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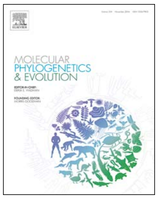

The systematics and biogeography of African tailorbirds (Cisticolidae: *Artisornis*) with comment on the choice of Bayesian branch-length prior when analyzing heterogeneous data

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ABSTRACT

The Long-billed Tailorbird (*Artisornis moreaui*), one of Africa's rarest birds, has a strikingly disjunct distribution, the origin of which has long puzzled biogeographers. One small population (subspecies *moreaui*) occurs in sub-montane forest in the East Usambara Mountains, a sky island near the coast of northern Tanzania, and another (subspecies *sousae*) on Serra Jeci in northwestern Mozambique, 950 km away. The African Tailorbird, the putative sister-species of Long-billed Tailorbird, also occurs in the East Usambara Mountains and on Serra Jeci, but in addition occupies all the Eastern Arc Mountain forests between these disjunct sites. Stuart (1981) hypothesized that the two tailorbird distributions could be explained by strong ecological competition, with African Tailorbird populations having eliminated Long-billed Tailorbird populations via competitive exclusion in montane forests between the East Usambara and Serra Jeci. If such competitive exclusion explains these geographic distributions, the co-occurrence of the two species in the East Usambara and at Serra Jeci may be ephemeral, with the status of Long-billed Tailorbird especially in doubt. We sought to (1) determine whether the two species of African tailorbirds are indeed sister-species, and (2) test predictions from Stuart's (1981) competitive exclusion hypothesis using genetic data. Phylogenetic analyses of our seven gene dataset (3 mtDNA, 4 introns; 4784 bp) indeed place these two species together in the genus *Artisornis*. Instead of finding shallow divergence among African Tailorbird populations and deep divergence between Long-billed Tailorbird populations as expected from Stuart's hypothesis, we recover deep genetic divergence and geographic structure among populations of both tailorbird species. This result is consistent with long-term co-existence of the two species at East Usambara and Serra Jeci. Observational data from both the East Usambara and Serra Jeci suggest that the two species have diverged in use of forest canopy strata. From a conservation standpoint, our results suggest that extinction of the Long-billed Tailorbird as a function of competition with African Tailorbird is highly unlikely, and should not be viewed as imminent. Threats to its survival are instead anthropogenic, and conservation measures should take this into account. Finally, our empirical results suggest that mis-specification of the branch-length prior in Bayesian analyses of mitochondrial DNA data can have a profound effect on the overall tree-length (sum of branch-lengths), whereas the topology and support values tend to remain more stable. In contrast, mis-specification of the branch-length prior had a lesser impact on all aspects of the nuclear-only DNA analyses. This problem may be exacerbated when mitochondrial and nuclear DNA analyses are combined in a total evidence approach.

1. Introduction

Resolving the systematics and biogeography of Old-World warblers, historically placed in the family Sylviidae, has proven challenging due to limited morphological divergence and considerable morphological convergence among these birds, the "Primitive Insect Eaters" of Mayr and Amadon (1951). Molecular-based systematic approaches have revealed that the Sylviidae, as defined in this "traditional" classification,

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is best broken into several families whose composition remains in a state of flux (e.g. Sibley and Alquist 1990; Sefc et al. 2003; Alström et al. 2006; Nguembock et al. 2007, 2008, 2012; Johansson et al. 2008; Cibois et al. 2010; Alström et al. 2011, 2013). One such family that has come to be defined with the aid of molecular characters is the Cisticolidae, a large radiation of primarily African warblers (Ryan 2006; Olsson et al. 2013).

Of the 27 cisticolid genera recognized by Ryan (2006), three are shared with Asia: prinias (*Prinia*), cisticolas (*Cisticola)* and the tailorbirds (*Orthotomus, Artisornis*). Recent studies have demonstrated that despite their similar stitched-leaved nest architecture, tailorbirds as traditionally circumscribed (e.g. Fry 1976; Sibley and Monroe 1990) are not monophyletic (Alström et al. 2006; Nguembock et al. 2007, 2008, 2012), with at least one species, the Mountain Tailorbird (*O. cucullatus*, which does not stitch its nest), falling outside the Cisticolidae.

The two African Tailorbird species (African Tailorbird *Artisornis metopias* and Long-billed Tailorbird *Artisornis moreaui*) differ from those in Asia by having 10 instead of 12 tail feathers (rectrices). Hall and Moreau (1962, 1970), Fry (1976) and Stuart (1981) emphasized the similarities of the two African tailorbirds with Oriental tailorbirds (*Orthotomus*) in their behavior, prominent slender bill, association with forest undergrowth, and general nest architecture. In contrast, Urban et al. (1997) and Ryan (2006) regarded the 10 rectrices (as opposed to 12) of the two African tailorbirds as diagnostic, and retained them in *Artisornis*. Molecular data has associated the African Tailorbird with two species of African warblers that were previously in the genus *Apalis* (now *Oreolais pulchra* and *O. ruwenzorii*), confirming that the African Tailorbird is more distantly related to Oriental tailorbirds (*Orthotomus*). Neither species of *Oreolais* stich their nests, suggesting that the stitched-leaved nest architecture of *Artisornis* nests likely reflects convergence or plesiomorphy (Nguembock et al. 2007; Olsson et al. 2013). Indeed, within the Cisticolidae, stitched-leaved nests occur in at least two additional genera (e.g. *Prinia subflava*, *Cisticola erythrops*; Ryan 2006), suggesting that this trait may be more labile than previously thought and may therefore be of more limited phylogenetic utility.

