Zoologica Scripta

Phylogeography and systematics of the Malagasy rock-thrushes (*Muscicapidae, Monticola*)

Astrid Cruaud, Marie Jeanne Raherilalao, Eric Pasquet & Steven M. Goodman

Submitted: 30 June 2011
Accepted: 2 September 2011
doi:10.1111/j.1463-6409.2011.00497.x

Cruaud, A., Raherilalao, M. J., Pasquet, E. & Goodman, S. M. (2011) Phylogeography and systematics of the Malagasy rock-thrushes (*Muscicapidae*, *Monticola*). —*Zoologica Scripta*, *40*, 554–566.

The patterns of genetic variation and the systematics of members of the widespread Old World genus *Monticola* (Family Muscicapidae) occurring on Madagascar remain unresolved. Herein, we address these questions by examining the phylogeography of Malagasy *Monticola* using two molecular markers (*ND2* and *ATP6*, 1.5 kb) from 60 individuals sampled across their known range. To clarify the relationships within the clade groupings, we use a statistical haplotype network and an analysis of the genetic structure of the different populations sampled. A morphological study was conducted in parallel that used many of the same individuals employed in the molecular study to examine potential differences between the recovered clades. Based on molecular genetics and morphology, *M. imerinus* is distinct from the *M. sharpei* complex, which is composed of five phylogroups: Group A (Central Highlands, typical *sharpei*), Group B (Central West, Bemaraha), Group C (Northern Highlands), Group D (Montagne d'Ambre, *erythronotus*) and Group E (Southwestern, *bensoni*). While molecular data show high levels of geographical structure, these differences exhibit low levels of intergroup genetic divergence (0.01–0.07%). We suggest that two species of *Monticola* occur on Madagascar, *imerinus* and *sharpei*, and the forms referable to *bensoni* and *erythronotus*, as well as unnamed populations from the Central West (Bemahara), should be considered as part of *M. sharpei* and are populations that are probably isolated and undergoing incipient speciation.

Corresponding author: *Steven M. Goodman, Field Museum of Natural History, 1400 South Roosevelt Road, Chicago, IL 60605, USA and Association Vahatra, BP 3972, Antananarivo (101), Madagascar. E-mail: sgoodman@fieldmuseum.org*
Astrid Cruaud, Département Systématique et Evolution, UMR 7205, Origine, Structure et Evolution de la Biodiversité, Case postale 51, 57 Rue Cuvier, 75231 Paris Cedex 05, France. E-mail: cruaud@supagro.inra.fr
Marie Jeanne Raherilalao, Département de Biologie Animale, Université d'Antananarivo, B.P. 906, Antananarivo (101), Madagascar and Association Vahatra, BP 3972, Antananarivo (101), Madagascar. E-mail: jraherilalao@vahatra.mg
Eric Pasquet, Département Systématique et Evolution, UMR 7205 « Origine, Structure et Evolution de la Biodiversité », Case postale 51, 57 Rue Cuvier, 75231 Paris Cedex 05, France. E-mail: eric.pasquet@mnhn.fr

Introduction

The avifauna of Madagascar, an island that has been isolated from continental landmasses for approximately 140 million years (de Wit 2003), holds a notably high percentage of endemic taxa, including several families and subfamilies of distinctly older radiations. Of the 285 bird species reported from the island, 210 are known to breed locally, and of these, 52% occur nowhere else in the world (Goodman & Hawkins 2008; Renoult 2009; Goodman *et al.* 2011). The phylogenetic affinities, origins and colonization history of the older groups in particular have been examined with molecular markers (e.g. Houde *et al.* 1997; Johnson *et al.* 2000; Cibois *et al.* 2001, 2010; Kirchman *et al.* 2001; Yamagishi *et al.* 2001; Sorensen & Payne 2005). Excluding studies exploring sister relationships between Malagasy and congeneric taxa in other areas of the Old World (e.g. Helbig & Seibold 1999; Groombridge *et al.* 2002; Voelker 2002; Sheldon *et al.* 2005), little attention has been devoted to the resolution of questions associated with the species limits of endemic birds, specifically phylogeographic studies (e.g. Goodman *et al.* 2001, 2011; Goodman & Weigt 2002; Fuchs *et al.* 2007). As much of

the conservation prioritization on Madagascar has been based on species distribution, with birds being amongst the targeted taxa (e.g. Kremen *et al.* 2008), refinement of information on the cladogenesis of endemic groups, particularly measures of genetic and morphological diversity, is critical to advance these programmes.

