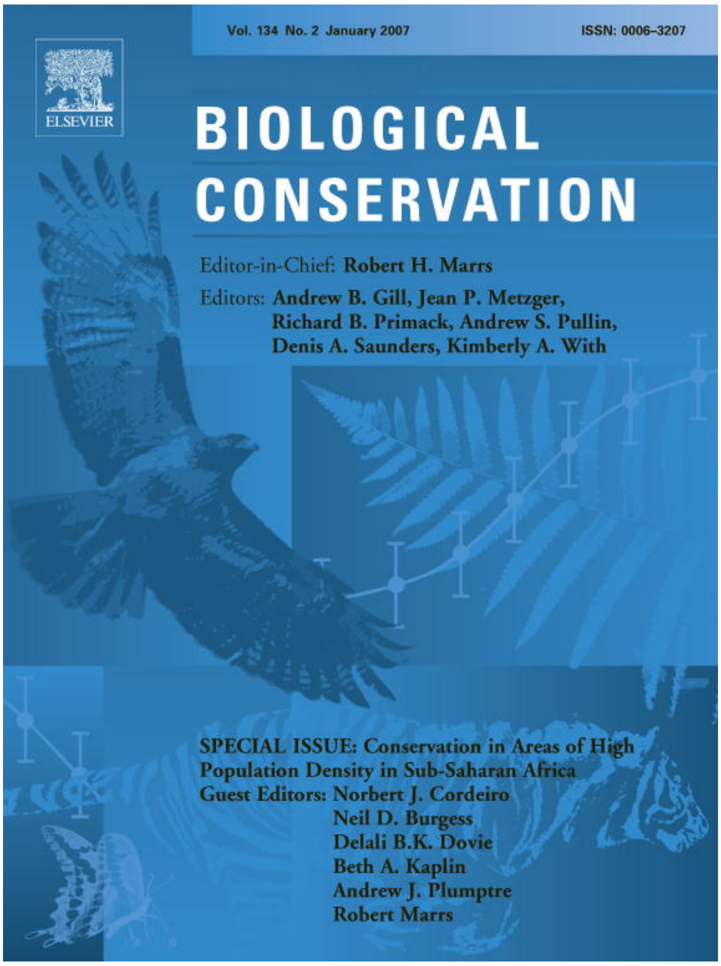

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The relevance of data on genetic diversity for the conservation of Afro-montane regions

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ABSTRACT

Molecular data are shedding new light on our understanding of genetic diversity and biological diversity in general. We examine results of recent genetic studies on African birds that document endemic diversity in small, isolated montane forests of Africa. These studies show that levels of genetic differentiation in these isolated montane regions are substantial and indicate little or no gene flow with their closest populations. Although this pattern of locally distributed montane taxa is not something that has gone unnoticed by traditional taxonomists, we argue that many of the small, often outlying areas run the risk of being devalued in conservation planning because these areas generally have comparatively low levels of overall diversity and endemism (especially at the species level). We strongly suspect that other organisms will possess similar patterns of differentiation in Afro-montane regions of Africa and we argue that this information can be effectively brought to bear to highlight the conservation significance of these smaller areas.

1. Introduction

The threats that are most apparent to the conservation of biological diversity are associated with human activities that destroy or alter that diversity (BirdLife International, 2004; Scharlemann et al., 2004; Burgess et al., 2006a; Ndangalasi et al., 2006). As important as these threats are, there are others. In the present paper, we examine genetic studies on African montane forest birds in order to illustrate a threat that too often goes unconsidered (e.g., Fox and Buckley, 2005), that of losing significant diversity because it is not recognized as important by standard conservation prioritization.

The literature on genetic structure in African birds is not large, because samples are often unavailable for many areas, making broad scale studies with samples from many geographic regions difficult. Still, there is an emerging body of work that has been greatly facilitated by the general collecting efforts of a few institutions. The data sets that we review illustrate the high levels of genetic structure that exist in these Afro-montane forest birds, and we address the implications of this structure for conservation planning.

At the outset, we emphasize that mitochondrial DNA (mtDNA), the type of genetic data focused on in this paper, comprises a single genetic locus. For this and other reasons,

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authors have cautioned about over-interpretation of these data in terms of inferring the evolutionary history of lineages (as opposed to only the history of mtDNA itself; e.g. Lovette, 2004). Although we agree with others that additional character data sets are always desirable (e.g., nuclear, vocal or morphological), we strongly believe that, even with these caveats, the comparative nature of these molecular data have substantial implications for addressing questions of conservation importance. By this we mean that genetic divergences and phylogenetic patterns among different lineages can be compared and contrasted. For instance, mitochondrial cytochrome *b* genes (cyt*b*) of humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*) exhibit about 10% uncorrected sequence divergence (Horai et al., 1995). Chimpanzees and bonobos (*Pan paniscus*) sequences exhibit 6% divergence. We mention these values simply to place into context the divergence between well-known lineages of organisms, whose differentiation is widely appreciated (and recognized taxonomically). Our point is that although low levels of genetic divergence do not necessarily mean populations are exchanging genes, high levels of divergence such as those mentioned above are an indication that populations have been evolving separately, and in our opinion, this is something that should be of interest in conservation planning.