In contrast to the established systematic position of the African Tailorbird (Nguembock et al. 2007, 2008; Olsson et al. 2013), the systematic position of the Long-billed Tailorbird continues to be debated. It has, to date, not been included in a molecular phylogeny, as no samples have been available due to its rarity. Originally described by Sclater (1931) as *Apalis moreaui*, and sometimes referred to as the Long-billed Apalis, it is one of Africa's rarest birds (Stattersfield and Capper 2000) and has a strikingly disjunct distribution. One small population (subspecies *moreaui*) occurs around Amani Forest and on Mount Nilo in the East Usambara Mountains, a montane sky island near the coast of northern Tanzania (Hall and Moreau 1962; Stuart 1981; Cordeiro et al. 2001), and another (subspecies *sousae*) on Serra Jeci (Njesi Plateau on older maps) in northwestern Mozambique, 950 km away (Benson 1945, 1946; Ryan and Spottiswoode 2003).

The remarkable contrasting distributions of the two African tailorbird species, with Long-billed Tailorbird restricted to only two small montane sky islands at the extreme northern and southern margins of the distribution of African Tailorbird (Fig. 1), has long intrigued ornithologists. Previous studies have suggested that strong ecological competition between the two tailorbird species is likely based on several lines of evidence, beginning with the morphological and behavioral similarities of the two species (Stuart, 1981). Further, it has been suggested that at the two locations where they co-occur, their niche differences take two different forms (Stuart, 1981; Cordeiro et al., 2001; Ryan and Spottiswoode, 2003), suggestive of alternate paths of ecological displacement (but see McEntee et al., 2005). In the East Usambara Mountains, the two species are partly elevationally segregated, with Long-billed Tailorbirds persisting at slightly lower elevations (c. 800 m and higher) than African Tailorbirds (c. 1000 m and higher; Cordeiro et al., 2001; Cordeiro, 2011). At Serra Jeci, the elevational band of forest is so narrow (primarily between 1600 and 1850 m) that it is unlikely to permit any elevational segregation. However Long-billed Tailorbirds are observed primarily in the mid-canopy there, and African Tailorbirds in the understorey (Benson, 1946; Ryan and Spottiswoode, 2003, JPM and E. Mulungu, pers. obs.). This situation may contrast with the East Usambaras (Ryan and Spottiswoode, 2003), where both species spend considerable time in the undergrowth (below 5 m), but Long-billed Tailorbirds also venture into the canopy (as high as c. 24 m; Cordeiro et al., 2001; McEntee et al., 2005). Stuart (1981), from consideration of the evidence for ecological competition, hypothesized that African Tailorbirds have eliminated Long-billed Tailorbirds from montane forests between East Usambara and Serra Jeci via competitive exclusion, resulting in the remarkable present disjunct distribution of Long-billed Tailorbird populations. If Stuart's hypothesis is correct, contemporary co-occurrence of the two species in the East Usambara and on Serra Jeci could be: (1) supported by unique conditions in these two montane highlands; (2) accommodated by ecological character displacement or adaptive phenotypic plasticity; or (3) ephemeral (Stuart, 1981), wherein African Tailorbird is competitively superior and, given more time, will cause extinction of the remaining two Long-billed Tailorbird populations. These possibilities are not mutually exclusive.

The use of molecular DNA sequence data provides a means to test between the alternate hypotheses of competitive exclusion by African Tailorbird and speciation with stable subsequent co-existence. Should on-going progressive competitive exclusion by African Tailorbird explain the distributions of the two tailorbird species, we would expect support for the following three predictions: (1) population histories should show signals of northward and southward expansion by African Tailorbird from the central Eastern Arc Mountains; (2) the divergence of the two extant Long-billed Tailorbird populations should pre-date the arrival and any subsequent divergence of African Tailorbirds in the East Usambara Mountains and on Serra Jeci; and (3) the inferred duration of co-existence in the East Usambara and on Serra Jeci should be relatively short. In contrast, co-existence of the tailorbirds in the East Usambara and Serra Jeci could be thousands of years old, indicative of successful resource partitioning with speciation. Molecular evidence for stable co-existence could come from geographically restricted and old lineage ages for populations of African and Long-billed Tailorbirds in either or both the East Usambara and Serra Jeci. Given the extremely small area of suitable habitat for both species at Serra Jeci (Ryan and Spottiswoode 2003), evidence for long-term coexistence there would be especially indicative of successful resource partitioning.

In this paper we first establish the systematic position of Long-billed Tailorbird among other 10-rectrix African warblers using an extensive mitochondrial and nuclear DNA dataset. Secondly, we make use of molecular data along with the three predictions delineated above to test Stuart's (1981) hypothesis that that African Tailorbirds have forced Long-billed Tailorbirds out of the understorey at Seri Jeci and potential through much of the central and southern Eastern Arc Mountains of Africa.

2. Material and methods

2.1. Sampling

We obtained samples of all taxa within the genus *Artisornis*, including both subspecies of Long-billed Tailorbird and all three subspecies of African Tailorbird (N to S: West Usambara Mountains n = 3, East Usambara Mountains n = 3, Rubeho Mountains n = 3, Udzungwa Highlands n = 2, Uluguru Mountains n = 3, Matengo Highlands n = 2, Serra Jeci n = 1; Table 1, Fig. 1). As suggested by others (Nguembock et al. 2008; Olsson et al. 2013), we expanded the ingroup sampling to include both species of the sister clade *Oreolais* (Black-collared "Apalis" *O. pulchra* and Ruwenzori "Apalis" *O. ruwenzorii*), as well as the White-chinned "Prinia" (*Schistolais leucopogon*), the Green Longtail (*Urolais*