A case in point are the rock-thrushes of the Old World genus *Monticola* Boie, with the Malagasy members formerly positioned in the endemic genus *Pseudocossyphus* Sharpe (Ripley 1964), but based on molecular markers are appropriately placed in *Monticola* (Goodman & Weigt 2002; Outlaw *et al.* 2007). Ambiguity exists associated with the taxonomic status of *Monticola bensoni* Farkas (1971); which according to certain authors is a distinct species, a synonym of *M. sharpei* (Gray, 1871), or a subspecies of *M. sharpei* (Goodman & Weigt 2002; Outlaw *et al.* 2007; IUCN 2010; Zuccon & Ericson 2010). *Monticola erythronotus* (Lavauden 1929), which was formerly considered a subspecies of *M. sharpei*, has been elevated to a full species and considered by IUCN (2010) as endangered. Finally, different ornithologists have discussed a potential undescribed form from the limestone areas of the central western portion of the island (Morris & Hawkins 1998; Jones & Swinnerton 2000).

Over the course of nearly two decades of fieldwork on Madagascar, new specimen material of *Monticola*, with associated tissue samples, has been gathered and provides an important source to examine phylogeographic patterns overlaid on morphological variation, and these aspects are the subjects of this paper. To date, the different published molecular genetic studies incorporating Malagasy *Monticola* had insufficient sampling from the island to resolve certain critical issues. Further, these projects focused on broader questions of species limits, biogeographic patterns and the phylogeny of the genus and its relationships to other members of the Muscicapidae and Turdinae (Goodman & Weigt 2002; Outlaw *et al.* 2007; Zuccon & Ericson 2010). Our intent here is to understand the level of genetic diversity, using two mitochondrial markers (*ND2* and *ATP6,* 1.5 kb), within and between the different proposed taxonomic forms of Malagasy *Monticola* and how these patterns relate to plumage coloration and morphometric variation.

Methods

The study organisms

Different forms of Malagasy *Monticola* have been named, and their taxonomic status has been in a state of flux over the past century. Based on morphological (Salomonsen 1934; Goodwin 1956; Farkas 1971) and molecular (Goodman & Weigt 2002; Outlaw *et al.* 2007; Zuccon & Ericson 2010) data, the Malagasy rock-thrushes are members of the genus *Monticola*, monophyletic with regard to Madagascar, and colonized the island an estimated 3.4 Ma via trans-oceanic dispersal from Africa.

Of the seven named forms occurring on the island, several exhibit differences in plumage coloration, size and habitat. Depending on the author, these morphotypes are considered as valid species, subspecies or synonyms. Here, we present a synopsis of the different described forms of Malagasy *Monticola*. All the localities mentioned hereafter are shown in Fig. 1.

1. *Monticola imerinus* (Hartlaub, 1860) Littoral Rock-thrush

Type locality – 'St. Augustins-Bai', southwest

syn. *Cossypha imerina* Hartlaub (1860)

syn. *Pseudocossyphus imerinus imerinus* Ripley (1964)

syn. *Pseudocossyphus imerinus* Langrand (1990)

IUCN status: Least Concern, version 3.1 (IUCN 2010).

This form is found in a distinct coastal habitat in the southwestern corner of the island, dominated by *Euphorbia* bushland, coral rag and dune habitat, and across an elevational range from sea level-200 m (Morris & Hawkins 1998). It is larger than the other forms of *Monticola* occurring on the island, particularly the bill, as well as having plumage differences.

2. *Monticola sharpei* (Gray, 1871) Forest Rock-thrush

Type locality – east central. This was subsequently restricted by Grandidier (1879, p. 370) to the forests east of Ambatondrazaka.

syn. *Cossypha Sharpei* Gray (1871)

syn. *Pseudocossyphus imerinus sharpei* Ripley (1964)

syn. *Pseudocossyphus sharpei* Langrand (1990)

IUCN status: Least Concern, version 3.1 (IUCN 2010).

This form has generally been considered as restricted to the humid forest formations of Madagascar, from the north-west, eastwards to the eastern mountains and running the complete length of the island. It occurs across an elevational range of 800–2500 m (Morris & Hawkins 1998). This species is distinctly more common in montane forests, as compared to more low-lying formations (Hawkins *et al.* 1998). Throughout this paper, when we use the name *sharpei*, we specifically refer to this form.

3. *Monticola erythronotus* (Lavauden 1929) Amber Mountain Rock-thrush

Type locality – Montagne d'Ambre

syn. *Cossypha sharpei erythronota* Lavauden (1929)

syn. *Pseudocossyphus imerinus erythronotus* Ripley (1964)

syn. *Pseudocossyphus sharpei erythronotus* Langrand (1990)

IUCN status: Endangered B1ab (iii) version 3.1 (IUCN, 2010).