Montane regions are spread across the entire continent and many of these regions have not been sampled recently in a manner that allows genetic studies on the populations they harbor. We review genetic structure for several lineages of birds found in two regions where data have been gathered, the Eastern Arc Mountains of East Africa and the Gulf of Guinea (Biafran) highlands of western Africa. We also include recent results from a poorly studied warbler group (*Bradypterus*) from the Albertine Rift region (Kahindo et al., unpub.). These data sets illustrate the significant levels of genetic structure that can exist and we discuss the implications that these results have for conservation prioritization in Afro-montane regions.

2. Studies of genetic structure in Afro-montane birds

2.1. *Greenbuls of the Eastern Arc mountains of East Africa*

Roy et al. (1998) presented sequence data from two mitochondrial genes (Cyt*b* and NADH2) for a set of montane greenbul (*Andropadus*) species. Their sampling was not large in terms of individuals per site but was substantial in including populations from numerous isolated montane forests of eastern Africa. Their results are striking. Several of the traditional species were comprised of highly divergent lineages in terms of their mitochondrial DNA (Figs. 1 and 2). The greatest divergences were between the large regional highlands such as the Albertine Rift compared to the Eastern Arc Mountains of Tanzania, but there was also evidence that smaller populations within regions were genetically differentiated from their neighbors (Fig. 2).

Within the mountain greenbul (*A. tephrolaemus*) samples from montane regions that included (north to south), Mount Meru (Kenya), the South Pare Mountains (northern Tanzania), the Uluguru Mountains (Tanzania), the Udzungwa Mountains (Tanzania) and Mt. Rungwe (southern Tanzania) exhibited, with only two exceptions, more than 10% sequence divergence between populations on different mountains. The two lower divergences were still 3% and 6%, which are comparatively high values in avian studies (Johns and Avise, 1998). The populations at the five sites had all been named as different subspecies based on morphological differences (Fig. 2), but the genetic data (coupled with the morphological data) are to us sufficient to argue that these taxa could be called species, which would recognize five locally distributed species of conservation concern in the different Eastern Arc mountain ranges. Given their restricted and localized distributions, all these taxa would qualify for inclusion as at least lower risk or near-threatened species (based on BirdLife International, 2000).

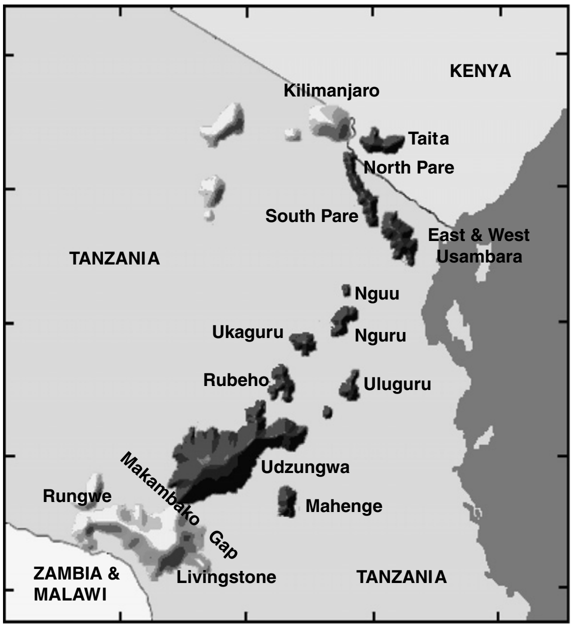

Fig. 1 – The Eastern Arc Mountains (dark grey) form a chain of isolated montane inselbergs that run from the Taita Hills in southeastern Kenya to the Makambako Gap between the Udzungwa and Rubeho-Livingstone Mountains in south central Tanzania.

