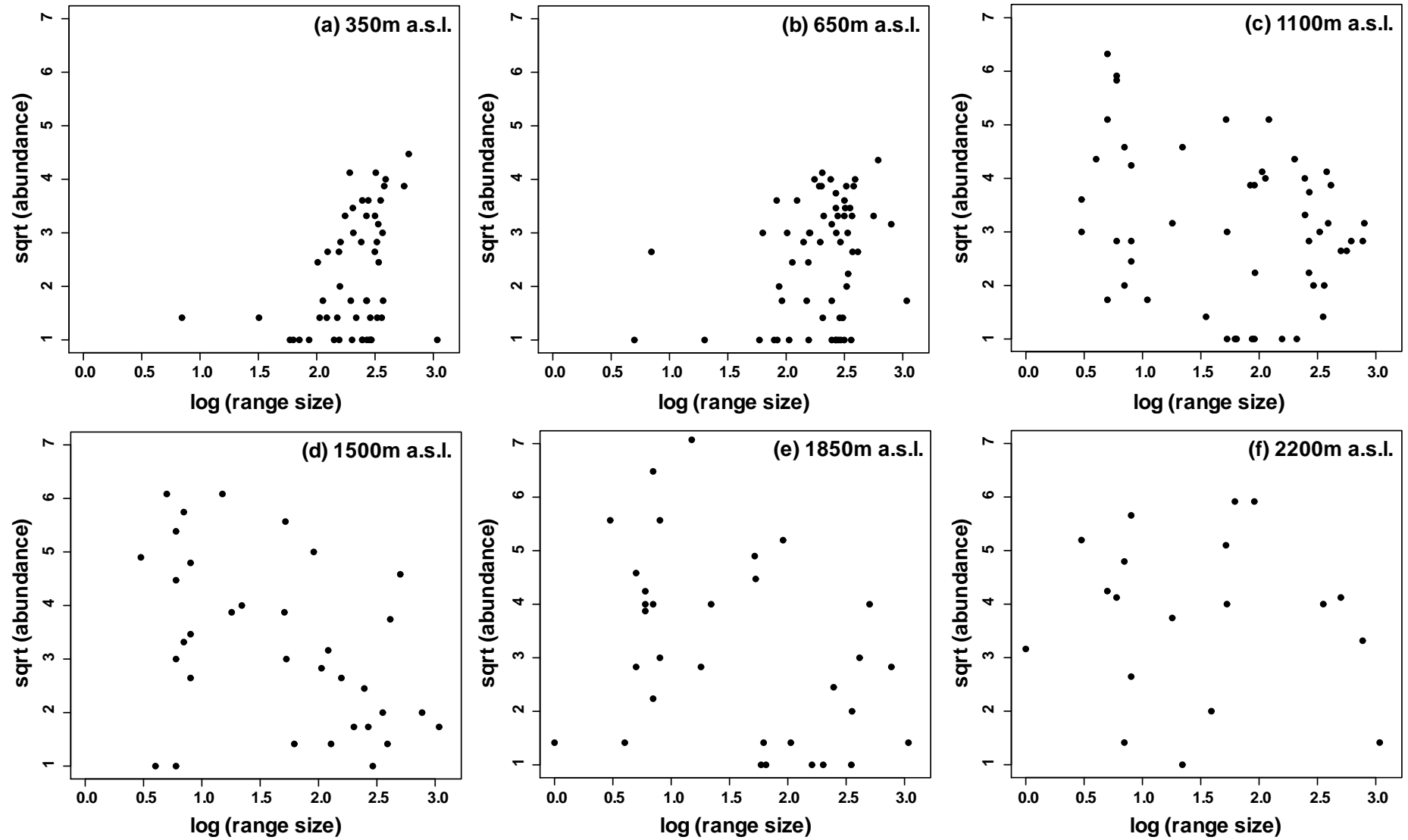
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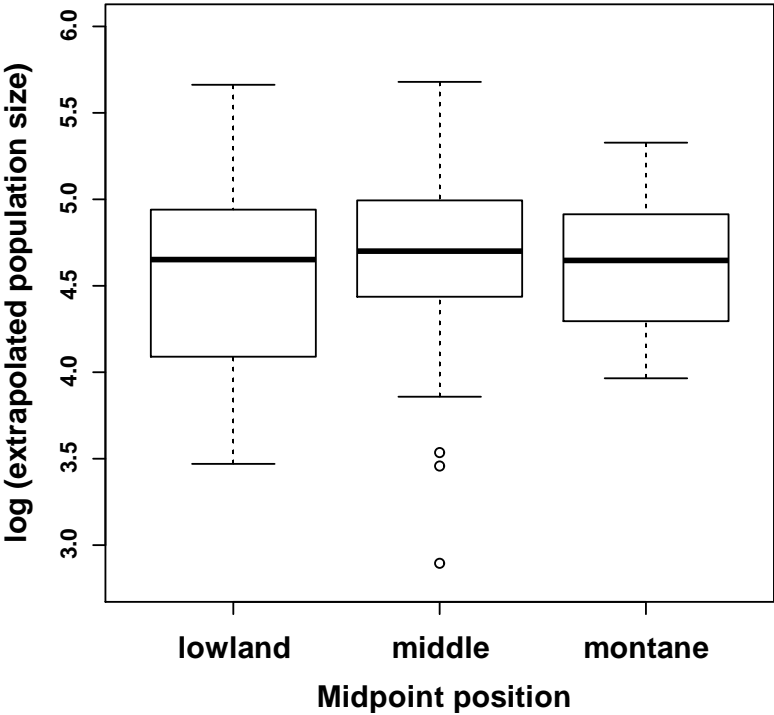
Fig. 4



502 Fig. 5



504 **Fig. 6**



505

Supplementary material

Appendix 1 Analyses utilizing abundance estimates based on a distance sampling protocol.

Fig. A1.1: Comparison between observed and distance sampling based estimates of mean abundances of passerine species occurring along the elevational gradient of Mt. Cameroon ($r = 0.63$, $n = 59$, $p < 0.001$). Estimates were based on detection functions fitted by the Distance v6.2 software (Thomas et al. 2010) for species with at least 10 detections. The outliers (depicted as stars) represent rarely or quietly vocalizing species (Cya_ori, Elm_alb, Mus_adu, Nes_she, Plo_ins), or species occurring in small flocks, i.e. with clustered occurrences (Phy_poe, Phy_pol, And_tep). The first five species have their elevational midpoint in the montane forest (above 1600 m a.s.l.), while the latter three have their elevational midpoint at mid-elevations (all have midpoint above 1300 m a.s.l.). Note the unrealistic mean abundance estimates based on detection functions (x-axis) for these species. Species abbreviations: And_tep: *Andropadus tephrolaemus*, Cya_ori: *Cyanomitra oritis*, Elm_alb: *Elminia albiventris*, Mus_adu: *Muscicapa adusta*, Nes_she: *Nesocharis shelleyi*, Phy_poe: *Phyllastrephus poensis*, Phy_pol: *Phyllastrephus poliocephalus*, Plo_ins: *Ploceus insignis*.

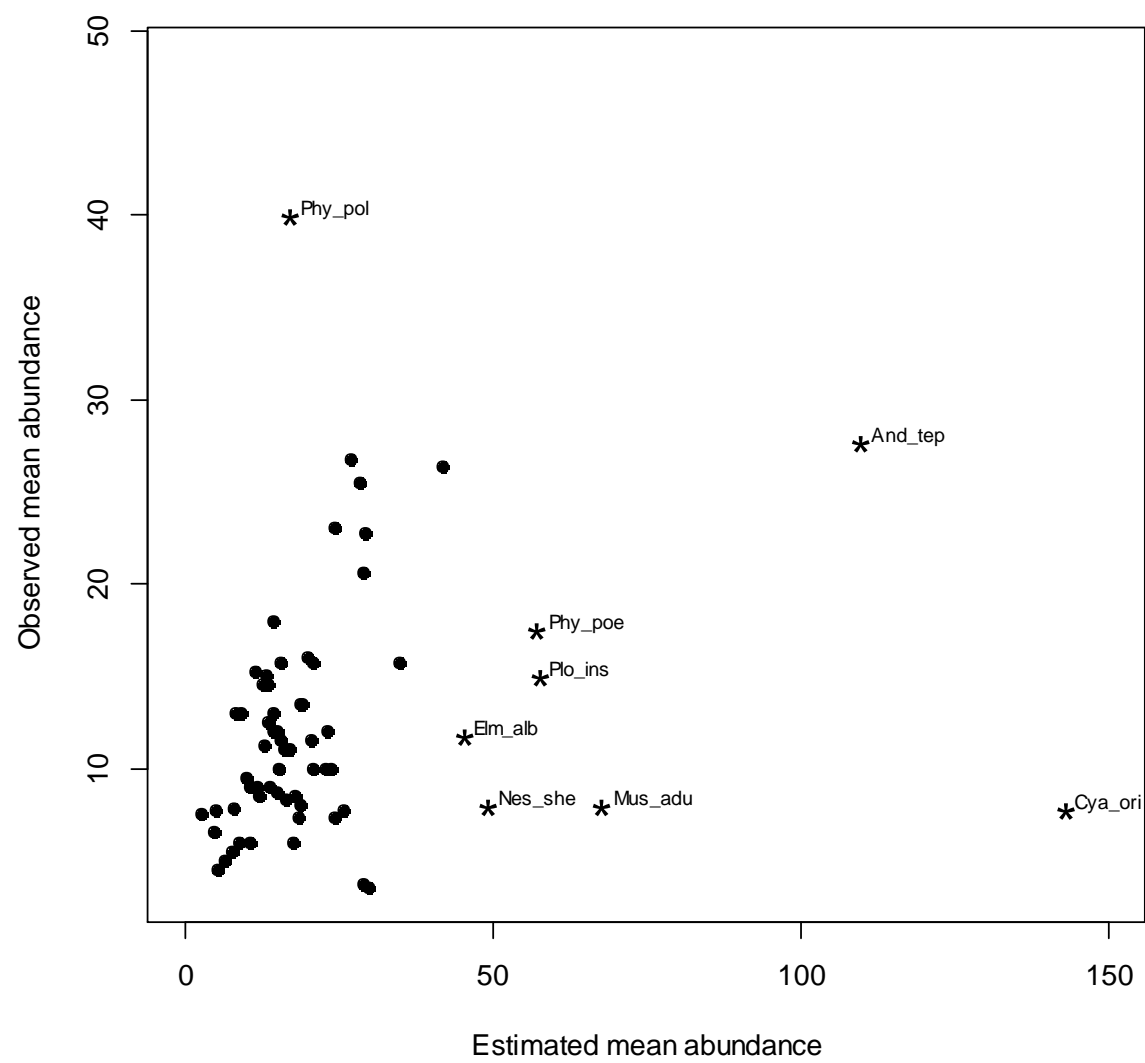


Fig. A1.2: Abundance-range size relationship of passerine species occurring along the elevational gradient of Mt. Cameroon (Spearman's $\rho = -0.25$, $n = 108$, $p < 0.05$). Abundance estimates are derived from a distance sampling protocol for species with at least 10 detections. Range sizes are log transformed, estimated abundances are square-root transformed.