This form is only known from montane forests on Montagne d'Ambre, an isolated volcanic mountain at the north end of the island and across the elevational range of 800–1300 m (Morris & Hawkins 1998). Its separation

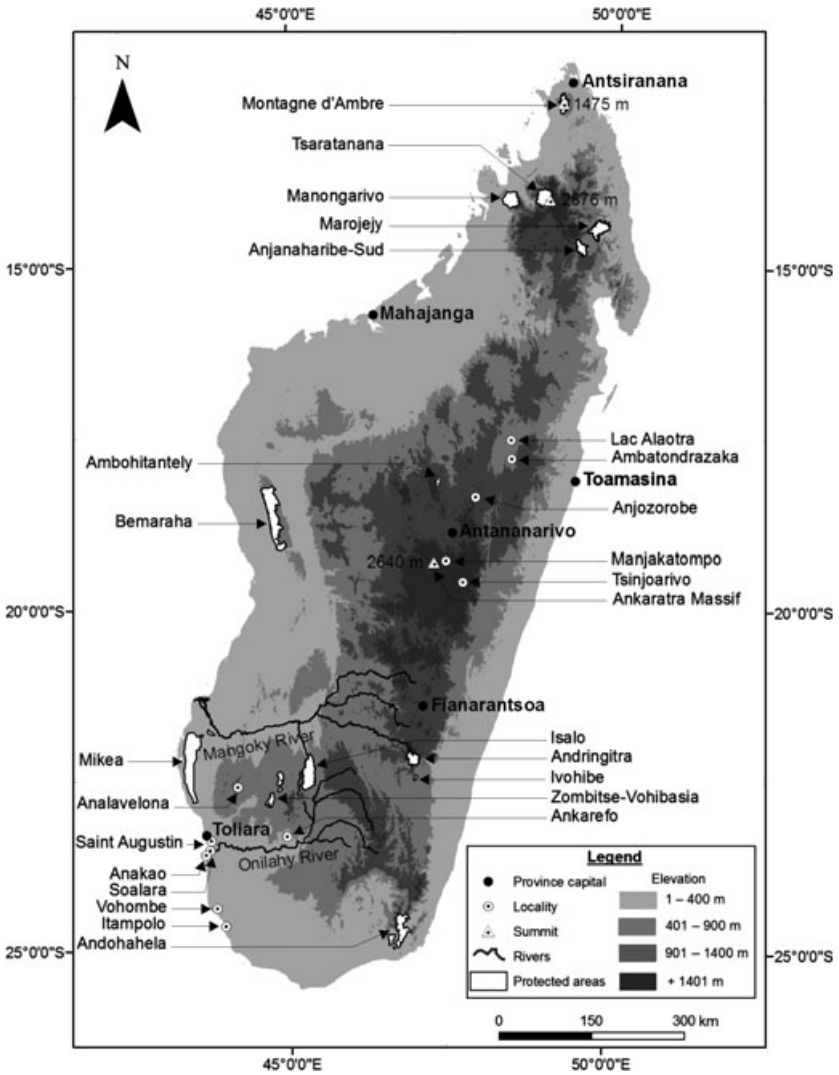

Fig. 1 Map of Madagascar showing different localities in the text associated with the distribution of *Monticola* species.

from *M. sharpei* and recognition as a distinct species were based largely on differences in plumage coloration (Lavauden 1929).

4. *Monticola sharpei interioris* Salomonsen (1934)

Type locality – Manjakatompo, Ankaratra Mountains

syn. *Monticola imerina interioris* Salomonsen (1934)

syn. *Pseudocossyphus sharpei salomonseni* Langrand (1990)

IUCN status: not assessed.

This form was named from the Ankaratra Massif in the Vakinankaratra mountain chain and occurs across an elevational range from 1600 to 2200 m (Milon *et al.* 1973; Goodman, unpublished data). Langrand (1990) also mentioned its occurrence in the Fianarantsoa area. It was distinguished from *sharpei* based on its slightly larger size and subtle plumage differences (Salomonsen 1934).

5. *Monticola bensoni* Farkas (1971)

Type locality – 'Ankarefu, Antinosy Cy'

syn. *Pseudocossyphus bensoni* Langrand (1990)

IUCN status: not explicitly treated as considered a form of *sharpei*.

As currently defined in the literature, *bensoni* inhabits semi-arid rocky country, often with sparse or open vegetation, and in numerous cases associated with cliffs and gorges, as well as dry deciduous forest from 700 to 1000 m (Langrand 1990; Langrand & Goodman 1996). It was distinguished from *sharpei* based on differences in plumage coloration, including aspects of the tail (Farkas 1971).

6. *Monticola sharpei salomonseni* Farkas (1973)

Type locality: 'Sianaka Forest, eastern Madagascar', also known as the Sihanaka Forest, which is to the east of Lac Alaotra.

IUCN status: not treated.

This form was described from the transitional zone between lowland and montane forest of eastern Madagas-

car and based on subtle plumage differences (Farkas 1973). It has not been subsequently recognized as valid. Further, Grandidier (1879) restricted the type locality of *sharpei* to the forests east of Ambatondrazaka, which is precisely the Sihanaka Forest. Hence, we treat the name *salomonseni* as a junior synonym of *sharpei*.

7. *Pseudocossyphus imerinus tsaratananae* Milon, Petter, and Randrianasolo (1973)
Type locality: 'massif du Tsaratanana'.
IUCN status: not treated.