2.2. *A recently described species of akalat from East Africa*

Building on a broader phylogenetic survey of the genus *Sheppardia* Akalats (Roy et al., 2000), Beresford et al. (2004) described a new species, the Rubeho akalat (*Sheppardia aurantiithorax*), with larger populations in the Rubeho highlands, Kiboriani Mountains and Ukaguru Mountains of the Eastern Arc Mountains of Tanzania, and a tiny population in the Uluguru's (Fig. 3A). This new species is morphologically and genetically differentiated (based on data from Cyt*b* and the nuclear intron 5 of the beta-fibrinogen gene) from neighboring sister species, *S. lowei* and *S. montana*, which also are confined to localized distributions in the Eastern Arc Mountains (Burgess et al., 2006b; Keith et al., 1992). The level of genetic divergence for the Cyt*b* sequences

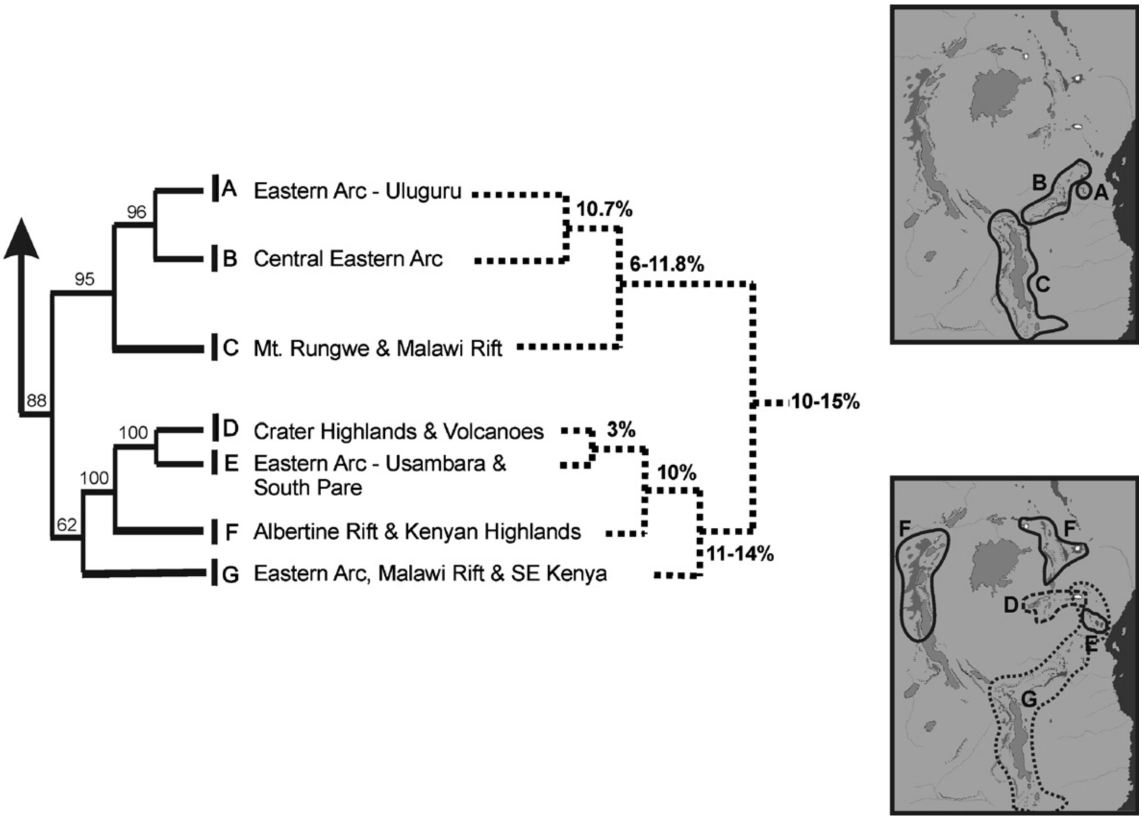

Fig. 2 – Relationships, area-cladograms, sequence divergence and estimated time of divergence for lineages within some montane greenbuls (genus *Andropadus*), based on data from Roy (1997) and Roy et al. (1998).

averaged about 5% between *aurantiithorax* and *lowei*. The limited distribution of the Rubeho akalat does not correspond to the distribution of any of the differentiated *Andropadus* greenbuls, which illustrates the complexity of biogeographic patterns in this region.

2.3. *Genetic structure in a group of African highland sunbirds*

The double-collared sunbirds, widespread across the Eastern Arc Mountains of Tanzania and southeastern Kenya, are characterized by regional variation in morphology and plumage. These differences have caused considerable dispute over their taxonomic status and the delineation of range boundaries. For example, it has been suggested that Moreau's sunbird (*Nectarinia moreaui*) is an atypical phenotype that has arisen from a hybridization event between the more widely distributed eastern double-collared sunbird (*N. mediocris*) and the Uluguru Mountain endemic Loveridge's sunbird (*N. loveridgei*; Hall and Moreau, 1970; Stuart and van der Willigen, 1980). In a recent revision of the eastern double-collared sunbird complex, Bowie et al. (2004) confirmed that Moreau's Sunbird is intermediate in shape and size between eastern double-collared sunbird and Loveridge's sunbird; nonetheless, discrete plumage characters separate all three taxa.