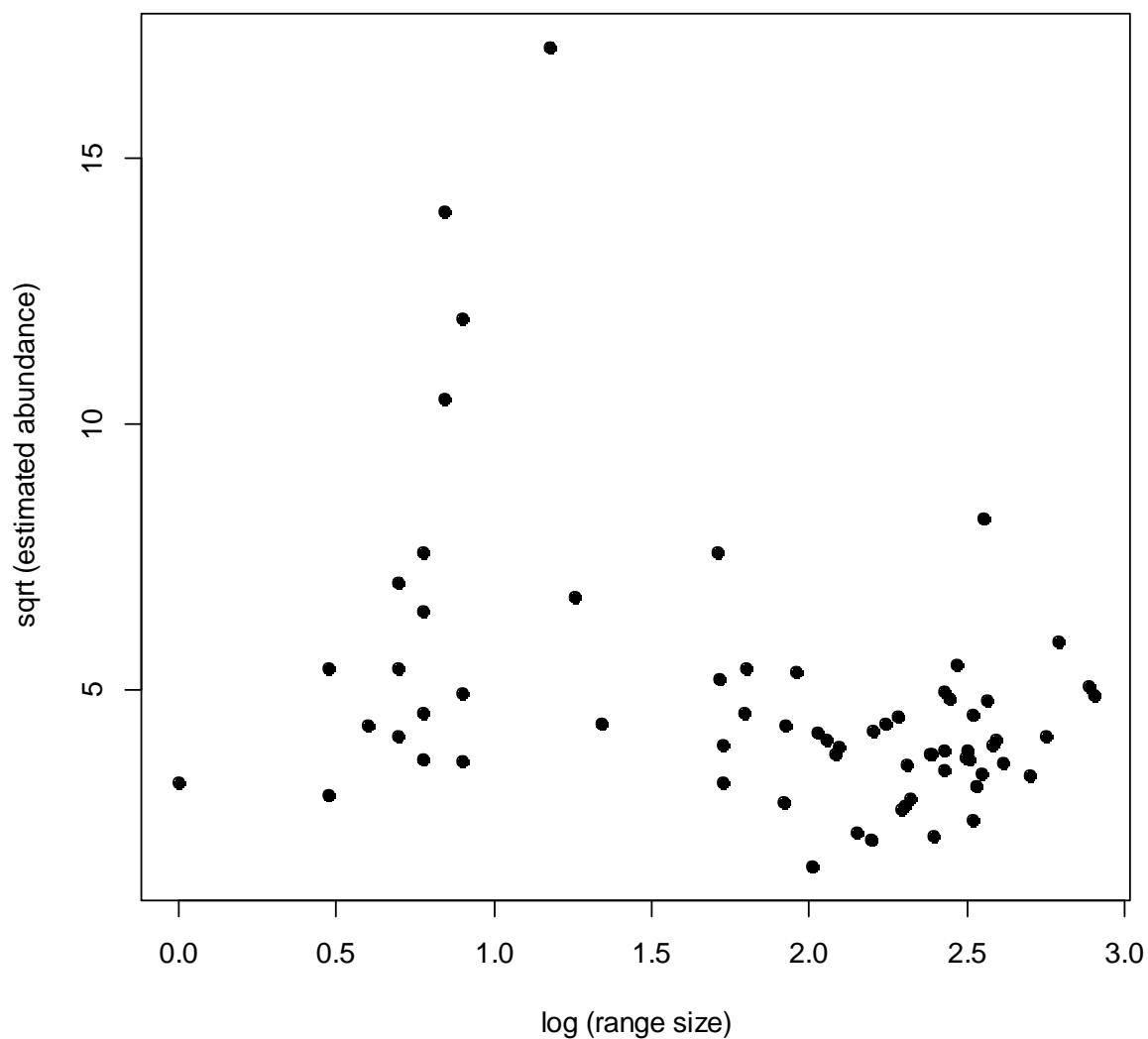
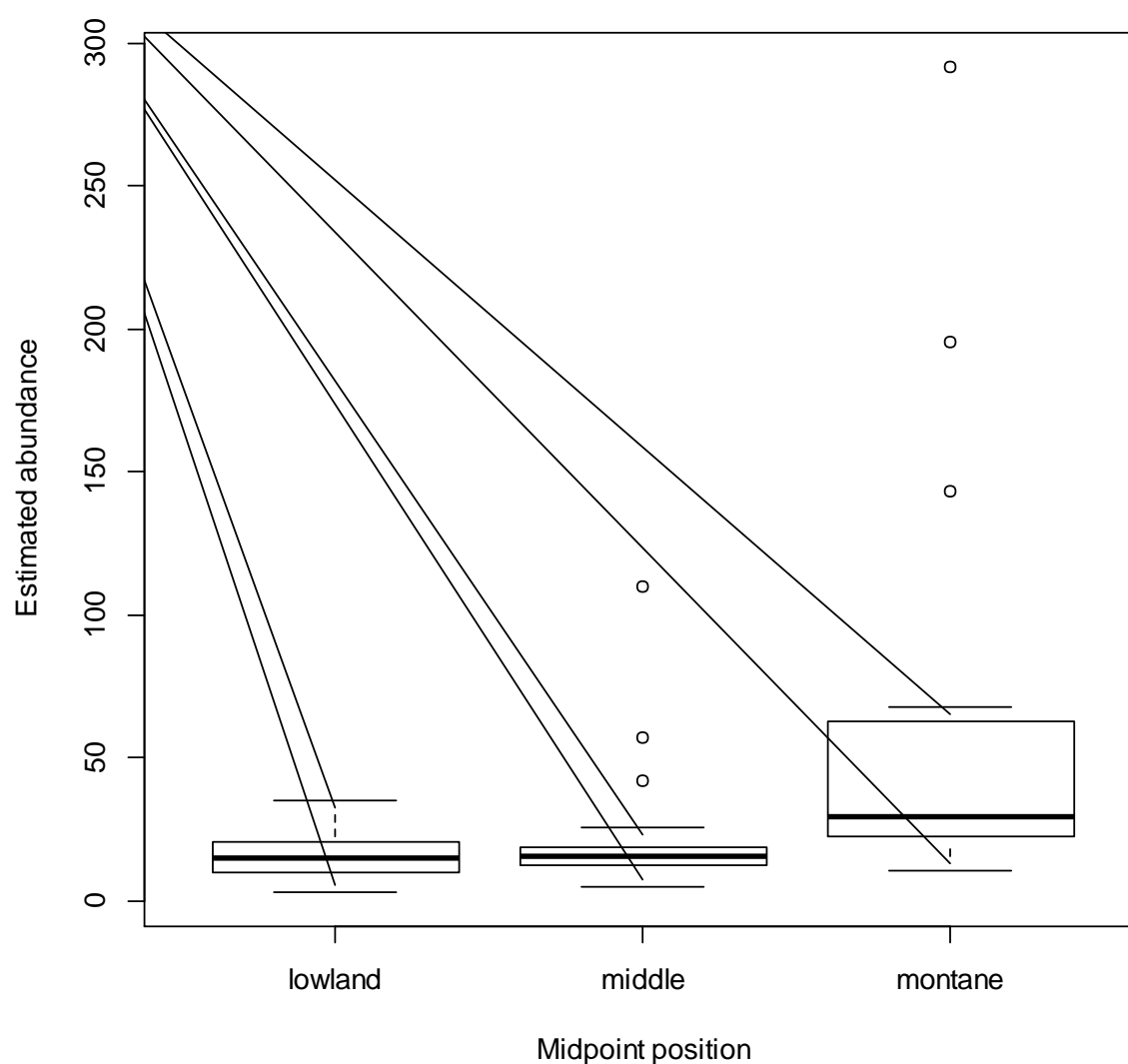


Fig. A1.3: Mean abundances of passerine species across elevations (Kruskal-Wallis chi-square: 18.00, $df = 2$, $p < 0.001$) divided into three groups based on the position of the midpoint of their elevational distribution on Mt. Cameroon (see Methods). Abundance estimates are derived from a distance sampling protocol for species with at least 10 detections.



CHAPTER 6

Djomo, N. E., Sedláček, O., Bayly, N., Albrecht, T., Ferenc, M., Reif, J., Motombi, F. N. & Hořák, D. 2014. Comparison of avian assemblage structures in two upper montane forests of the Cameroon volcanic line: lessons for bird conservation. *Biodiversity and Conservation* 23(6): 1469–1484.

Comparison of avian assemblage structures in two upper montane forests of the Cameroon volcanic line: lessons for bird conservation

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Abstract The Cameroon volcanic line montane forests host specific avian assemblages with many endemic species. Such unique bird assemblages deserve adequate description for proper protection. For this purpose, we sampled birds in the upper montane forests of Mts Cameroon and Oku situated at ~2,250 m. We combined point counts and continuous observations to describe species composition and estimate densities of particular species. In total, we recorded 106 species; 45 only on Mt Oku, 21 only on Mt Cameroon, and 40 common to both mountains. The higher species richness on Mt Oku was due to non-forest

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species that invaded the forest interior due to recent human disturbance. Endemic species of the Cameroon volcanic line and montane non-endemic species had higher abundances than widespread species in general. As a result, we did not find a positive abundance–range-size relationship for both locations. Our findings support a previously made observation that montane species of the Cameroon volcanic line have higher densities compared to widespread species. However, we also show that the structures of avian assemblages vary between sites as species spatial turnover was lower on Mt Cameroon than on Mt Oku and species common to both were more abundant on Mt Cameroon. This could be attributed to the more pristine forest on Mt Cameroon, with higher annual rainfall but also due to lower human impact and the existence of a continuous forest. Conservation action within the broader landscape context is thus necessary to secure diverse montane forests in West-Central Africa in the future.

Keywords Assemblage structure · Species richness · Abundance–range size relationship · West-Central Africa · Range-restricted species

Introduction

Recent macroecological analyses of global geographical distribution of avian diversity revealed that the patterns of species richness cannot be explained fully by climatic variation (Storch et al. 2006). Instead, the information about topographic relief should be incorporated into the models to predict correctly the extraordinary high diversity in tropical mountain regions (Rahbek and Graves 2000; Davies et al. 2007). It appears that tropical mountains serve as generators of diversity and recent scientific efforts are focused on understanding the mechanisms behind (Fjeldså et al. 2012). Mountains close to the Equator are exceptional not only in overall species richness of birds but also because of their unusually high levels of endemism (Omme et al. 2005). Such species are of concern to conservation biologists as they are highly vulnerable to extinction; for instance, due to climate change (Malcolm et al. 2006). However, the peculiarity of tropical mountain assemblages of birds is further accentuated by a specific and still poorly known abundance structure.

Based on a few recent studies we know that species with tiny spatial distributions tend to be very abundant locally where they occur (Reif et al. 2006; Romdal and Rahbek 2009; Williams et al. 2009; Fjeldså et al. 2010). This finding goes against one of the best-documented general relationships in macroecology—the abundance range size relationship, which assumes that the geographical range of species should positively correlate with their local abundances (Brown 1984; Gaston and Blackburn 2000). To explain this phenomenon, it has been suggested that tropical mountain endemics are phylogenetically old species which are probably well specialized for local environmental conditions, and this may enhance their resilience by maintaining high demographic connectivity throughout their distributional ranges (Fjeldså et al. 2012). However, we are still far from understanding the processes responsible for high abundances of endemic species. Limitations in our current knowledge of the structure of avian assemblages in tropical mountain forests remain because of the physically demanding field work in these areas and the limited research effort in remote tropical regions in general. Besides, factors influencing community-wide patterns in tropical bird assemblages seem to be less predictable than those

observed in northern temperate zones as marked differences are reported among sites (Karr 1976; Keast 1985), as well as at the same site from year to year (Brosset 1981; Stiles 1983). This lack of knowledge hinders the formulation of hypotheses about maintenance and origin of diversity in tropical mountain forests and also impedes the adoption of adequate conservation actions.

From a global perspective, Afrotropical mountain forests deserve more attention as they show high levels of spatial isolation and endemism resulting in unique assemblage structures. Montane forest communities in Africa occur above 1,600 m a.s.l. (Thomas 1986; Smith et al. 2000; Wethered and Lawes 2003, 2005) and form the so-called Afromontane archipelago (White 1981; Grimshaw 2001; Taylor et al. 2012), as individual forest blocks are separated from each other by surrounding lowlands. In West-Central Africa this Afromontane archipelago mostly follows the Cameroon volcanic line including Mt Cameroon and the islands of Bioko and São Tomé (Scatena et al. 2010). The montane forests here have some peculiar characteristics (cooler climate and higher humidity) that clearly distinguish them from other tropical forests and are particularly rich, with high numbers of endemic plant, bird, amphibian, reptile, mammal and insect species (Dowsett-Lemaire and Dowsett 2000, unpubl. data). The Cameroon volcanic line is thus considered a ‘hotspot’ for biodiversity and endemism on a continental scale for a wide variety of taxa (Fishpool and Evans 2001; Brooks and Thompson 2001). With respect to birds, it contains 28 restricted-range endemic species including the Mount Cameroon Francolin *Francolinus camerunensis*, the Mount Cameroon Speirops *Speirops melanocephalus* and the Bannerman’s Turaco *Tauraco bannermani* and ranks third for important bird areas in mainland Africa in terms of restricted range species (after the Albertine Rift Mts and the Eastern Arc Mts, Dowsett-Lemaire and Dowsett 2000).

The general objective of the present study is to provide information about the structure of avian assemblages inhabiting afromontane forests at the same elevation but located on different mountains. We carried out this study on the two highest peaks of the Cameroon volcanic line—Mt Cameroon and Mt Oku. These two mountains are part of the same range but at different positions, with Mt Cameroon located on the Atlantic coast and Mt Oku further inland, which gives rise to different climates, land use histories and landscape contexts. Therefore, we aim to enhance our incomplete knowledge of unique montane communities but also provide a starting point for the clarification of the role of the large scale landscape context in shaping the structure of local avian assemblages in the Cameroon volcanic line. Specifically, our goal is to: (i) describe species composition of two avian montane assemblages and provide information about densities of their members, (ii) assess the level of species spatial turnover between mountains, (iii) test for differences in species-area relationships, and (iv) evaluate whether abundances of restricted range species are higher than those of widespread ones which would have implications for nature conservation.

Methods

Study areas

The study was performed in the forests of Mt Cameroon and Mt Oku in the Cameroon volcanic line. Mt Cameroon, also known as Mt Fako, is one of Africa’s largest volcanoes (4,095 m a.s.l.) that rises from lowland tropical rain forest at sea level and extends inland from the gulf of Guinea in the bight of Biafra (DeLancey and DeLancey 2000). Mt Oku,

also known as Kilum mountain, is located in the western highland plateau of Cameroon. It is the second highest mountain in mainland West Africa and rises from grassland to 3,011 m a.s.l (Fiona et al. 2000).