Milon *et al.* (1973) distinguished this form based on colour differences, and there is no evidence that a type specimen was designated. Best considered a *nomen nodum*.

Morphological study

Taxonomic sampling. Museum specimens were examined from the following museums: American Museum of Natural History, New York (AMNH); The Natural History Museum, London, formerly British Museum (Natural History) [BMNH]; Field Museum of Natural History, Chicago (FMNH); Muséum national d'Histoire naturelle, Paris (MNHN); and Département de Biologie Animale, Université d'Antananarivo (UADBA).

Measurements were taken by SMG from dried museum specimens following the techniques described by Baldwin *et al.* (1931). In the field, mass was measured with a spring balance to the nearest 0.5 g. Univariate statistical analyses were conducted for each of the measured variables with samples being segregated by sex and groups derived from genetic markers. To examine morphological differences between the different groups of Malagasy *Monticola*, a principal component analysis was conducted using the statistical package STATISTICA, version 7.0 (StatSoft, Inc., Tulsa, OK, USA); data were log-transformed, and the unrotated option was used. Only adult specimens were used in these analyses.

Molecular study

Taxonomic sampling. The vast majority of the *Monticola* tissue samples were small pieces of muscle saved in lysis buffer and obtained from 60 different individuals from across the island (Fig. 2b, Appendix S1). Associated voucher specimens for the molecular study are housed in the UADBA or FMNH. Single individuals belonging to *M. solitarius* and *M. gularis* were used as outgroups.

Laboratory protocols

Total DNA was extracted from frozen or alcohol-preserved tissues using a CetylTrimethylAmmonium Bromide (CTAB)-based protocol (Winnepenninckx *et al.* 1993) with an overnight Proteinase K (0.1 mg/mL) digestion. PCR amplification of partial sequences of two mitochondrial genes (*ND2* coding for the subunit 2 of the mitochondrial NADH dehydrogenase and *ATP6* coding for the subunit 6 of the ATP synthase) was performed using primers pairs L5219Met and H6313Trp (Sorenson *et al.* 1999) for *ND2*, and A8PWL (5′-CCTGAACCTGACCATGAAC-3′) and CO3HMH (5′-CATGGGCTGGGGTCRACTATGTG-3′) (Seutin & Bermingham unpublished) for *ATP6*.

PCR cycling conditions started with an initial 4-min denaturing step at 94 °C followed by 35 amplification cycles of 30-s denaturing at 94 °C, 40-s annealing at 56 °C, 45-s extension at 72 °C and final extension step at 72 °C for 5 min. PCR products were purified using exonuclease I and phosphatase and sequenced directly using the BigDyeTerminator V3.1 kit (Applied Biosystems, Foster City, CA, USA) and an ABI3730XL sequencer at Genoscope, Evry, France. Both strands for each overlapping fragment were assembled using the sequence-editing software GENEIOUS v3.7 (Drummond *et al.* 2007). All sequences have been deposited in GenBank (Appendix S1)

Phylogenetic analyses

Sequences were aligned using Clustal W 1.81 default settings (Thompson *et al.* 1994). Alignments were translated to amino acids using MEGA 4 (Tamura *et al.* 2007) to detect frameshift mutations and premature stop codons, which may indicate the presence of pseudogenes. Phylogenetic analyses of combined mitochondrial data set were conducted using both parsimony and maximum likelihood (ML) methods. Parsimony analyses were conducted under TNT version 1.1 (Goloboff *et al.* 2008). Analyses were performed with unordered, equally weighted and non-additive characters, all substitutions equally weighted. Traditional heuristic searches were conducted using 1000 'random addition sequences' to obtain initial trees and 'tree bisection and reconnection' as branch swapping option. Robustness of topologies was assessed by bootstrap procedures using 1000 replicates.

The most appropriate model of evolution for the data set was identified using the Akaike information criterion implemented in MRAIC.PL 1.4.3 (Nylander 2004). We performed ML analyses and associated bootstrapping using the MPI-parallelized RAxML 7.0.4 (Stamatakis 2006a). GTRCAT approximation of models was used for ML bootstrapping (Stamatakis 2006b; 1000 replicates).

Distance analyses

Minimum intergroup divergence and maximum intragroup divergence were calculated for each group highlighted in the phylogenetic analysis. All the divergences were calculated using a K2P distance model in MEGA version 4. As commonly accepted, if these groups correspond to different species, the sequences divergences should be much greater between groups than within them (Hajibabaei *et al.* 2006).