Molecular analyses of 728 bp of mtDNA (NADH3 and Control Region) suggest that Moreau's sunbird is a valid taxon and the sister species to Loveridge's sunbird (Fig. 3B). Further, eastern double-collared sunbird haplotypes can be divided into three distinct clades, separated from each other by substantial genetic divergence (8–10% sequence divergence, Fig. 3B). Moreover, these three clades each can be identified by discrete plumage characters, which led Bowie et al. (2004) to recommend recognition of three species. Thus, where two or three species were recognized previously, Bowie et al. (2004) now argue for the recognition of five species: *N. mediocris* restricted to the highlands of Kenya and the crater highlands of Tanzania, *N. usambarica* restricted to the Taita, Pare and Usambara Mountains, *N. fuelleborni* of the southern Eastern Arc and Malawi Rift, *N. moreaui* of the central Eastern Arc and *N. loveridgei,* endemic to the Uluguru Mountains (Fig. 3B).

2.4. *Genetic structure in a group of Afro-montane thrushes*

Few species of African birds have undergone more taxonomic revision than the olive thrush *Turdus olivaceus*. This turmoil has been 'driven' by disagreement on how to partition the striking phenotypic variation among allopatric populations (see Clement and Hathway, 2000; Keith and Urban, 1992; Keith et al., 1992 for reviews). The current consensus is to recognize one species, *T. olivaceus*, split into three assemblages: (1) the *olivaceus* group restricted to southern Africa, (2) the *swynnertoni* group of the Zimbabwean and southern Malawi highlands and (3) the *abyssinicus* group of the montane highlands of eastern and central Africa.