The study areas were located on Mt Cameroon (4°08.67'N 9°07.31'E) at an altitude of ~2,250 m a.s.l and on Mt Oku (6°12.06'N 10°31.03'E) at an altitude of 2,240 m a.s.l. On Mt Cameroon, field work was carried out in the upper montane forest interior close to Mann's spring, which is a natural spring situated at the border of the forest and montane grassland, and on Mt Oku in the Kilum Ijim upper montane forest interior. Unbroken high-montane forests stretch downhill from these sites, although their edges have been degraded to varying degrees by fires invading from the savannah on Mt Cameroon and by small scale human clearance for farming and cattle grazing on Mt Oku. On Mt Cameroon, average rainfall at the foot of the mountain is up to 10,000 mm per year and falls to 2,000 mm per year in the northeast portion of the massif (Payton 1993, unpubl. data). Its montane forest is found at relatively low elevations, generally above 800 m, but on its seaward slope montane trees appear as low as 500 m, possibly because of extensive cloud cover and frequent mists (Graham et al. 2005). Important trees here include *Schefflera abyssinica*, *S. manni*, *Prunus africana* and *Podocarpus* spp. Habitats also include montane *Sporobolus* grasslands and *Gnidia* woodlands (Njabo 2006). Average annual rainfall is over 2,400 mm per year (Forboseh et al. 2003) in the Kilum Ijim forest on Mt Oku and the canopy of the forest is unusually open. Important trees throughout include *Carapa procera*, *S. abyssinica*, *S. manni*, *Syzygium guineense bamendae* and *P. africana*. There is extensive *Arundinaria* bamboo forest above 2,600 m (Njabo 2006).

Bird sampling

Fieldwork was carried out during the dry season on both mountains. On Mt Cameroon, we performed the fieldwork at the beginning of the dry season as well as at the turn of dry and wet seasons in November 2011 (OS, DH, TA, MF, EDN) and February 2004 (NB, FNM), respectively. On Mt Oku, we sampled birds at the beginning of the dry season in November 2008 (OS, DH, JR, TA). These periods correspond to the breeding season of the majority of birds in the montane forests of the Cameroon volcanic line (Serle 1981; Tye 1986). During field surveys we always employed two methodological approaches: point counts and random walks. We used these two methods to maximize detection of birds in the dense forest and estimate abundances precisely. For point counts we established a line transect with a random starting point containing 16 census points within the forests interior on both mountains (only 15 points were established in 2004 on Mt Cameroon and point locations were different from those in 2011). The distance between neighbouring points was 150 m which is enough to avoid counting the same individual twice (Huff et al. 2000). We conducted three visits to each census point recording all birds (both visually and acoustically) within a 50 m radius for 15 min. For further analyses we used information about the maximum number of species for all three visits recorded at particular points and the maximum estimated number of individuals per species for density estimates. We believe that abundance estimates for particular species are adequate for inter-specific comparisons (cf. Raman 2003). We therefore decided to use a narrow fixed radius (50 m) in which the detectability for all species was almost the same (Reif et al. 2006). We performed all visits during morning hours (between 06:00 and 10:00), changing the order of points visited to factor out the effect of daytime.

We also recorded all birds heard or seen both during the day and at night during the entire duration at Mann's spring (1 week in 2004 and 2011, respectively) and on Mt Oku

(2 weeks in 2008) through random walks. Species detected through random walks were added to those detected through point counts and that constituted our checklist. Note that the abundance information and all the analyses (except for overall species counts) are based on data collected during point counts only.

Data analysis

In order to describe the structure of local avian assemblages, we employed fundamental macroecological analytical tools such as abundance–range size relationship (hereafter ARSR) and species–area relationship (hereafter SAR); two important tools for determining the minimum area for biodiversity conservation. The ARSR is based on the prediction that local abundances of particular species are related to their geographical ranges (Gregory and Gaston 2000). The SAR is simply the observation that the number of species in a region is a positive function of the area of the region and gives information on species turnover (Storch et al. 2012), as well as enabling the prediction of the expected loss of species richness from a region undergoing specified levels of area reduction (habitat loss) (Connor and McCoy 2001).

For analyses, we classified species according to their geographical ranges and conservation status using the information available on the BirdLife International website (BirdLife International 2012) and cross-checked the distributional data with maps from Sinclair and Ryan (2003). We also classified the species according to diet type (see supplementary material): (i) invertebrate feeders (feeding mainly but not exclusively on invertebrates), (ii) frugivorous species (feeding mainly but not exclusively on fruits), (iii) nectarivorous species (feeding mainly but not exclusively on nectar), (iv) carnivorous species (feeding mainly but not exclusively on small vertebrates), (v) granivorous species (feeding mainly but not exclusively on seeds), and (vi) mixed diet species based on information from the Birds of Africa (Fry and Keith 2004). Moreover, we sorted all species into three categories of range-size according to Reif et al. (2006): (i) species endemic to the Cameroon volcanic line (hereafter ED), (ii) montane species not endemic to the Cameroon volcanic line (hereafter MR), (iii) species widespread throughout Africa (hereafter WD). Species with ranges at elevations mostly above 1,600 m a.s.l were considered to be montane species (Graham et al. 2005).

Data analyses were done in STATISTICA 6.0 software and R 2.15.2. (R Development Core Team 2012) and we employed only common statistical procedures such as linear regression and analysis of variance. We used species abundances as the response variables and range sizes as categorical predictor. We used non-parametric alternatives of the tests when data did not fit a normal distribution. For data analyses of species densities and ARSR, we excluded aerial feeders and raptors because of the probability of counting the same individual at more than one census point. For a better illustration of the ARSR we used a variable called ‘Abundance–Range Size Ranking Difference’ (Reif et al. 2006). Species were ordered according to abundance and range-size respectively and if a positive ARSR is assumed, the abundance rank for a particular species will correspond to its range-size rank. We then calculated the difference between the two rankings for each species. The absolute value of the difference shows the degree of deviation from positive ARSR, while its sign indicates whether the species abundance is higher or lower than expected by range size (Reif et al. 2006). We used the SAR to estimate the species turnover along our point count transects. It was computed by sampling points along the transect (one to sixteen) in order to estimate how the number of species increases with an increase in area represented by the number of points summed. While calculating SAR we summed species numbers for all possible sets of adjacent points (pairs, triples, quadruples etc.) and then calculated an average number of species per point, pair of points, trio of points etc. This

procedure enabled us to determine the similarity of species diversity on both mountains. We calculated Sørensen's similarity coefficient β for comparing the similarity of two samples (see Eq. 1 below). This is a simple measure of species turnover, ranging from a value of 0 where there is no species overlap between the assemblages, to a value of 1 when exactly the same species are found in both assemblages used for comparing.

$$\beta = 2C/S1 + S2 \quad (1)$$

where S1 is the total number of species recorded in the first assemblage, S2 is the total number of species recorded in the second assemblage, and C is the number of species common to both assemblages.

Results

Overall description

In total, we recorded 16 species endemic to the Cameroon volcanic line, 17 non-endemic Afrotropical montane species, and 73 widespread species to give a total of 106 species belonging to 42 families for both study sites. Twenty one species were detected only on Mt Cameroon, 45 only on Mt Oku and 40 on both mountains. Fifty species were detected through point counts on both mountains and the rest through random walks. Both sources of information were added together to make up the checklist. All 106 species recorded were made up of 48 invertebrate feeders, 14 frugivores, three nectarivores, 16 carnivores, nine granivores and 16 mixed diet species (see Table S1).

Mt Cameroon

In total, we found 61 species on Mt Cameroon (Table 1). In 2004 we had 46 species of which 36 were found in 2011. In 2011 we had 51 species of which 15 were not found in 2004. The highest number of species (23) belonged to the guild of invertebrate feeders (Fig. 1).

There was no significant difference in the average abundances of species common to both years, paired t test: $t = 1.05$, $df = 20$, $P = 0.307$ (Table 1). The overall number of individuals of all species detected during point counts was 462 individuals in 2011 and 458 in 2004. The number of species was a positive function of the area indicating that species numbers increased with area sampled as shown by SAR (to be comparable with Mt Oku, analysis includes only point count data from 2011; Fig. 2). The most abundant species were the Western Mountain Greenbul *Andropadus tephrolaemus* (ED) (68 individuals in 2004 and 61 in 2011), the Northern Double-Collared Sunbird *Cinnyris reichenowi* (MR) (46 in 2004 and 58 in 2011) and the African Hill Babbler *Pseudoalcippe abyssinica* (MR) (35 in 2004 and 35 in 2011). These species also had the highest occupancies, being present at all points (Table 1). For further calculations we used information about abundances from point counts done in 2011 only as those were performed at the beginning of dry season and thus are comparable with Mt Oku. Differences in the average abundances among species groups as classified according to range size were not significant (ANOVA: $F_{2,23} = 0.535$, $P = 0.593$, Fig. 3a). The pattern of ARSR showed negative trend but it was not statistically significant (Pearson coefficient = -0.334 , $n = 26$, $P = 0.09$). However, the abundance–range size ranking difference showed significant differences among groups,

Table 1 List of bird species recorded using different methods on Mt Cameroon and Mt Oku

Species	Point count	Checklist	Occupancy			Average abundances		
			Mt Oku		Mt Cameroon	Mt Oku		Mt Cameroon
			2008	2004	2011	2008	2004	2011
<i>Accipiter melanoleucus</i>		MO–MC ^b						
<i>Alcedo leucogaster</i>		MO						
<i>Alethe poliocephala</i>		MC ^b						
<i>Andropadus montanus</i>	MO	MO–MC ^b	9			0.81		
<i>Andropadus tephrolaemus</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	15	15	16	2	4.27	3.81
<i>Andropadus virens</i>	MC ^a	MC ^a		5			0.33	
<i>Anthus cinnamomeus</i>		MO–MC ^{a,b}						
<i>Anthus trivialis</i>		MC ^a						
<i>Apalis cinerea</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	16	14	15	1.56	1.8	1.63
<i>Apalis jacksoni</i>		MO						
<i>Apalis pulchra</i>	MO	MO	16			1.63		
<i>Apaloderma vittatum</i>	MO	MO	1			0.06		
<i>Apus affinis</i>		MC ^a						
<i>Apus barbatus</i>		MO						
<i>Batis minor</i>		MO						
<i>Bradypterus bangwaensis</i>	MO	MO	5			0.31		
<i>Bradypterus lopezi</i>	MC ^{a,b}	MC ^{a,b}		11	16		1.4	1.69
<i>Bubo poensis</i>		MC ^a						
<i>Buteo auguralis</i>		MO–MC ^{a,b}						
<i>Campephaga petiti</i>		MO						
<i>Caprimulgus nigriscapularis</i>		MO–MC ^b						
<i>Caprimulgus tristigma</i>		MO						
<i>Centropus monachus</i>		MO						
<i>Chloropeta natalensis</i>		MO						
<i>Chrysococcyx klaas</i>		MO						
<i>Cinnyris bouvieri</i>		MO						
<i>Cinnyris reichenowi</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	16	14	16	2.88	3.07	3.63
<i>Circus aeruginosus</i>		MO						
<i>Circus pygargus</i>		MC ^a						
<i>Cisticola brunnescens</i>		MO						
<i>Cisticola chubbi</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	8	12	10	0.56	1.8	1.06
<i>Colius striatus</i>		MO						
<i>Columba sjostedti</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	2	14	2	0.13	3.33	0.13
<i>Coracina caesia</i>	MO	MO–MC ^a	5			0.31		
<i>Corvus albus</i>		MO						
<i>Corythaeola cristata</i>		MC ^{a,b}						
<i>Cossypha isabellae</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	4	5	15	0.31	0.33	1.44
<i>Cossypha niveicapilla</i>	MO	MO	1			0.06		
<i>Cryptospiza reichenowi</i>	MO	MO–MC ^{a,b}	6			0.43		
<i>Cyanomitra oritis</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	9	4	6	0.75	0.27	0.44
<i>Dendropicos elliotii</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	2	1	8	0.13	0.07	0.56
<i>Dendropicos fuscescens</i>	MO	MO	1			0.06		