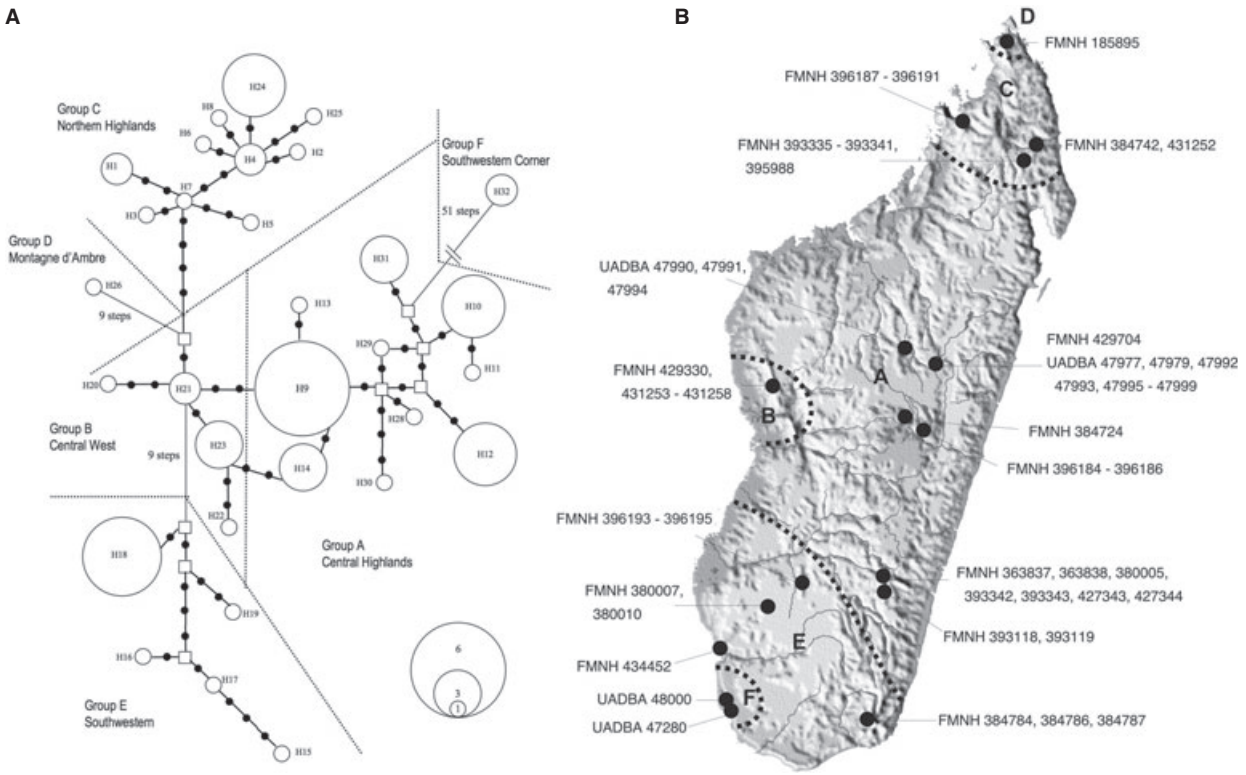

Fig. 2 Phylogeographic structure of the Malagasy *Monticola*. —a. Haplotype network – Circles at nodes are proportional in size to the number of individuals with that haplotype. Haplotypes within the interior of the network and not detected in the sample are represented by small white boxes. Mutational steps are represented by small black circles. Codes refer to haplotype numbers in Appendix S1.—b. Map of the sampling site localities – Capital letters and dotted lines show the different groups derived from Fig. 2 used for the AMOVA analysis.

Phylogeographic analyses

Given that networks allow a more detailed display of population information than strict bifurcating trees (Posada & Crandall 2001), a statistical parsimony network was reconstructed for the whole data set. We used the median-joining reconstruction method implemented in the software NETWORK 4.6 (available at http://www.fluxus-engineering.com; Bandelt *et al.* 1999). ϵ was initialized to zero, and characters were considered equally weighted.

We used hierarchical analysis of molecular variance (AMOVA, Excoffier *et al.* 1992) to test several hypotheses of geographical structure and to define phylogeographic lineage breaks. Analyses were performed using the software ARLEQUIN version 3.5.1.2 (Excoffier *et al.* 2005). The sampling sites were grouped by geographical regions (Central Highlands, Central West, Northern Highlands, Montagne d'Ambre, Southwestern and Southwestern Corner), following the structure of the haplotype network (see Results). We used the same substitution model as for the ML analyses, and levels of significance were determined through 1000 random permutation replicates.

Results

Sequence data

The final matrix contained 60 ingroup and two outgroup species for a total length of 1532 bp. Of these, 293 bp were variable and 135 bp parsimony informative. Alignment revealed no indels. The best-fitting model chosen by MrAIC for the whole data set was GTR+G.