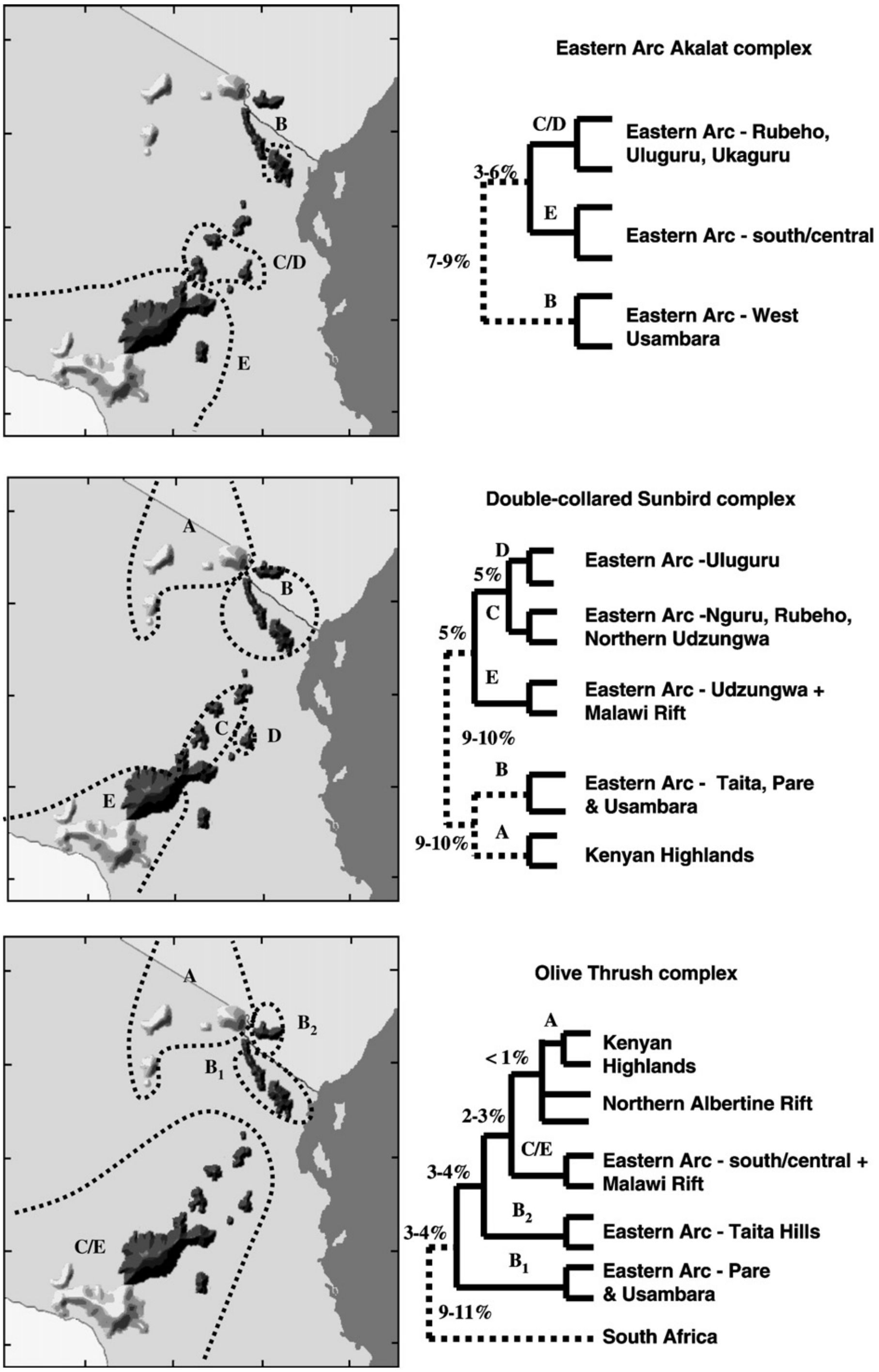

Fig. 3 – Insights into the evolutionary history of three species complexes (A) akalats (Beresford et al., 2004), (B) eastern double-collared sunbirds (Bowie et al., 2004) and (C) Olive Thrushes (Bowie et al., 2005) within the Eastern Arc. Dotted lines on the maps demark taxon boundaries for areas labeled on the phylogenies. Dotted lines in the phylogenies correspond to nodes that are hypothesized to be older than three million years based on a molecular clock.

Bowie et al. (2005) obtained mtDNA sequences (NADH2 and NADH3 genes) from 63 individuals encompassing 16 taxa (species and subspecies) in the *olivaceus* species complex (plus seven outgroup species), in order to investigate phylogenetic relationships among the various taxa. Particular emphasis was placed on the phylogenetic affinities and taxonomic status of the endangered Taita thrush (*T. helleri*).

Phylogenetic hypotheses generated using parsimony, maximum likelihood, and Bayesian Inference identified a number of discrete clades corresponding to recognized subspecies (Fig. 3C). Northern (*abyssinicus* group) and southern populations (*olivaceus* + *swynnertoni* group) of olive thrush differ by 9–10% in sequence divergence (Fig. 3C). Furthermore, all analytical methods suggested that mtDNA sequences of *helleri* (Taita Hills) and *roehli* (Usambara and Pare Mountains) are both reciprocally monophyletic, and 2.5–10.5% divergent from all other forms of olive thrush (Fig. 3C). Both *helleri* and *roehli* are surrounded in adjacent highlands by populations of olive thrush that represent a more recent radiation, suggesting that *helleri* and *roehli* may be relict taxa that have maintained their genetic integrity. The results of this study support previous arguments (Bowie et al., 2003) for recognizing the arid/woodland inhabitant *T. smithi* as a species distinct from other southern African forest populations of *T. olivaceus* (including the *swynnertoni* group of southern Malawi and Zimbabwe). Results further suggest that *T. abyssinicus* restricted to the Kenya-Tanzania volcanic Highlands, Albertine Rift and central Eastern Arc, *T. helleri* endemic to the Taita Hills in SE Kenya and *T. roehli* restricted to the Pare and Usambara Mountains be accorded species rank.

2.5. Genetic structure in Afro-montane warblers

The genus *Bradypterus* has a wide distribution across tropical Africa and Asia and is well represented on major mountains in Africa, thus offering another lineage in which ecological processes and affinities between areas can be assessed. The taxonomic arrangement of African *Bradypterus* has been based on assessments of morphology and songs with historic debate as to the limits of some species and the affinities of some populations (Urban et al., 1997). Genetic data are contributing to the understanding of relationships within this group and further documenting the distinctiveness of some highland populations.

Our studies (Kahindo et al., unpublished data) in the Albertine Rift region have uncovered mtDNA sequence divergence (for the genes, NADH3 and ATPase 6) within Afro-montane *Bradypterus* varying from 1% for intraspecific comparisons to 13% between species. The inclusion of *B. caudatus* from the Philippines raises the latter value to 15.8%. High values of sequence divergence support a pre-Pleistocene diversification of the lineages currently recognized as species.