Table 1 continued

Species	Point count	Checklist	Occupancy			Average abundances		
			Mt Oku	Mt Cameroon		Mt Oku	Mt Cameroon	
				2004	2011		2004	2011
<i>Dendropicos goertae</i>	MO	MO	1			0.06		
<i>Elminia albiventris</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	4	5	10	0.31	0.47	0.88
<i>Emberiza tahapisi</i>		MO						
<i>Estrilda astrild</i>		MO–MC ^a						
<i>Estrilda nonnula</i>		MO–MC ^{a,b}						
<i>Euplectes capensis</i>		MC ^{a,b}						
<i>Euschistospiza dybowski</i>		MO						
<i>Falco biarmicus</i>		MO						
<i>Falco subbuteo</i>		MC ^b						
<i>Falco tinnunculus</i>		MO						
<i>Ficedula hypoleuca</i>		MO						
<i>Francolinus squamatus</i>		MO–MC ^{a,b}						
<i>Hirundo fuligula</i>		MO						
<i>Hirundo rustica</i>		MO–MC ^a						
<i>Indicator willcocksi</i>	MC ^b	MC ^b			3			0.19
<i>Kakamega poliothorax</i>	MO–MC ^b	MO–MC ^{a,b}	1		1	0.06		0.06
<i>Laniarius atroflavus</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	16	15	16	1.25	3.4	2
<i>Laniarius poensis</i>		MC ^a						
<i>Lanius collaris</i>		MO						
<i>Linurgus olivaceus</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	14	5	11	0.88	0.53	1
<i>Malaconotus gladiator</i>		MO						
<i>Merops variegatus</i>		MO						
<i>Milvus migrans</i>		MO						
<i>Motacilla flava</i>		MO–MC ^{a,b}						
<i>Muscicapa adusta</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	7	12	11	0.5	1.2	1
<i>Nesocharis shelleyi</i>	MO	MO	1			0.06		
<i>Onychognathus walleri</i>	MC ^b	MO–MC ^b			6			2.19
<i>Oriolus nigripennis</i>		MO						
<i>Otus icterorhynchus</i>		MC ^b						
<i>Parus albiventris</i>	MO	MO	1			0.06		
<i>Phoeniculus bollei</i>		MO						
<i>Phyllastrephus poensis</i>	MO	MO	1			0.06		
<i>Phylloscopus sibilatrix</i>		MO						
<i>Phylloscopus trochilus</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	1	5	1	0.06	0.33	0.06
<i>Platysteira cyanea</i>	MC ^{a,b}	MC ^{a,b}		8	13		0.8	1.06
<i>Platysteira laticincta</i>	MO	MO	4			0.25		
<i>Ploceus bannermani</i>	MO	MO	10			0.69		
<i>Ploceus insignis</i>	MO–MC ^a	MO–MC ^{a,b}	2	3		0.13	0.27	
<i>Ploceus melanogaster</i>	MC ^{a,b}	MO–MC ^{a,b}		1	3		0.07	0.25
<i>Pogoniulus bilineatus</i>	MO	MO–MC ^a	2			0.13		
<i>Pogoniulus coryphaeus</i>	MO–MC ^b	MO–MC ^{a,b}	3		11	0.19		0.75
<i>Psaldiprocne fuliginosa</i>	MC ^{a,b}	MC ^{a,b}		2	1		0.27	0.13

Table 1 continued

Species	Point count	Checklist	Occupancy			Average abundances		
			Mt Oku	Mt Cameroon		Mt Oku	Mt Cameroon	
			2008	2004	2011	2008	2004	2011
<i>Pseudoalcippe abyssinica</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	16	15	16	2.31	2	2.19
<i>Pycnonotus barbatus</i>	MO–MC ^b	MO–MC ^b	5		2	0.38		0.13
<i>Quelea erythrops</i>		MC ^a						
<i>Saxicola rubetra</i>		MC ^a						
<i>Saxicola torquata</i>	MC ^b	MO–MC ^b			1			0.06
<i>Schoutedenapus myoptilus</i>		MC ^a						
<i>Scopus umbretta</i>		MO						
<i>Serinus burtoni</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	7	3	2	0.44	0.2	0.13
<i>Serinus mozambicus</i>	MO	MO	1			0.06		
<i>Speirops melanocephalus</i>	MC ^{a,b}	MC ^{a,b}		7	5		1.53	0.63
<i>Spizaetus africanus</i>		MC ^a						
<i>Streptopelia semitorquata</i>		MO						
<i>Sylvia borin</i>		MO						
<i>Tauraco bannermani</i>	MO	MO	3			0.38		
<i>Tauraco macrorhynchus</i>		MC ^{a,b}						
<i>Tchagra australis</i>		MO						
<i>Treron calva</i>	MO	MO–MC ^{a,b}	2			0.13		
<i>Turdus pelios</i>	MC ^{a,b}	MC ^{a,b}		11	10		1.33	0.69
<i>Turtur tympanistria</i>	MO	MO–MC ^b	3			0.19		
<i>Tyto alba</i>		MC ^{a,b}						
<i>Urolais epichlora</i>	MO–MC ^{a,b}	MO–MC ^{a,b}	9	14	12	0.63	1.47	1.13
<i>Zosterops senegalensis</i>	MO	MO	15			1.69		

Information about occupancies (number of census points at which the species was recorded during point counts, maximum is 16 for all surveys except for Mt Cameroon in 2004 when it was 15) and averages abundances per point are provided

MC recorded on Mt Cameroon

MO recorded on Mt Oku

^a Recorded during the first survey in 2004

^b Recorded during the second survey in 2011

Kruskal–Wallis test: $H = 10.9$, $df = 2$, $n = 26$, $P = 0.004$ (Fig. 3b). Endemics and MR showed positive rankings whereas WD had negative rankings.

Mt Oku

On Mt Oku we found 85 species of which 40 were detected by point counts. The overall species abundance detected was 366 individuals. The highest number of species (20) belonged to the guild of invertebrate feeders (Fig. 1).

The number of species also increased with area sampled as shown by SAR (Fig. 2). The most abundant species were *C. reichenowi* (46), *P. abyssinica* (37) and *A. tephrolaemus* (32). Species with the smallest range sizes also had the highest occupancies (Table 1). The ARSR on Mt Oku was also not statistically significant (Pearson coefficient = -0.23 , $n = 40$,

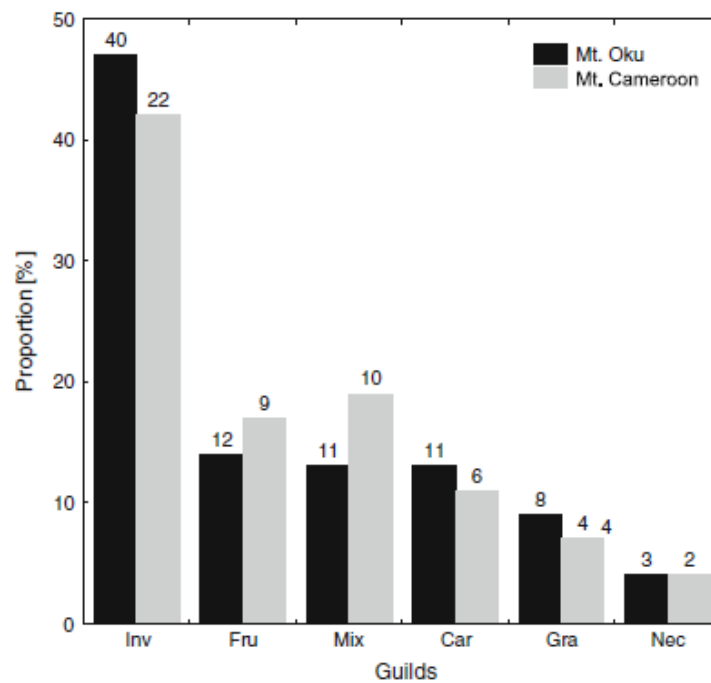


Fig. 1 Relative composition of different guilds in the montane forests of Mt Cameroon and Mt Oku. *Inv* invertebrate feeder, *Fru* frugivorous, *Mix* mixed diet, *Car* carnivorous, *Gra* granivorous, *Nec* nectarivorous. The number of species per guild for each mountain can be seen in each column. *Dark bars* represent Mt Oku and *light bars* Mt Cameroon

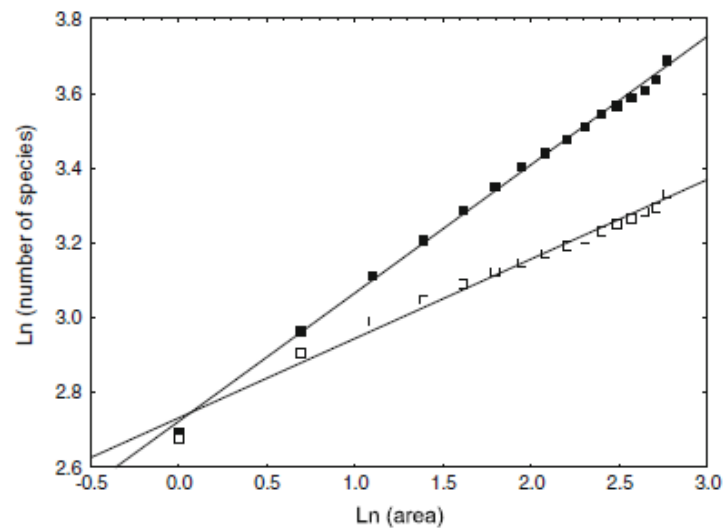


Fig. 2 Species–area relationships (in ln–ln scale) for birds of Mt Cameroon (slope = 0.212) and Mt Oku (slope = 0.343). Differences in compositional changes are evident both in absolute numbers of species and in the different slopes for the mountains. *Dark squares* represent Mt Oku and *open squares* represent Mt Cameroon

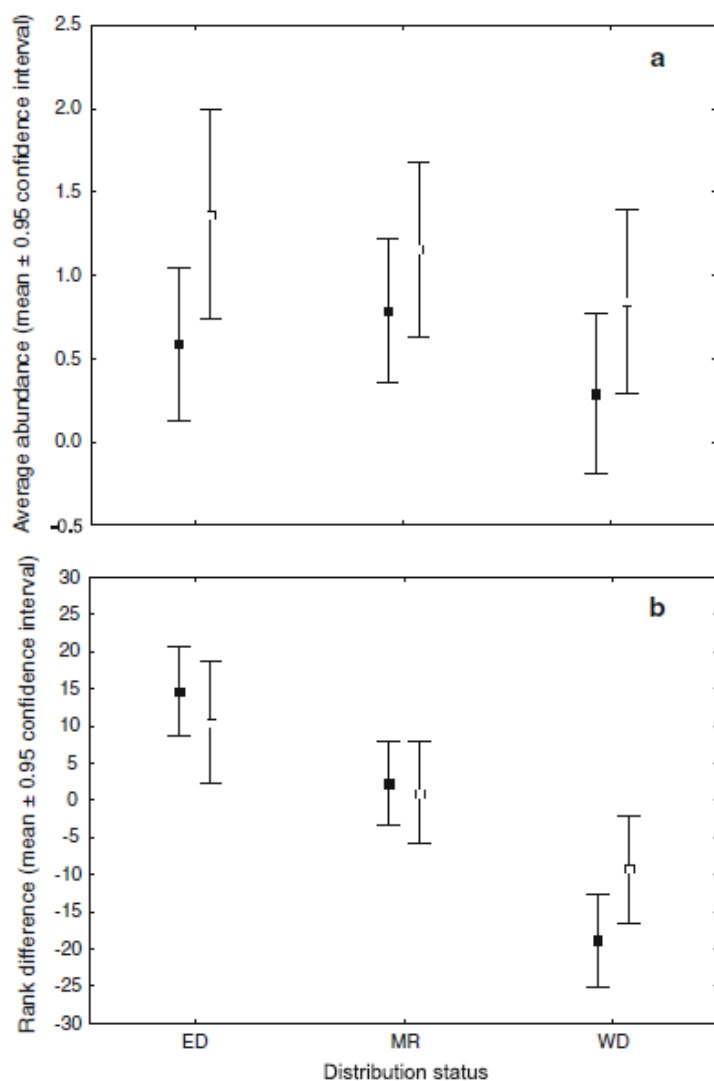


Fig. 3 Abundances according to range-sizes. Differences in the average abundances per point between the endemics (ED), montane (MR) and widespread (WD) species on Mt Cameroon ($P = 0.59$) and Mt Oku ($P = 0.18$) (a). Abundance–range-size ranking differences in the three groups of the bird assemblages in both montane forests (b). Dark squares represent Mt Oku and open squares represent Mt Cameroon

$P = 0.14$). The difference in the average abundances among the species groups as classified according to range size was also non-significant (ANOVA: $F_{2,37} = 1.81$, $P = 0.18$, Fig. 3a). The analysis revealed a significant difference among species groups in the abundance–range size ranking, Kruskal–Wallis test: $H = 21.6$, $df = 2$, $n = 40$, $P < 0.001$ for Mt Oku (Fig. 3b). Endemics and MR showed positive rankings whereas WD had negative rankings.