Phylogenetic analyses

Parsimony (MP) and ML analyses produced similar topologies, and we arbitrarily chose to map node support values on the ML topology (Fig. 3). As has been shown in broad-scale phylogenetic studies of the genus *Monticola* or thrushes in general (Outlaw *et al.* 2007; Zuccon & Ericson 2010), the monophyly of the Malagasy *Monticola* is well supported (BP_{ML} = 100, BP_{MP} = 100). Individuals belonging to *M. imerinus* formed a strongly supported

Fig. 3 Phylogenetic tree showing the relationships amongst the Malagasy *Monticola*. Bootstrap supports (more than 65) are indicated at nodes (ML/MP).

clade (Group F) sister to all other sequenced individuals (BP_{ML} = 100, BP_{MP} = 100). The analyses highlighted five different groups within the *sharpei* complex. Each group appeared restricted to a geographical region (Fig. 2b): Group A: Central Highlands, Group B: Central West (Bemaraha), Group C: Northern Highlands, Group D: Montagne d'Ambre and Group E: Southwestern. Groups C and E appeared monophyletic with strong support (BP_{ML} = 90, BP_{MP} = 84 and (BP_{ML} = 100, BP_{MP} = 97, respectively). Within the Group E, specimens identified as *M. sharpei* and *M. bensoni* appeared intermixed. Although specimens collected in an open area of ericoid savannah in the summital zone of Andringitra were previously identified as *bensoni* (Langrand & Goodman 1996), one of these (FMNH 380005) is nested within the Central Highland birds (Group A), rather than with those

Table 1 Patterns of mitochondrial divergence for the 60 specimens of Malagasy *Monticola* based on K2P distances

	Group A	Group B	Group C	Group D	Group E	Group F
Maximum intragroup divergence	0.004	0.003	0.004	N/A	0.006	0.000
Minimum intergroup divergence	0.001	0.001	0.003	0.007	0.007	0.034
Closest relative (shortest distance)	Group B	Group A	Group B	Group B	Group B	Group A

from the Southwestern (Group E), which contains those classically identified as *bensoni*. To assess whether outgroup choice affected the overall level of phylogenetic resolution, analyses were conducted with *M. imerinus* as the outgroup, and this did not enhance the resolution of the phylogenetic tree.

The K2P pairwise genetic distances within all the groups were low (Table 1). For Groups A, B, C and D, the maximum intragroup divergence exceeded the minimum intergroup divergence. Group F (*M. imerinus*) appeared well separated from the other groups (minimum intergroup divergence = 0.034, maximum intragroup divergence = 0.00).

Haplotype networks

The phylogeographic analyses detected 32 mtDNA haplotypes. A visual inspection of the haplotype network revealed a general low level of divergence (Fig. 2a), confirming the results of the phylogenetic analyses. The network showed a deep split between the Group F (*M. imerinus*) and members of the *M. sharpei* complex. There is little divergence between Groups A (Central Highlands) and B (Central West). The Group E (Southwestern) is separated from the next closest cluster (Groups A + B) by nine mutational steps. Group B is separated from (i) Group C (Northern Highlands) by one missing haplotype and five mutational steps and (ii) Group D (*M. erythronotus*, Montagne d'Ambre) by the same above-mentioned missing haplotype and nine mutational steps.

We used analysis of molecular variance to test several hypotheses of geographical structure and to define phylogeographic lineage breaks. As individuals referable to *M. imerinus* were clearly divergent from the others, they were excluded from the analyses. The different comparisons were as follows: (i) (Northern Highlands + Central Highlands) versus Southwestern, (ii) Northern Highlands versus Central Highlands versus Southwestern, (iii) Northern Highlands versus Montagne d'Ambre versus Central Highlands versus Southwestern and (iv) Northern Highlands versus Montagne d'Ambre versus Central Highlands versus Central West versus Southwestern (Table 2). While standard phylogenetic and phylogeographic approaches indicate little significant historical structure, the AMOVA showed significant differentiation between the specimens from Montagne d'Ambre, Northern Highlands, Central Highlands and Southwestern groups. In all cases, variation within groups (ΦCT), amongst populations within groups (ΦSC) and within populations (ΦST) was significant.

Morphological variation

Specimens assigned to the different groups, as defined by the molecular analysis presented above, showed sexual dimorphism in certain regions (Northern Highlands, Montagne d'Ambre and *M. imerinus*), but not in others (Central Highlands; Appendix S2). Hence, in subsequent morphological comparisons, the sexes are separated. Analyses were conducted to compare possible differences in external measurements between birds. Populations classically placed in *M. sharpei interioris* and nominate *M. sharpei* could not be statistically separated from one another and are combined in Appendix S2. This conclusion is in parallel to the molecular results, which shows that an individual based on its collection site falls within the range of *interioris* (FMNH 384724), but is nested within *sharpei* (Fig. 3).