Within the central African swamp group, *baboecala, carpalis, graueriand grandis*, there is support for a single clade, with the western *B. grandis* more closely related to the East African *B. carpalis* and the southern race of *B. baboecala* than the Albertine Rift endemic *B. graueri*. The highest intraspecific sequence divergence was within *baboecala* (11.1% between *B. b. centralis* and *B. b. benguellensis*, a taxon endemic to the Angolan highlands), which clearly suggests that the taxon *baboecala* may be comprised of multiple distinct lineages with restricted ranges. The enigmatic *B. alfredi*, which is known from a few specimens scattered from western Ethiopia and Sudan, to NW Zambia is genetically distinct from other African taxa that have been surveyed with levels of divergence varying from 10% to 12% from other taxa. We do not currently know what kind of genetic structure exists within this taxon, but its scattered distribution suggests that several locally distinct populations/species may exist.

In the mountains of eastern Africa, our genetic data support the distinctiveness of the taxon currently called *B. lopezi barakae*, which is confined to the Albertine Rift (Urban et al., 1997) and is 11% divergent from Eastern Arc lineages. This suggests that *B. lopezi* may not be monophyletic as currently recognized (Urban et al., 1997). Within *B. cinnamomeus*, sequence divergence averages 4–7% between three major groups: the Albertine Rift, the Eastern Arc, and the highlands of southern Tanzania and Malawi. Recognition of these genetically (and at least for *barakae*, morphologically) distinctive taxa as species would add two more montane endemics to the Albertine Rift avifauna.

2.6. Genetic structure in two montane species from the Biafran forests and highlands

Smith et al. (2000) examined genetic structure in mountain greenbuls (*Andropadus tephrolaemus*) and Cameroon blue-headed sunbirds (*Nectarinia ortis*) from six sites on different mountains in the Biafran Highland region, including the highlands on the island of Bioko. Using Cyt*b* and control region mtDNA sequences, both species exhibit divergence between populations on Bioko, Mount Cameroon and what they termed the northern mountains (comprised of Mt. Kupe, Mt. Oku, Bakossi Mountains and Tchabal Mbabo). Genetic divergences between these lineages averaged about 4%. This is estimated because the authors do not provide a distance matrix, and sequences of the entire data set are not deposited on GenBank. An additional observation about these data is scant haplotype sharing between their northern mountain sites which is consistent with little or no gene flow between these isolated mountains. Smith et al. (2000) compared their phylogenetic data with species diversity data and suggested that Mount Cameroon and Bioko were higher priorities than the sites in the north.

Although we do not disagree with the overall assessment of Smith et al. (2000), we would point out that both study taxa

Table 1 – Summary implications of distinct lineages documented in the reviewed studies on genetic structure of some Afro-montane birds

Taxon	Region	No. of lineages based on mtDNA	Source
Andropadus tephroleamus	Eastern Arc Mts.	5	Roy et al. (1998)
Sheppardia ssp.	Eastern Arc Mts.	3	Beresford et al. (2004)
Nectarinia mediocris	Eastern Arc/Kenyan Highlands/Malawi	5	Bowie et al. (2004)
Turdus helleri/roehli	Taita Hills/N. Tanzania	2	Bowie et al. (2005)
Bradypterus cinnamoneous	Albertine Rift/Eastern Arc/Malawi	3	Kahindo et al., unpubl. data
Nectarinia ortis	Gulf of Guinea Highlands	4	Smith et al. (2000)

In most cases, the taxa had been recognized as single biological species.

exhibit genetic differentiation between all three areas, and there appears to be no gene flow between populations of Mount Cameroon and the northern mountains. Thus, the northern mountains appear to constitute a historically distinct area that has experienced significant isolation, yet harbors lower species diversity than Bioko and Mount Cameroon. Furthermore, it appears that there are very low levels of haplotype sharing between the individual sites (their Table 1) comprising the northern mountains. For example, in the sunbird, *N. oritis*, all but one of the six Cyt*b* haplotypes from Mt. Kupe and all three of the Bakossi Mountian haplotypes are endemic to their respective sites, therefore, it should not be overlooked that these northern mountain sites are both genetically distinct from Bioko and Mt. Cameroon and appear to have little historical gene flow between each other. These data suggest unique genetic diversity exists in at least four distinct montane areas of this region.

3. Discussion

The data reviewed in this paper can be roughly summarized to give an idea of how many lineages are uncovered by the genetic data for several currently recognized biological species (Table 1). This is not a simple comparison to undertake, but from the six data sets, there is evidence for breaking up six montane biological species (with sampling sometimes only including a portion of the overall range) into 18 species based on the genetic data, thus there may be a threefold underestimate of diversity for such lineages. We do not assume that this will be the pattern across all avian lineages found in these regions (e.g., Bowie et al., 2006), but we doubt that such differentiation will be uncommon. The primary point for the present is that many of these genetically distinct lineages are locally distributed in small, often outlying highland areas; a pattern also documented recently by Dillon and Fjeldså (2005). There are currently insufficient data to assess whether other habitats might exhibit similarly high levels of genetic structure. On other continents such as South America, it appears that savanna avifaunas generally may not have as much genetic structure as forest avifaunas (Bates et al., 2003, 2004), but more studies are needed.