Study sites comparison

More than 50 % of species present on Mt Oku were also present on Mt Cameroon (Sørensen's similarity coefficient $\beta = 0.55$) but each mountain had some species peculiar

to it. On Mt Cameroon these were: *S. melanocephalus*, Mountain Saw-Wing *Psolidoprocne fuliginosa* and Cameroon Scrub-Warbler *Bradypterus lopezi*, while on Mt Oku these were *T. bannermani*, Bangwa Forest Warbler *Bradypterus bangwaensis*, Black-collared Apalis *Apalis pulchra*, White-headed Wood Hoopoe *Phoeniculus bollei* and the Banded Wattle-eye *Platysteira laticincta* amongst others (Table 1). Both mountains had similar assemblage structure with approximately the same number of species per guild except for the invertebrate feeders that were almost twice as numerous on Mt Oku as on Mt Cameroon (Fig. 1).

Species spatial turnover was higher on Mt Oku than on Mt Cameroon (Fig. 2). There was a significant difference in abundances of particular species common to both mountains (paired *t* test: $t = 2.85$, $df = 18$, $P = 0.010$) being higher on Mt Cameroon.

Discussion

We recorded a total of 106 bird species, 21 only on Mt Cameroon, 45 only on Mt Oku and 40 common to both mountains. Mt Cameroon had a higher proportion of endemic species than Mt Oku while Mt Oku had a higher number of WD species than Mt Cameroon. Our results indicate that, even though the field effort was comparable between sites, the total number of species detected on Mt Oku was higher when compared to Mt Cameroon but the species abundances were higher on Mt Cameroon than on Mt Oku. On both mountains, restricted-range species had higher abundances than widespread species and species turnover was higher for the mountain situated in the mosaic landscape than for that found surrounded by pristine forest. This is somewhat counter intuitive as the type of forest is the same for both sites. We suggest four possible explanations for the difference in number of species between the mountains. First, the different geographical locations of the mountains are responsible, with the local bird assemblages potentially reflecting different species pools. The difference in species pool could also be caused by the location of Mt Oku within the savannah, and as a result, savannah species which are mostly WD enrich its bird assemblage. Second, the lower species richness on Mt Cameroon might be a result of its geographical isolation as the theory of island biogeography would predict (MacArthur and Wilson 1967). Indeed, geographically outlying mountains like Mt Cameroon generally have a different species composition to those like Mt Oku which are connected to mountains in the main massif (Graham et al. 2005). According to the theory, possible mechanisms behind might be related to lower probability of colonisation of an isolated mountain by new species, higher rates of extinction, or evolution of independent evolutionary lineages. The third explanation includes differences in climatic conditions between sites. As mentioned above, Mt Cameroon located by the sea has a relatively humid and warm climate while Mt Oku situated inland is cooler and drier. Such conditions can theoretically support different number of species but based on published information one would expect the opposite relationship between relative humidity and species richness than that observed here (Graham et al. 2005). The final explanation relates to the broader landscape context of the two mountains. In our opinion the landscape composition surrounding the mountains under study is crucial to explaining the observed differences. Mt Cameroon rises from lowland forest and thus its montane forest at upper elevations is surrounded by a lowland forest belt. Therefore, the probability that non-forest species (usually widespread and generalist species) enter the montane forest interior is low. The opposite situation can be found on Mt Oku where the forest patch is surrounded by a savannah matrix and human settlements and non-forest generalist species can easily invade

montane forest community. This explanation is supported by data presented here as the difference in species richness between the mountains is mostly due to widespread species common on Mt Oku. In conservation efforts, species richness is frequently used as a measure of environmental quality (Sodhi and Ehrlich 2010). In this case, we show that locally high species richness might be a result of habitat degradation or large scale fragmentation and the presence of restricted-range species is then a more reliable clue for evaluating the conservation importance of a locality.

Our analysis did not suggest any differences in utilization of food resources by birds between the study sites. Invertebrate feeders were the most abundant guild for both forests and this finding is in congruence with information published for lowland forests in Cameroon (De-Iongh and Van Weerd 2006).

Besides the overall number of species, we endeavoured to estimate spatial turnover in species richness (β -diversity) using point count data. We found that the slope of SAR was higher on Mt Oku than on Mt Cameroon suggesting higher species turnover among points on the first mountain. The higher species turnover observed on Mt Oku could be related to several attributes of the local montane forest community as it has been shown that high species turnover is connected to high habitat heterogeneity (e.g. McKnight et al. 2007; Jankowski et al. 2009). The structure of the forest itself is quite similar on both mountains, however, the entire forest environment seems to be more heterogeneous on Mt Oku. Due to a number of human activities, the Mt Oku forest environment is more frequently broken by edge habitats, pathways or even pastures. Although birds were counted in the forest interior only, the local presence of individual species might be affected by larger scale effects. As a result, some forest interior points may not be suitable for some forest specialist species. Alternatively, non-forest specialists common in the surrounding savannah and agricultural landscape (Fotso 2001) might invade the margins of montane forest interior and thus influence the composition of forest avian assemblages (Forbeseh et al. 2003; but see Hořák et al. 2010). The relative area of true interior forest can be limited when the forest block is surrounded by non-forests environments which can again influence populations of true forest specialists. In contrast, Mt Cameroon's montane forest is surrounded by pristine mid-elevation forest and lowland forest (Ekobo 2003), which protects the montane assemblages from open landscape effects.

We found that Mt Cameroon montane forest hosts both higher overall abundances and a higher number of individuals per species for species common to both mountains. The differences in abundances of birds between the mountains may therefore tell us something about habitat suitability and thus be of importance to conservation science (Sodhi and Ehrlich 2010). Our results indicate that Mt Cameroon forest can support more individuals per species. We have two possible but not mutually exclusive explanations for this observation. First, it can reflect differences in resource availability between the mountains. Higher temperature and rainfall on Mt Cameroon could enhance resource availability via increased primary productivity (Graham et al. 2005), which could in turn support more individuals. Second, the montane forest on Mt Cameroon is part of a forest block forming a vast area of suitable habitats for forest species. The lower abundances of birds inhabiting the montane forest on Mt Oku might therefore be associated with higher levels of habitat degradation at a large spatial scale and could indicate that the montane forest on Mt Oku is of lower quality from an avian point of view.

In order to focus on restricted-range species, we divided birds into three categories depending on their geographical distribution. Similar to our previous study performed in the montane forest mosaic in the Bamenda highlands (Reif et al. 2006), we found that endemics to the Cameroon volcanic line and montane restricted non-endemics are more

abundant than widespread species. Other studies reports similar observation from other African mountains. Sekercioglu and Riley (2005) found that endemic species are among the most abundant in the Kumbira Forest in the Angola Escarpment. Similarly, endemic and non-endemic montane species had higher counts than widespread species on the Namuli Massif in northern Mozambique (Ryan et al. 1999). Also Owunji et al. (2005) reported high detection rates of endemic species in montane forest environments in the Albertine Rift, where endemic species form a substantial part of bird assemblages at elevations between 2,100 and 2,600 m a.s.l. Finally, Fjelds  and Rab l (1995) and Fjelds  (1999) found that endemic species of the Eastern Arc Mountains are more abundant than widespread species in the mature montane forest. It follows that high local abundances of restricted-range species is quite common and even ubiquitous in Afromontane regions.

Our results have serious implications for nature conservationists. We found that scarce remnants of upper montane forests on two of the highest peaks in the Cameroon volcanic line still host a high diversity of restricted-range bird species confined to West-Central Africa. Moreover, members of local avian assemblages can be found in relatively high numbers and this is possibly related to their long term adaptations to the local environment. There are, however, two threatening facts that seem to neutralize this relatively positive information about African birds. First, we found considerable differences in avian assemblage compositions between the study sites suggesting that montane forest of the same mountain range can differ substantially. Second, although our results show that abundances of range-restricted species are still relatively high in the montane forests of the Cameroon volcanic line, significant differences can be found between locations. We believe that these differences can be attributed to landscape scale effects especially to different levels of habitat degradation and fragmentation on the mountains. More conservation efforts are needed in the montane forests of the Cameroon volcanic line to save the last remnants of this unique environment. In addition, more information from other montane forest sites could help to elucidate spatial variation in montane forest bird assemblages. Such data would allow for a proper understanding of the mechanisms leading to observed differences and enable the adoption of appropriate conservation actions.

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Table S1. Characteristics of all species recorded on Mt Cameroon and Mt Oku.

Species	^a Diet type	Geographical range (km ²)	^b Distribution status	^c Conservation status
<i>Accipiter melanoleucus</i>	Car	9,070,000	WD	LC
<i>Alcedo leucogaster</i>	Car	2,740,000	WD	LC
<i>Alethe poliocephala</i>	Inv	1,590,000	WD	LC
<i>Andropadus montanus</i>	Fru	61,300	ED	NT
<i>Andropadus tephrolaemus</i>	Fru	59,500	ED	LC
<i>Andropadus virens</i>	Mix	6,120,000	WD	LC
<i>Anthus cinnamomeus</i>	Inv	>200,000	WD	LC
<i>Anthus trivialis</i>	Inv	12,300,000	WD	LC
<i>Apalis cinerea</i>	Inv	458,000	MR	LC
<i>Apalis jacksoni</i>	Inv	497,000	MR	LC
<i>Apalis pulchra</i>	Inv	100,000	MR	LC
<i>Apaloderma vittatum</i>	Inv	486,000	MR	LC
<i>Apus affinis</i>	Inv	22,200,000	WD	LC
<i>Apus barbatus</i>	Inv	1,070,000	WD	LC
<i>Batis erlangeri</i>	Inv	>200,000	WD	LC
<i>Bradypterus lopezi</i>	Inv	393,000	WD	LC
<i>Bradypterus bangwaensis</i>	Inv	6,900	ED	NT
<i>Bubo poensis</i>	Car	3,800,000	WD	LC
<i>Buteo auguralis</i>	Car	7,040,000	WD	LC
<i>Campephaga petiti</i>	Inv	509,000	WD	LC
<i>Caprimulgus nigriscapularis</i>	Inv	826,000	WD	LC
<i>Caprimulgus tristigma</i>	Inv	4,550,000	WD	LC
<i>Cinnyris reichenowi</i>	Nec	243,000	MR	LC
<i>Cinnyris bouvieri</i>	Nec	355,000	WD	LC
<i>Centropus monachus</i>	Car	2,870,000	WD	LC
<i>Chloropeta natalensis</i>	Inv	3,740,000	WD	LC
<i>Chrysococcyx klaas</i>	Inv	14,000,000	WD	LC
<i>Circus aeruginosus</i>	Car	13,500,000	WD	LC
<i>Circus pygargus</i>	Car	9,420,000	WD	LC
<i>Cisticola brunnescens</i>	Inv	1,560,000	WD	LC
<i>Cisticola chubbi</i>	Inv	44,500	MR	LC
<i>Colius striatus</i>	Fru	7,960,000	WD	LC
<i>Columba sjostedti</i>	Fru	44,200	ED	LC
<i>Coracina caesia</i>	Inv	905,000	MR	LC
<i>Corvus albus</i>	Mix	>500,000	WD	LC

<i>Corythaeola cristata</i>	Fru	3,850,000	WD	LC
<i>Cossypha isabellae</i>	Inv	51,500	ED	LC
<i>Cossypha niveicapilla</i>	Inv	5,180,000	WD	LC
<i>Cryptospiza reichenovii</i>	Gra	436,000	MR	LC
<i>Cyanomitra oritis</i>	Nec	65,600	ED	LC
<i>Dendropicos elliotii</i>	Inv	799,000	WD	LC
<i>Dendropicos fuscescens</i>	Inv	12,500,000	WD	LC
<i>Dendropicos goertae</i>	Inv	8,170,000	WD	LC
<i>Elminia albiventris</i>	Inv	225,000	MR	LC
<i>Emberiza tahapisi</i>	Gra	6,950,000	WD	LC
<i>Estrilda astrild</i>	Gra	5,860,000	WD	LC
<i>Estrilda nonnula</i>	Gra	1,220,000	WD	LC
<i>Euplectes capensis</i>	Mix	2,640,000	WD	LC
<i>Euschistospiza dybowskii</i>	Gra	755,000	WD	LC
<i>Falco biarmicus</i>	Car	17,900,000	WD	LC
<i>Falco subbuteo</i>	Car	9,910,000	WD	LC
<i>Falco tinnunculus</i>	Car	37,600,000	WD	LC
<i>Ficedula hypoleuca</i>	Inv	3,550,000	WD	LC
<i>Francolinus squamatus</i>	Inv	2,590,000	WD	LC
<i>Hirundo fuligula</i>	Inv	9,510,000	WD	LC
<i>Hirundo rustica</i>	Inv	43,400,000	WD	LC
<i>Indicator willcocksi</i>	Inv	3,270,000	WD	LC
<i>Kakamega poliothorax</i>	Inv	141,000	MR	LC
<i>Laniarius atroflavus</i>	Mix	54,100	ED	LC
<i>Laniarius poensis</i>	Mix	169,000	MR	LC
<i>Lanius collaris</i>	Car	7,180,000	WD	LC
<i>Linurgus olivaceus</i>	Gra	215,000	MR	LC
<i>Malaconotus gladiator</i>	Mix	7,200	ED	VU
<i>Merops variegatus</i>	Inv	4,200,000	WD	LC
<i>Milvus migrans</i>	Car	> 5,000,000	WD	LC
<i>Motacilla flava</i>	Inv	> 5,000,000	WD	LC
<i>Muscicapa adusta</i>	Inv	2,390,000	WD	LC
<i>Nesocharis shelleyi</i>	Fru	31,200	ED	LC
<i>Onychognathus walleri</i>	Mix	308,000	WD	LC
<i>Oriolus nigripennis</i>	Mix	2,050,00	WD	LC
<i>Otus icterorhynchus</i>	Car	671,000	WD	LC
<i>Parus albiventris</i>	Inv	322,000	MR	LC
<i>Phoeniculus bollei</i>	Inv	1,290,000	WD	LC
<i>Phyllastrephus poensis</i>	Inv	44,400	ED	LC
<i>Phylloscopus sibilatrix</i>	Inv	4,060,000	WD	LC
<i>Phylloscopus trochilus</i>	Inv	15,800,000	WD	LC