Table 2 Results from the hierarchical analysis of molecular variance (AMOVA) of different phylogroups of Malagasy *Monticola*

	(North + Central Highlands) vs Southwestern			**North vs Central Highlands versus Southwestern**			**North Highlands versus Ambre versus Central Highlands versus Southwestern**			**North Highlands versus Ambre versus Central Highlands versus Central West versus Southwestern**		
Source of variation	% variation	Fixation index	*P*-value	% variation	Fixation index	*P*-value	% variation	Fixation index	*P*-value	% variation	Fixation index	*P*-value
Between regions	58.56	ΦCT = 0.59	<0.001	67.56	ΦCT = 0.68	<0.001	71.75	ΦCT = 0.72	<0.001	72.22	ΦCT = 0.72	<0.001
Between sampling sites	29.63	ΦSC = 0.72	<0.001	17.14	ΦSC = 0.53	<0.001	13.11	ΦSC = 0.46	<0.001	10.91	ΦSC = 0.39	<0.001
Within sampling sites	11.81	ΦST = 0.88	<0.001	15.29	ΦST = 0.68	<0.001	15.14	ΦST = 0.85	<0.001	16.86	ΦST = 0.83	<0.001

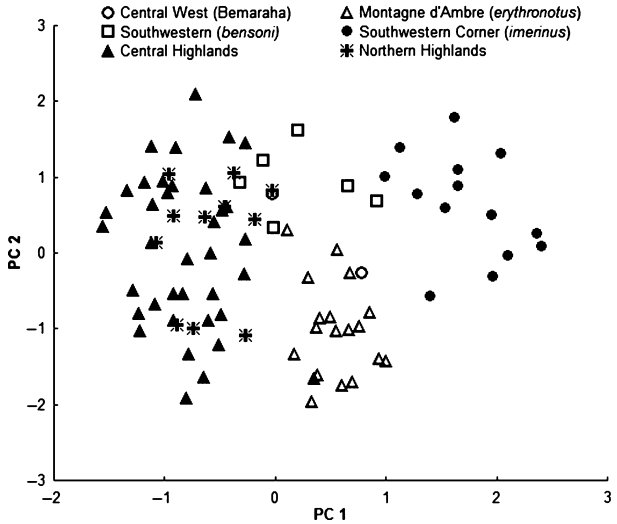

Fig. 4 Projection of first two unrotated principal components of log-transformed bill and tarsus measurements of specimens belonging to the *Monticola sharpei* complex. See Table 3 for the variables used in the analysis and the associated loadings.

Morphologically, birds referable to *M. imerinus* (Group F) can be easily separated from the other groups by their distinctly longer bill (Appendix S2). The birds from the Central West (Group B) are notably larger, particularly compared to those from the Central Highlands (Group A) and Northern Highlands (Group C). Further, even though the sample size is not large, birds from the South-west (Group E) are also larger on average than those from the Central Highlands (Group A) and Northern Highlands (Group C) and approach those from the Central West (Group B).

To examine in closer detail size variation in the different groups, a principal component analysis (PCA) was conducted using the tarsus and the three different bill measurements for adult male specimens. The wing and tail measurements were excluded from this analysis as they showed considerable levels of variance (Appendix S2). The comparisons of factors 1 and 2 for the bill and tarsus measurements showed some clear separation between specimens assigned to different phylogroups (Fig. 4). The first two unrotated principal components (PCs) accounted for 94.4% of the total variance in bill and tarsus morphology (Table 3) and separated the specimens into several different groups (Fig. 4). All of the variables associated with bill morphology showed heavy loadings on PC1, but only tarsus loaded notably on PC2. The following conclusions can be drawn from this analysis

1 Birds placed in Group F (*M. imerinus*) showed complete separation from the other groups;
2 Those from Group D (*M. erythronotus*) were largely separated from the other groups, with the exception of one individual from Group B (Central West, Bemaraha);
3 There was broad overlap between birds from Group A (Central Highlands) and Group C (Northern Highlands);
4 Group E (Southwestern, *bensoni*) falls in a intermediary position between Group F (*M. imerinus*) and Groups A and C (Central and Northern Highlands); and
5 Group B (Central West, Bemaraha) broadly overlaps with Group E (Southwestern).

Table 3 Factor loadings from principal component analysis of log-transformed bill and tarsus measurements of specimens belonging to the *Monticola sharpei* complex. A graphical representation of the first two principal components (PC) is presented in Fig. 4

Variable	PC 1	PC 2
Exposed culmen	0.934	0.198
Bill from skull	0.967	0.101
Bill from nostril	0.936	0.217
Tarsus	0.618	−0.786
Explained variance	3.066	0.714
Proportion of total variation explained	76.7%	94.4%

Plumage colour variation

In Table 4, we present a summary of differences in adult male specimens between the different groups derived from the molecular markers (Fig. 3). The reference specimens used in these comparisons are also illustrated in Fig. 5. In general, males from Group A (Central Highlands), Group B (Central West) and Group C (Northern Highlands) are very similar in coloration, with the exception that Group C tends to be more saturated in coloration. Group D (Montagne d'Ambre, *erythronotus*) is distinctly more rufous and notably different in coloration from the first three groups. Individuals from Group E (Southwestern, *bensoni*) are paler than those from the first three groups.