The high levels of genetic differentiation that have been found in these afro-montane studies are consistent with recently observed correlations between levels of genetic differentiation and latitude in a broad survey of vertebrates (Martin and McKay, 2004). The significance of the genetic data summarized above gains additional context when we reconsider the degree of divergence in the mitochondrial cytochrome *b* gene between humans, chimpanzees and bonobos. We mentioned these values simply to emphasize that the levels of genetic divergence being uncovered among African highland birds are as substantial as those found between chimpanzees and bonobos (6%); two mammals that we as humans can appreciate as being separate species with noticeable differences in many traits (De Waal and Lanting, 1997). Although there is often at least some morphological differentiation associated with the large genetic divergences between populations of Afro-montane birds, we would argue that the genetic data in and of themselves are sufficient to characterize these populations as evolutionarily distinct lineages; such that their unequivocal isolation (manifested as divergence) make these distinctive lineages worthy of conservation concern.

There is a growing literature discussing how to treat such divergent populations taxonomically (e.g. Beresford et al., 2004; Bowie et al., 2004; Dillon and Fjeldså, 2005); we have not focused on that issue here, but acknowledge its critical importance. For example, in a recent analysis of Sub-Saharan bird distribution patterns, Dillon and Fjeldså (2005) demonstrate that the phylogenetic species concept (PSC) recognizes more areas as possessing endemic species than the biological species concept (BSC) does, but they dismiss these results as trivial because overall patterns of species richness remain largely the same. Their results demonstrate that details on endemism within larger, traditionally recognized priority areas (such as general Afro-montane regions) become highlighted by the PSC. In our opinion, this illustrates why the PSC is more appropriate than the BSC for conservation. Our review suggests that they were, however, conservative in their designation of distinctive lineages (Phylogenetic species). Of the 23 taxa that we suggest could be designated Phylogenetic species (Table 1), only 16 were recognized by Dillon and Fjeldså (2005) www.oikos.ekol.lu.se/appendix, No. E4344. Even with this possible underestimate of Phylogenetic species, Dillon and Fjeldså (2005) also provide solid evidence against a primary concern BSC adherents have frequently expressed regarding the PSC (e.g., Collar, 1996). This is that the PSC will recognize so many areas that it overwhelms our ability to conserve.

We feel that Dillon and Fjeldså (2005) provide a wonderful data set that emphasizes the need for more studies of genetic structure. It is fundamentally important to determine whether establishing a management plan to conserve one species on five mountains, or five species each restricted to a single mountain, is appropriate for the taxonomic group at hand. However, whatever we choose to call these differentiated populations (we would call them five phylogenetic species), the genetic data offer evidence that these populations are both isolated and have diverged from one another. In addition, these populations often have divergent morphological characters.

3.1. *Specific implications for conservation in Africa*

In discussing the broader implications of these data for conservation, we draw on our experiences with conservation planning in Africa. As conservationists rush to make decisions in what is often called a "crisis discipline" (Hunter, 1996; Meffe and Carroll, 1997; Primack, 1998), it may be extremely important in a figurative sense to occasionally stop, take a deep breath, and consider the broadest possible picture. Prioritization is one of the ways in which conservationists are most proactive these days, particularly in the tropics (e.g., Pain et al., 2005). Workshops are commonplace and at these workshops, agendas are set for future actions and allocation of resources based on a few days of meetings with stakeholders and generally interested parties. One of us (JMB) attended an April, 2003 workshop in Entebbe, Uganda, whose goal was to develop a strategic plan for the Albertine Rift. This magnificent montane region is defined, with some difficulty around the edges, as the highlands that stretch from northern Uganda and the eastern Democratic Republic of Congo, south through Rwanda, Burundi, western Tanzania and northern Zambia. Like the Eastern Arc Mountains, this is, in a sense, a continental archipelago. Based on biogeographic patterns of many groups, including birds, it is clear that there are historical, but poorly understood, connections between the Albertine Rift region and other Afro-montane areas (Bowie, 2003; Bowie et al., 2006). From a modern conservation perspective, the region is faced with the fact that areas with some of the highest endemism in Africa are also surrounded by some of the highest human population densities (Balmford et al., 2001; Burgess et al., 2006a; Plumptre et al., 2003, 2006).

The Entebbe workshop itself is evidence that the Albertine Rift region is receiving attention as a region of high conservation concern; nevertheless, what concerned us was that during breakout sessions to discuss a logical framework leading to an action plan for the Albertine Rift, it was strongly suggested that several isolated areas in the southern part of the Rift be left out of the discussions because of their lack of connectivity to other areas. This is where planners may make errors in judgment that could affect the conservation of distinctive biotic diversity.