<i>Platysteira cyanea</i>	Inv	5,600,000	WD	LC
<i>Platysteira laticincta</i>	Inv	1,900	ED	EN
<i>Ploceus bannermani</i>	Mix	10,900	ED	VU
<i>Ploceus insignis</i>	Mix	247,000	MR	LC
<i>Ploceus melanogaster</i>	Mix	220,000	MR	LC
<i>Pogoniulus bilineatus</i>	Fru	7,150,000	WD	LC
<i>Pogoniulus coryphaeus</i>	Fru	307,000	MR	LC
<i>Psaldiprocne fuliginosa</i>	Inv	3,500	ED	LC
<i>Pseudoalcippe abyssinica</i>	Mix	498,000	MR	LC
<i>Pycnonotus barbatus</i>	Fru	19,600,000	WD	LC
<i>Quelea erythrops</i>	Gra	10,500,000	WD	LC
<i>Saxicola torquata</i>	Mix	19,500,000	WD	LC
<i>Saxicola rubetra</i>	Mix	5,330,000	WD	LC
<i>Schoutedenapus myoptilus</i>	Inv	385,000	MR	LC
<i>Scopus umbretta</i>	Car	19,900,000	WD	LC
<i>Serinus burtoni</i>	Gra	401,000	MR	LC
<i>Serinus mozambicus</i>	Gra	9,530,000	WD	LC
<i>Speirops melanocephalus</i>	Mix	150	ED	VU
<i>Spizaetus africanus</i>	Car	1,920,000	WD	LC
<i>Streptopelia semitorquata</i>	Fru	13,800,000	WD	LC
<i>Sylvia borin</i>	Inv	9,650,000	WD	LC
<i>Tauraco bannermani</i>	Fru	2,000	ED	EN
<i>Tauraco macrorhynchus</i>	Fru	1,270,000	WD	LC
<i>Tchagra australis</i>	Inv	8,300,000	WD	LC
<i>Treron calva</i>	Fru	11,400,000	WD	LC
<i>Turdus pelios</i>	Mix	8,380,000	WD	LC
<i>Turtur tympanistria</i>	Fru	8,130,000	WD	LC
<i>Tyto alba</i>	Car	63,300,000	WD	LC
<i>Urolais epichlora</i>	Inv	48,900	ED	LC
<i>Zosterops senegalensis</i>	Inv	8,340,000	WD	LC

^a Car = carnivorous, Inv = invertebrate feeder, Mix = mix diet species, Gra = granivorous, Fru = frugivorous, Nec = nectarivorous

^b WD = widespread, MR = montane restricted non-endemic, ED = endemic to the Cameroon Mountains

^c LC = least concerned, VU = vulnerable, EN = endangered, NT = near threatened

CONCLUSIONS

Ecologists and biogeographers since von Humbolt have been interested in studying species distribution patterns around the globe. Questions such as, why are some species very common while others are rare or why are common species very abundant while rare species scarce, have been intensely investigated at different spatial scales but still not fully elucidated.

In this thesis, I found that avian diversity on Mt. Cameroon decreases with elevation with a low elevation plateau. The pattern can be said to be driven mostly by two factors: temperature and biotic interactions (predation and parasitism). Temperature on Mt. Cameroon decreases with elevation, and limits the number of species that can physiologically tolerate the much colder higher elevations. Given that there is a positive relationship between temperature and diversity, temperature therefore appears to be one of the determinants of the diversity pattern. Biotic interactions on the other hand, are known to be correlated with a change in species richness, and are stronger in sites with more species. This implies the greater biotic interactions at lower elevations on Mt. Cameroon promote coexistence, specialization and reduce competition.

Concerning nest predation risk on Mt. Cameroon, I did not find a decreasing predation with elevation for all artificial nests types, but different nest type-elevation interactions. These differences in predation risk of different nest types were mostly due to the changing structure of the surrounding vegetation along elevations. The vegetation layers seem to be of vital importance for breeding success. I found a low level of haemosporidian prevalence in avian hosts. This was probably because of the scarcity of dipteran ornithophilic vectors on Mt. Cameroon, which is surprisingly very dry despite the fact that it is situated in one of the wettest regions in the world. Host-parasite reciprocal specialization was very high, probably because of the recent speciation of the infected birds, which have higher probabilities of infection due to still adapting immune systems to parasites. I found these haematozoa to be specialized for few but abundant host species that mostly forage at ground level. This environment, in ways still to be elucidated, does not impose intense pressure on males of the only monochromatic montane species that spans the entire gradient, to develop pronounced morphological competitive traits as is usually the case in other tropical environments, and at higher latitudes. From a methodological point of view, field sexing of this species is still possible by using a combination of traits (tail length, bill height and wing length) in a discriminant function.

Concerning bird assemblages, the abundance – range size relationship is distorted towards higher elevations in the montane forest. Interestingly, the total assemblage abundances do not differ between elevations and population size estimates of species occupying different parts of the gradient remain relatively constant. This deviation in the montane forest is because montane species are very abundant. I found that the level of degradation of montane habitats can serve as an indicator of environmental stress for true forest species because pristine montane forests have more abundant forest species but degraded montane forests have higher species richness.

In conclusion, there probably are other factors that act in concert with temperature and biotic interactions to drive the observed avian diversity pattern on Mt. Cameroon. The observed patterns of assemblage structures are caused mostly by high abundances of montane species, which might be a result of the long-term isolation and ecological specialization of these species on Mt. Cameroon, but it also due to a competitive release in species poor montane locations which possibly is facilitated by an extinction filter. More attention should be focused on insular biodiversity hotspots like Mt. Cameroon because these are centers of endemism and generators of diversity.

APPENDIX

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A comparison of point counts with a new acoustic sampling method: a case study of a bird community from the montane forests of Mount Cameroon[§]

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Acoustic signals are frequently used for estimating avian species richness, abundance and community composition. However, sampling by traditional methods of bird surveys is often limited by availability of experienced researchers in the field, especially in the tropics. New bioacoustic approaches offer some solutions to such limitations and provide opportunities for more extensive spatial and temporal sampling. In our study, we compared results of traditional point counts with simultaneous acoustic samples obtained by automated soundscape recording units in the montane forest of Mount Cameroon. We showed that the estimates of species richness, abundance and community composition based on point counts and *post-hoc* laboratory listening to acoustic samples are very similar, especially for a distance limited up to 50 m. Species that were frequently missed during both point counts and listening to acoustic samples were typically those with relatively quiet songs. Abundances were rather underestimated by listening to acoustic samples in the most abundant species, including those occurring in flocks and species with low singing activity. Despite some possible biases, we demonstrated that the method based on listening to acoustic samples is relatively effective and offers a useful alternative approach for surveying Afromontane bird communities.

Keywords: abundance, automatic recording units, montane forest, point count, species richness, species turnover

Introduction

Point counts with distance sampling are the most frequently used method for estimating avian species richness, abundance and community composition (Buckland 2006; Simons et al. 2007). However, field sampling of avifauna by such traditional methods is often limited by the availability of experienced observers (Hobson et al. 2002). The development of alternative sampling approaches during the last decade, including methods based on automatic recordings, brings new opportunities for investigation of bird communities, especially in the tropics (Venier et al. 2011; Celis-Murillo et al. 2012; Sueur et al. 2012). New bioacoustic approaches offer more cost-effective, time-efficient, and spatially and temporally extensive sampling (Haselmayer and Quinn 2000; Hobson et al. 2002; Celis-Murillo et al. 2009). Devices suitable for acoustic sampling of bird communities produce soundscape recordings, i.e. sample all sounds produced in a given environment including background noise (Sueur et al. 2012). Advantages of using automatic soundscape recording include the possibility to schedule recording over multiple time periods with a single visit, the production of permanent, verifiable records, the control for observer variability, and the possibility to employ field assistants with limited bird identification and survey

skills (Hutto and Stutzman 2009; Blumstein et al. 2011; Rempel et al. 2013). Permanent recordings also could be made easily available for the use of other researchers and for future comparisons.

However, before automatic soundscape recording is accepted as a rigorous technique and applied more generally, there is a need to evaluate its performance, compare outcomes with those of conventional census methods and identify possible biases (Hobson et al. 2002; Acevedo and Villanueva-Rivera 2006; Hutto and Stutzman 2009; Rempel et al. 2013). Recent studies conducted in different habitats in the temperate zone generally revealed that listening to recordings enables detection of a similar number of species as revealed during point counts in the field (Hobson et al. 2002; Rempel et al. 2005; Celis-Murillo et al. 2009; but see Hutto and Stutzman 2009). Rempel et al. (2013) also showed that data recorded by different microphone systems do not differ much from actual number of bird species detected by observers. The only study from the tropics (Yucatan Peninsula), conducted by Celis-Murillo et al. (2012), also brought promising results; these authors showed that species richness, species composition and detection probabilities of 15 bird species did not differ

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between a quadraphonic acoustic recording system and point counts in six structurally different vegetation types, excluding tropical forest. However, performance of acoustic monitoring has never been tested in tropical rainforests and the specific environment of tropical montane forests, especially with regard to distance-related limitations of the method. For example, sound transmission conditions in the tropical forest interior differ from other temperate and drier tropical environments in many aspects, such as structure and density of vegetation, humidity or ambient noise, and can be influenced by species community composition, bird vocal activity and song structure (e.g. Eve 1991; Mathevon et al. 2008).

Our study was situated in pristine montane forest of Mt Cameroon, which is recognised to form part of one of the most important areas of bird endemism in Africa (Fishpool and Evans 2001; BirdLife International 2013). Our general objective was to compare the results of automatic acoustic sampling in estimating alpha, beta and gamma diversity, species composition and abundances of the bird community with simultaneously conducted point counts and to evaluate spatial limits of acoustic sampling. In particular, we aimed to determine if the two survey methods generated similar estimates of (1) the number of species (hereafter 'species richness') at particular census points, (2) community similarity among sites, and (3) total abundances of the species in the study area. In addition, we aimed to determine (4) if and how these estimates differ for different sampling extents, and (5) sources of bias for particular species.

Material and methods

Study site

The study was conducted in the interior of the primary upper montane forest of Mt Cameroon National Park, South-West Region, Cameroon. The site was located on the south-western slope of the mountain close to Mann's Spring (4°08.67' N, 9°07.31' E) at an altitude of approximately 2 250 m above sea level (asl). Average annual precipitation at this altitude on Mt Cameroon is about 3 000 mm and persistent mist and cloud cover usually occurs. The rainy season lasts from late March to the beginning of November, with a peak during July–September (Payton 1993; Fonge et al. 2005). The montane forest extends from c. 1 600 m up to 2 300 m asl at the study site with small fragments up to 2 500 m asl (Cable and Cheek 1998). The forest at the study site represents a typical upper Afromontane forest with discontinuous canopy, which is 10–15 m high, and a high frequency of large trees (Proctor et al. 2007). Trees carry a heavy load of epiphytes, particularly mosses and ferns. The understory consists of dense, tall herbs and shrubs, about 2 m tall (Thomas 1986). The most abundant tree species in the study area included *Schefflera abyssinica*, *S. manni*, *Prunus africana* and *Podocarpus* spp.

A total of c. 375 bird species have been recorded from the Mt Cameroon area, 61 of which are recorded at c. 2 300 m asl (Bayly and Njie Motombe 2004; our unpublished data), although the latter figure includes montane grassland species and Palearctic migrants. There is a high level of endemism among the avifauna of

Mt Cameroon, with 20 species confined to the Cameroon Mountains Endemic Bird Area and two species (Mount Cameroon Francolin *Francolinus camerunensis* and Mount Cameroon Speirops *Speirops melanocephalus*) only found on Mt Cameroon. The majority of these endemics are confined to montane forest (BirdLife International 2013).