There is no doubt that these outlying areas, the northern Zambian highlands, Mount Kabobo and the Marungu Highlands in the south, and the Lendu Plateau in the north do not have the high levels of species diversity that exist in larger protected areas in the core of the Albertine Rift. However, their lack of connectivity is shown at the level of subspecific taxonomy in some groups such as birds (Hall and Moreau, 1970). Unfortunately, there have been few recent assessments of these outlying areas (or even some of the larger "core" parts) of the Rift, because the region has been through a disastrous period of war. It also should be noted that the outlying areas generally do not possess populations of the two flagship species of the Albertine Rift (chimpanzees and mountain gorillas, the Marungu Highlands do have chimpanzees), but even based on our presently poor knowledge, these areas are known to have endemic taxa of birds.

We argue that it is important not to marginalize conservation efforts of these outlying, and isolated mountainous areas. Ernst Mayr (1963) in his seminal works on speciation reviewed how geographically isolated populations could be important entities for generating diversity. To our knowledge the importance of geographic isolation has never been refuted as an important factor in generating diversity. It is certainly true that many isolated populations may represent sinks, no matter what actions humans do or do not take, but who among us can predict the evolutionary futures of such isolates? Africa possesses many such fringe sites, including Mount Rungwe, and the Ufipa Plateau on the fringes of the Malawi Rift and Eastern Arc Mountains, the Mahale Mountains (an outlier of the Albertine Rift) in Tanzania, and the Nyika plateau in Malawi; the list is not short, nor is it limited only to montane habitats (Dillon and Fjeldså, 2005). An oft-stated goal in conservation biology is to try to preserve the processes associated with the generation and maintenance of biotic diversity. The more depauperate areas on the fringe of larger conservation "hotspots" or isolated from the apparent "ecoregions" to which they belong may simply represent unimportant isolates and evolutionary dead ends. However, it is equally possible that they represent important sources of evolutionary potential and as such it is important not to let them slip completely out of view during prioritization for conservation.

The genetically distinct populations of birds we have reviewed could be examples of such evolutionary potential. For the Eastern Arc Mountains, the four bird data sets we review, greenbuls (Roy et al., 1998), sunbirds (Bowie et al., 2004), thrushes (Bowie et al., 2003, 2005) and akalats (Beresford et al., 2004; Roy et al., 2000), isolated mountain ranges are shown to harbor populations that may have been evolving separately for as long as 5 million years (Figs. 2 and 3). The Taita thrush (*Turdus helleri*), a globally critically-endangered species is a case in point, being restricted to the Taita Hills, the northern most outlier of the Eastern Arc. The Eastern Arc is a region whose already high levels of endemicity continue to grow with new discoveries (e.g., Matthee et al., 2004; Bowie and Fjeldså, 2005; Jones et al., 2005; Stanley et al., 2005, and citations therein) of locally distributed taxa, and other groups of organisms appear differentiated on even finer scales in these mountains (Menegon et al., 2004).

The Eastern Arc has recently received much needed attention from the international community as a global conservation priority (e.g. Special Volume 87 parts 1–2 of the Journal of East African Natural History – Burgess et al., 1998, 2006b; Myers et al., 2000), but emphasis cannot be given only to the larger blocks of forest such as the Uluguru, Usambara and Udzungwa Mountains, which harbor most of the endemic species without sacrificing genetically distinct lineages on smaller adjacent mountain areas (like the South Pares and the Rubehos), including those like Mt Rungwe which are outliers of the Eastern Arc Mountains. The Usambara Mountains harbor distinct lineages of greenbul (*Andropadus usambara*), sunbird (*Nectarinia usambarica*) and thrush (*Turdus roehli*), all of which extend to the Pare Mountains (Figs. 1–3). If the more northern Pare Mountains are considered unimportant outliers due to their relative poor species richness then 50% of the range of these three taxa mentioned above would be lost.

The smaller isolates of the Eastern Arc and the Albertine Rift have not been completely ignored, but as priorities are set, they could be lost, especially if we remain unconvinced that these smaller isolated areas within larger designated "hotspots" have evolutionary potential. By their very history they will tend to have low scores for many of the commonest measures (species diversity and species endemism) used to assess the relative values of different sites. If we learn that these small isolates harbor genetically and evolutionarily distinctive populations, as the studies summarized here document (Beresford et al., 2004; Bowie et al., 2004, 2005; Roy et al., 1998, 2000), it will be important to use these data to argue for the conservation of these smaller isolated and often peripheral areas.

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