Field sampling

Field work was carried out between 9 and 15 November 2011, at the beginning of the dry season. This period corresponds to the breeding season of the majority of montane forest birds of the Cameroon mountains (Serle 1981; Tye 1986). We sampled bird communities using conventional point counts as described by Bibby et al. (2000a). Point counts are a suitable sampling method in closed forest habitats with high canopies, particularly rainforests, and can be used for estimating species abundances (Bibby et al. 2000b). We selected 16 census points spaced 150 m apart. The distance between census points was specified so as to diminish the probability of multiple counting of individuals while remaining logistically tractable for the study. Point counts were performed between 06:00 and 10:00 in the morning. We conducted three 15-minute point counts at each census point ($n = 16$), resulting in 48 point samples. No census point was sampled twice on the same day. Point counts were conducted by two groups of researchers (two or three persons) led by two researchers who primarily sampled the bird community (OS and DH). OS collected 28 and DH collected 20 samples. Each researcher conducted at least one of the three samples at each census point. We recorded all heard and seen individual birds during point counts. If an individual was both heard and seen, it was considered to be recorded acoustically. Each point count was divided into three 5-minute intervals, and the bird community was sampled separately for each interval. The distance to each bird detected was recorded as either less than 50 m or more than 50 m. A range finder was used to calibrate the 50 m distance at each census point.

Simultaneously to conducting each point count, a 15 min acoustic sample (AS) was obtained using SongMeter recording units (SM2, Wildlife Acoustics, Inc., Concord, MA, USA) with two sensitive omnidirectional microphones (see Sueur et al. 2012 for detailed description of the devices). The devices were mounted on the nearest tree stem at a height of approximately 180 cm and recordings commenced and ended at the same moment as each point count. The sampling frequency of the acoustic samples was 44.1 kHz and the samples were saved in WAV format on 32 GB SDHC cards.

Data processing and analyses

As was done with sample point data, the 48 acoustic samples were each divided into three 5-minute samples using GoldWave 5.67 software (<http://www.goldwave.com>). These samples were randomly renamed from 1 to 144, so that they could be processed 'blindly'. Samples were studied by OS who listened to the original WAV files using a computer (played in GoldWave) and stereo channel headphones under standardised conditions. The recording was played with a volume approximately simulating real

noise, and each individual bird that was heard was noted to compile a list of species and the number of individuals of each species recorded on each acoustic sample. All detections of individuals were divided into two categories according to the clarity of its vocalisations: clearly audible individuals (approximately up to 50 m) and individuals that were not clearly audible (more than 50 m).

The three 5-minute acoustic samples made during a point count were grouped together and the cumulative species richness for 5-, 10- and 15-minute sampling periods was calculated. For comparison of species richness detected during point counts and listening to acoustic samples we used all 48 original 15-minute samples (three repeats at 16 census points). We treated these samples as independent simply because the aim was to compare the species richness estimated by two methods at the same time. However, community similarity analysis was based on census points ($n = 16$), where the species composition was grouped for all three visits at a census point. Similarly, species abundances (number of individuals of each species) per census point were estimated as the maximum estimated abundances for particular species recorded during the three visits at a census point. Total abundance of

a species for the whole study site was estimated as the sum of these maximum per-point abundances.

To compare species richness and species abundances estimated by point counts and acoustic sampling, we employed basic statistical tools such as paired *t*-tests and Pearson's correlations. There was no need to transform the species richness data because it fitted a normal distribution. The similarity of bird communities between all particular census points was estimated using the Sørensen index (Sørensen 1957). All statistical analyses were conducted using R 2.15.0 software (R Development Core Team 2011). Means are presented with standard deviations (SD).

Results

We recorded a total of 30 bird species during point counts. All species, with one exception (the uncommon Black-billed Weaver *Ploceus melanogaster*), were also detected using acoustic sampling. Almost all species recorded during point counts were detected only (18 species) or mostly (more than 73% of individuals in seven species) by vocalisations. Only five species were seen during a point count more often than they were heard (Table 1).

Table 1: A comparison of the two methods (point counts and acousting sampling) used for estimating number of detections for point samples ($n = 48$) and total abundances at census points ($n = 16$, three controls) for all bird species. Two distances from observer/recorder were distinguished: within a radius of 50 m (clearly audible individuals in acoustic samples) and at any distance. The % Vocalising column shows the proportion of individuals for a particular species that were detected by vocalisation during point counts in the field for any distance from the observer

Species	Number of detections ($n = 48$)				Abundance ($n = 16$)				% Vocalising
	Point count		SongMeter		Point count		SongMeter		Point count
	50 m	All	50 m	All	50 m	All	50 m	All	Total
<i>Andropadus tephrolaemus</i>	48	48	47	47	49	51	34	34	98.5
<i>Apalis cinerea</i>	41	47	38	45	25	39	17	28	96.5
<i>Bradypterus lopezi</i>	37	40	38	40	28	36	23	34	100
<i>Cinnyris reichenowi</i>	47	47	47	47	53	54	37	37	100
<i>Cisticola chubbi</i>	26	36	30	35	17	28	13	21	100
<i>Columba sjostedti</i>	2	2	1	1	2	2	1	1	0
<i>Cossypha isabellae</i>	21	23	15	15	17	18	13	13	93.1
<i>Cyanomitra oritis</i>	10	10	4	4	6	6	3	3	33.3
<i>Dendropicos ellioti</i>	13	14	9	10	7	8	8	9	85.7
<i>Elminia albiventris</i>	19	20	20	20	12	13	14	14	92
<i>Francolinus squamatus</i>	0	4	0	3	0	5	0	3	100
<i>Indicator willcocksi</i>	5	9	5	9	5	8	6	9	100
<i>Kakamega poliothorax</i>	2	2	2	2	1	1	1	1	100
<i>Laniarius atroflavus</i>	42	48	40	48	34	52	19	36	100
<i>Linurgus olivaceus</i>	15	17	20	21	14	14	16	16	100
<i>Muscicapa adusta</i>	15	16	18	18	10	15	15	15	72.7
<i>Onychognathus walleri</i>	6	7	4	6	35	48	11	16	100
<i>Phylloscopus trochilus</i>	1	5	1	2	1	5	1	2	100
<i>Platysteira cyanea</i>	19	40	24	40	17	30	16	25	100
<i>Pogoniulus coryphaeus</i>	21	36	23	32	12	24	14	20	95.5
<i>Psalidoprocne fuliginosa</i>	1	1	1	1	1	1	2	2	0
<i>Pseudoalcippe abyssinica</i>	46	48	46	48	34	45	27	38	100
<i>Pycnonotus barbatus</i>	4	4	4	4	2	2	2	2	100
<i>Saxicola torquata</i>	3	4	3	3	1	2	1	1	100
<i>Serinus burtoni</i>	2	2	2	2	2	2	2	2	100
<i>Speirops melanocephalus</i>	7	7	9	9	11	11	12	12	100
<i>Tauraco macrorhynchus</i>	2	2	0	2	2	3	0	4	0
<i>Turdus pelios</i>	16	16	11	11	11	12	1	1	100
<i>Urolais epichlora</i>	21	30	23	28	18	22	15	17	100
<i>Ploceus melanogaster</i>	1	1	0	0	1	1	0	0	0

The cumulative species richness detected within 50 m of census points during point counts increased from 6.85 ± 2.08 (5 min) to 8.85 ± 2.20 (10 min) and to 10.23 ± 2.46 (15 min) per point sample ($n = 48$). Almost identical results were obtained for clearly audible birds during acoustic sampling, with species richness increasing from 6.88 ± 2.21 (5 min) to 8.85 ± 2.18 (10 min) and to 10.06 ± 2.28 (15 min) per point sample (Figure 1a). We observed no significant difference in species richness estimated by the two methods for any of the three time intervals (paired t -test, $df = 47$; 5 min: $t = 0.09$, $p = 0.9$; 10 min: $t = 0$, $p = 1$; 15 min: $t = -0.80$, $p = 0.5$). The species richness detected for particular 15-minute samples by the two methods was also significantly correlated ($r = 0.82$, $p < 0.001$; Figure 2a). The number of cases above (15)

and below (20) the line of direct correlation (slope = 1.0) were similar, suggesting that the two methods produced a comparable amount of inaccuracies in estimation of the species richness.

For birds detected at any distance from the observer, the cumulative number of bird species detected during point counts increased from 8.60 ± 2.01 (5 min) to 10.81 ± 2.18 (10 min) and 12.21 ± 2.47 (15 min) per point sample ($n = 48$). During acoustic sampling, the cumulative species richness increased from 8.44 ± 2.12 (5 min) to 10.35 ± 1.98 (10 min) and 11.48 ± 2.05 (15 min) per point sample (Figure 1b). We detected significantly higher cumulative species richness during the point counts compared with acoustic sampling after 10 min and 15 min, respectively (paired t -test, $df = 47$; 10 min: $t = -2.25$, $p = 0.03$; 15 min:

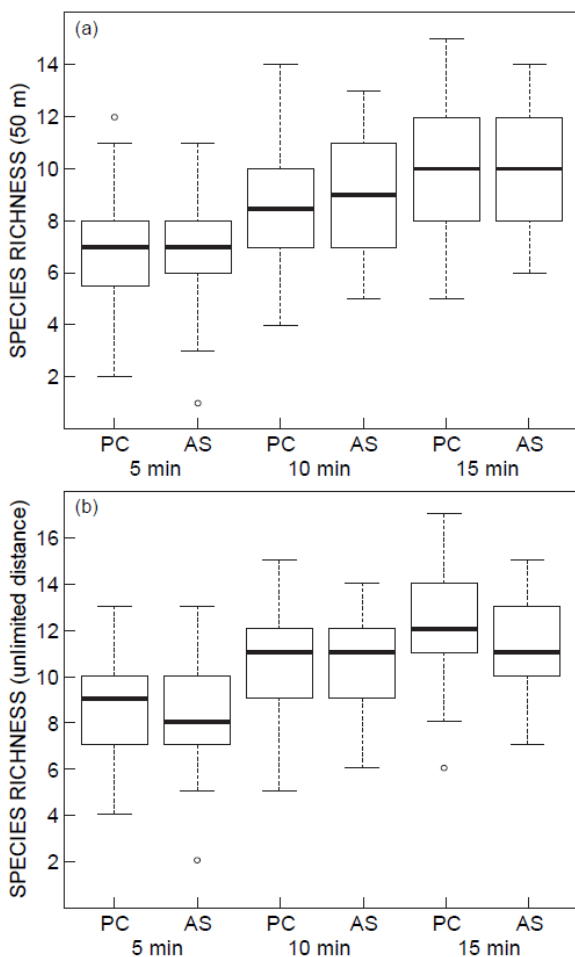


Figure 1: Cumulative species richness recorded at particular point samples ($n = 48$) using point counting in the field (PC) and listening to acoustic samples (AS) during 5-, 10- and 15-minute intervals within a radius of (a) 50 m from the observer/recorder (clearly audible individuals in acoustic samples) and (b) any distance from the observer/recorder. The boxplots show the median, interquartile range (box), and the minimum and maximum values (whiskers)

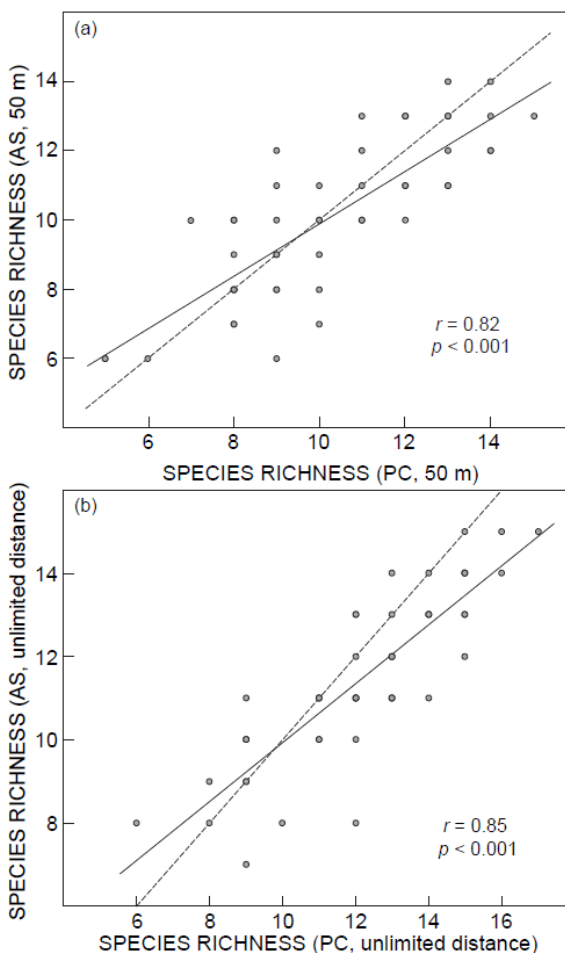


Figure 2: Correlation (solid line = trend in the data) of species richness recorded at particular point samples ($n = 48$) during 15 min. using point counting (PC) in the field and listening of acoustic samples (AS) within a radius of a) 50 m from observer/recorder (clearly audible individuals in acoustic samples) and b) any distance from observer/recorder. Dashed line shows the trend with the slope 1.0

$t = -3.89$, $p < 0.001$), but not after only 5 min (paired t -test, $df = 47$; 5 min: $t = -0.85$, $p = 0.40$). The species richness detected for particular 15-minute samples by the two methods was significantly correlated ($r = 0.85$, $p < 0.001$; Figure 2b). However, the number of cases below (29) the direct correlation (slope = 1) were comparably higher than those above the line (9) showing that for unlimited distance, acoustic sampling tends to overlook some species vocalising at distances greater than 50 m.

Species with a lower detectability during acoustic sampling compared to point counts were the Mountain Robin-Chat *Cossypha isabellae*, Cameroon Sunbird *Cyanomitra oritis*, Elliot's Woodpecker *Dendropicos ellioti* and African Thrush *Turdus pelios* (see Table 1 for raw data). On the other hand, species with more detections during acoustic sampling were Chubb's Cisticola *Cisticola chubbi*, Brown-throated Wattle-eye *Platysteira cyanea* (both only up to 50 m), Oriole Finch *Linurgus olivaceus*, Dusky Flycatcher *Muscicapa adusta* and Mount Cameroon Speirops *Speirops melanocephalus* (see Table 1 for raw data).

Bird community similarity (Sørensen index) among particular sampling sites was significantly correlated for estimations using point counts and listening to acoustic samples for both 50 m radius ($r = 0.79$, $p < 0.001$; Figure 3a) and unlimited distance ($r = 0.69$, $p < 0.001$; Figure 3b). However, the bird community similarity among individual census points tends to be underestimated if calculated from data based on listening to acoustic samples. This discrepancy appears to be more pronounced for the unlimited distance data set (Figure 3a and b).

We also calculated total abundances of particular species for the whole study site as a sum of maximum abundances estimated for 16 census points (Table 1). We observed a strong correlation between species abundances estimated by the two methods for both 50 m radius ($r = 0.92$, $p < 0.001$; Figure 4a) and unlimited distance ($r = 0.93$, $p < 0.001$; Figure 4b). However, the number of points above the direct correlation line (slope = 1.0) was lower for both distances (50 m: 10 above, 12 below; unlimited distance: 9 above, 16 below), showing that acoustic sampling underestimates overall abundances of several bird species (Figure 4a and b). Species whose abundances have been typically underestimated by acoustic sampling were mainly species occurring in flocks (Waller's Starling *Onychognathus walleri* and Western Mountain Greenbul *Andropadus tephrolaemus*), most abundant species with more individuals singing at a census point (Northern Double-collared Sunbird *Cinnyris reichenowi*) including duet species (Yellow-breasted Boubou *Laniarius atrofasciatus* and Grey Apalis *Apalis cinerea*), and a species that was identified only by warning calls (African Thrush *Turdus pelios*).

Discussion

The use of acoustic signals for detecting birds is crucial for surveys focused on estimating community composition, species richness and abundances of particular species (Dawson and Efford 2009). This holds true especially in densely vegetated habitats, including tropical woodlands and rain forests, where most individuals are more easily detected by sound than by sight (Celis-Murillo et al.

2012). During our field surveys, we recorded c. 93% of all individuals acoustically and more than half of all species was detected exclusively by voice. All species (with one exception, the uncommon Black-billed Weaver *Ploceus melanogaster*) that were detected during point counts were also recorded by listening to acoustic samples. This suggests that employing soundscape recordings is a reliable approach to produce complete checklists of bird communities, especially at places with a high rate of singing activity of most of the community members (Celis-Murillo et al. 2012).

Our study design was, however, focused mainly on estimating species richness and community composition of particular census points and evaluating the spatial limits of the method based on listening to acoustic samples. Estimates of local species richness were similar for point

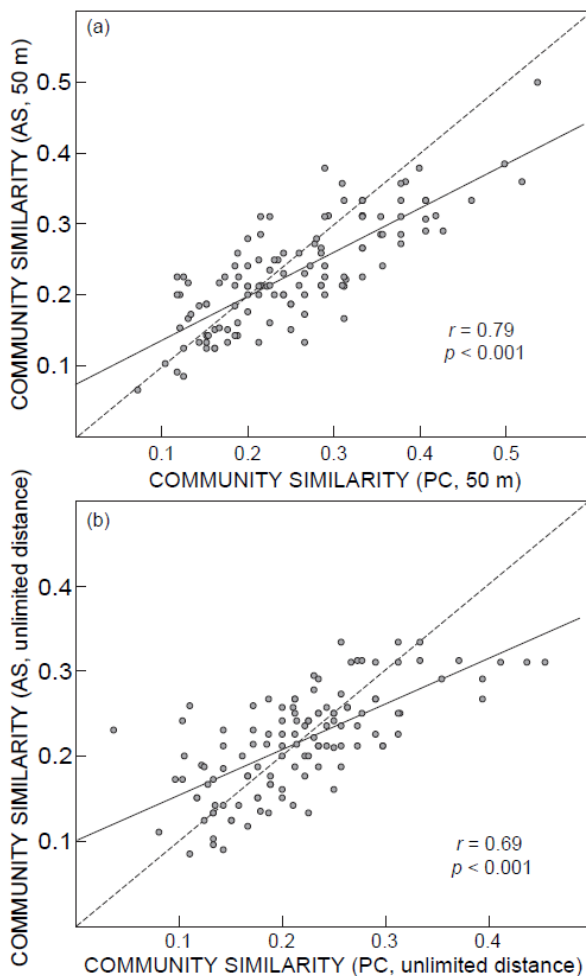


Figure 3: Correlation of bird community similarity (Sørensen index) among particular point samples ($n = 48$) estimated by point counting (PC) in the field and listening to acoustic samples (AS) within a radius of (a) 50 m from the observer/recorder (clearly audible individuals in acoustic samples) and (b) any distance from the observer/recorder. The dashed line shows the trend with the slope 1.0

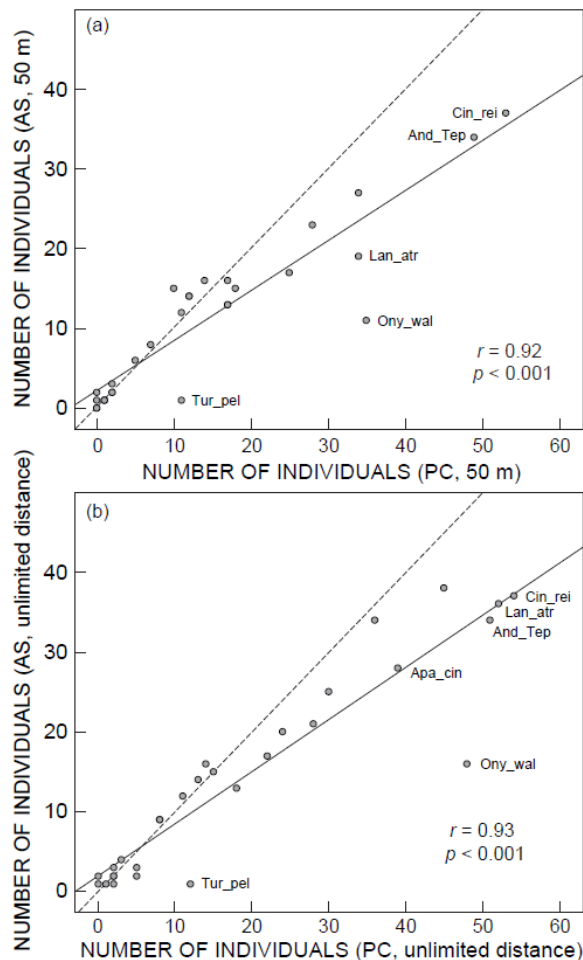


Figure 4: Correlation of total abundances of particular bird species estimated for 16 census points using point counting (PC) in the field and listening to acoustic samples (AS) within a radius of (a) 50 m from the observer/recorder (clearly audible individuals in acoustic samples) and (b) any distance from the observer/recorder. The dashed line shows the trend with the slope 1.0. Abbreviations correspond to the first three letters of the genus and species epithets listed in Table 1

count surveys and listening to acoustic samples in our study. This holds true especially for the distance up to 50 m, total species richness estimates for the 15-minute period, as well as cumulative estimates for all three 5-minute periods. Still, both methods provided similar diversity estimates for any distance. However, listening to acoustic samples tended to miss some individuals singing at greater distances. We observed such an underestimation in cumulative species richness estimates for 10- and 15-minute periods. It might be explained by the fact that the signal-to-noise ratio significantly decreases the detectability of some bird species beyond the 50 m distance (Rempel et al. 2013). Our previous studies that focused on investigation of bird community structures in the montane forests of the

Cameroon volcanic line (Reif et al. 2006, 2007; Hořák et al. 2010; Djomo et al. 2014) showed that the narrow fixed radius of 50 m represents a reasonable compromise in montane rain forest as the detectability of all bird species seems to be comparable for this distance. On the other hand, a radius covering a much smaller area (e.g. 25 m) might not provide sufficient data on species richness and abundances.

An important question is how to estimate an approximate radius of 50 m during listening to acoustic samples. This undoubtedly requires a good knowledge of the singing activity of all species of a given community, especially with regard to species-specific song volume and its transfer efficiency in a given environment (Catchpole and Slater 2008). However, our experience of listening to SongMeter acoustic samples showed that most of the bird species are clearly audible for closer distances of approximately 50 m and individuals singing at a greater distance are well distinguishable. Two groups of birds seem to deviate from this rule in our study. (1) Bird species with loud vocalisations, e.g. *Platysteira cyanea*, and species that duet, namely *Laniarius atrofasciatus* or *Cisticola chubbii*. Our analysis showed that there is a tendency to include these species more frequently at closer distance (clearly audible) during listening to acoustic samples compared with reality. For this reason, these species can sometimes produce false positive records for closer distances and may contribute to slight overestimation of species richness. (2) Group of birds with relatively quiet singing. Surprisingly, according to our analysis this latter group of species can be relatively easily missed both during point counts (e.g. Oriole Finch *Linurgus olivaceus* and Dusky Flycatcher *Muscicapa adusta*) and listening to acoustic samples (e.g. *Cossypha isabellae*). Acoustic samples were also less efficient in detection of non-breeding species that vocalised only by short warning calls during our survey period (e.g. *Cyanomitra oritis* and *Turdus pelios*), and also less detectable was the tapping of woodpeckers (*Dendropicos ellioti* in the present case). It has been previously suggested that species with inconspicuous singing are more often missed by observers in the field when several species are singing and calling at the same time (Hutto and Stutzman 2009). Celis-Murillo et al. (2009) also suggested that the first several minutes of a bird survey might be challenging for observers because of the large number of new detections. They also noted that an advantage of acoustic samples is that sounds can be replayed to allow detection of individuals that might otherwise have been overlooked. Our results only partly conform with these studies, because we experienced that some individuals of species with inconspicuous singing may be missed also during listening to acoustic samples.

Listening to acoustic samples also produced similar bird species checklists for particular census points if compared with data obtained by point count surveys. Therefore, we suggest that recordings can be used for an accurate estimation of bird community composition at local scales. We also showed that data based on listening to acoustic samples produce reliable estimates of beta diversity among particular census points. However, beta diversity tends to be slightly higher when estimated by listening to acoustic samples, especially for the sampling at any distance. This is likely caused by false negative detections for further distances.

Our study is the first to employ acoustic sampling for estimation of avian community structure in tropical Africa. Moreover, we are among the first showing that acoustic sampling provides a good estimate of species abundances for the purpose of interspecific comparisons. However, listening to acoustic samples rather failed in detecting more conspecifics singing at one particular census point (see also Celis-Murillo et al. 2009) and therefore typically led to underestimation of the total abundances of the most common species. In our study area, this was true mainly for species moving in flocks (*Onychognathus walleri* and *Andropadus tephrolaemus*), species with lekking singing behaviour (*Cinnyris reichenowi*) and abundant duetting species (*Laniarius atroflavus* and *Apalis cinerea*). Number of individuals was undoubtedly underestimated also for non-breeding species that had no or low singing activity (e.g. *Turdus pelios* and *Cyanomitra oritis*).

We conclude that listening to acoustic samples offers an alternative and useful approach for surveying bird communities that might accelerate the collection of basic information on community structures in poorly known Afrotropical regions and habitats. In addition, it is helpful when there is a need to monitor species-rich communities throughout the year (Sueur et al. 2012). Furthermore, the method produces archival records of surveys, providing an opportunity for detailed reanalyses of recordings such as automatic detections of particular species (e.g. Kasten et al. 2010; Goyette et al. 2011) and estimates of acoustic species richness (Depaertere et al. 2012; Gasc et al. 2013). These are gradually developing fields of research, which will present opportunities for a variety of studies much needed in the afrotropical region.

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