Discussion

There have been diverging opinions amongst bird taxonomists and biologists as to the number of species or forms of *Monticola* occurring on Madagascar. In part, the dividing point between these different views is based on morphological, largely plumage coloration (Langrand 1990; Morris & Hawkins 1998; Sinclair & Langrand 1998), as compared to genetic markers (Goodman & Weigt 2002; Outlaw *et al.* 2007; Zuccon & Ericson 2010). Inherent in these different perspectives is phenotypic versus genetic differences, and a number of recent studies have shown that aspects of feather coloration in birds is not necessarily linked to neutral markers (e.g. Kruckenhauser *et al.* 2004;

Table 4 Patterns of male plumage coloration in the different groups of Malagasy *Monticola sharpei* complex based on the genetic analyses (Fig. 2) and with the principal reference specimen listed. Also see Fig. 5 for colour illustrations of some of these groups

	Group A Central Highlands	Group B Central West (Bemaraha)	Group C Northern Highlands	Group D Montagne d'Ambre (*erythronotus*)	Group E Southwestern (*bensoni*)
Reference specimen	FMNH 427384	FMNH 431254	FMNH 431252	FMNH 384798	FMNH 396194
Crown	Blue-grey	Blue-grey	Blue-grey	Blue-grey	Light blue-grey
Central back	Blue-grey	Blue-grey	Dark blue-grey	Rufous	Light blue-grey
Lower back	Blue-grey tinged with dull brown	Blue-grey tinged with dull brown	Dark blue-grey tinged with dark grey	Rufous	Light blue-grey
Throat	Medium blue-grey	Medium blue-grey	Medium blue-grey	Medium blue-grey	Light blue-grey
Abdomen	Orange-rufous	Orange-rufous	Orange-rufous	Orange-rufous	Light orange-rufous
Wing coverts	Blue-grey	Blue-grey	Dark blue-grey	Rufous	Light blue-grey

Lehtonen *et al.* 2009). The principal questions with regard to Malagasy *Monticola* being:

1 If birds previously referred to the form *bensoni* should be considered a synonym of *sharpei*, a subspecies of *sharpei* or a distinct species.
2 The taxonomic status of birds from Montagne d'Ambre, falling under the name *erythronotus*, which show notable divergence in plumage coloration from other *Monticola* on the island.
3 The taxonomic status of birds from Bemaraha (Central West), which has not been previously named, as no specimens to our knowledge were available for morphological and genetic comparisons, and previous inferences were based on birds in the hand or photographs.

In the current study, we have been able to sequence 60 samples of Malagasy *Monticola*, including new material from Montagne d'Ambre, Bemaraha, and from elsewhere on the island, as well as examine and measure a good proportion of the world's museum skin specimens to assemble a morphological data set to address these questions.

Geographical distribution of birds referable to M. bensoni and level of divergence from M. sharpei

The holotype locality of *bensoni* is in the southwestern portion of the island (Collar & Tattersall 1987; Langrand & Goodman 1996), presumably in open canyon country and part of the southern extension of the Isalo Massif. Subsequently, this form was found in the Parc National de l'Isalo, in a similar habitat (Farkas 1971) and several sites further to the north towards the interior portion of the Mangoky River (Langrand & Goodman 1996). Even though birds referred to *bensoni* were found in transitional dry deciduous forest, the habitat preference of *bensoni* has been assumed to be open habitat. This combined with subtle differences between *sharpei* and *bensoni* with regard to size and plumage coloration (Langrand & Goodman 1996) yielded problems in the identification of certain specimens used in previous molecular studies (Goodman & Weigt 2002; Outlaw *et al.* 2007; Zuccon & Ericson 2010). Birds found in an open area of ericoid savannah above the forest line on the Andringitra Massif were identified as *bensoni* (Langrand & Goodman 1996). However, as shown here, using molecular markers, the single individual for which tissue is available from the upper reaches of Andringitra (FMNH 380005) is nested within the Central Highland birds (Group A), rather than with those from the Southwest (Group E), which contains those classically identified as *bensoni* (Fig. 3). Further, specimens (FMNH 384784, 384786 and 384787) collected in the humid forests of the Parc National d'Andohahela, which were previously inferred to be *sharpei* based on distribution and habitat (Hawkins & Goodman 1999), fall within those from the Southwest (Group E). On the basis of current information, Group E (*bensoni*) birds occur from near the mid-portion of the Mangoky River, south across the Isalo Massif to the Onilahy River (the type locality of Ankarefo) and west through the dry deciduous forests of the Zombitse-Vohibasia National Park (including the Vohimena Massif), the humid forest "oasis" of the Analavelona Massif (Goodman & Raherilalao unpublished data; Projet ZICOMA 1999) and terminating in the *Euphorbia* scrub near St. Augustin. The southeastern limit of this form is the humid forests of Parc National d'Andohahela (Parcel 1), which is in close proximity to the ecotone between dry and humid forests. Of all of the described forms of Malagasy *Monticola*, *bensoni* occurs in the greatest range of habitat types.

We have no evidence of sympatry between *M. imerinus* and *bensoni* (Group E). Older skin specimens referable to *M. imerinus* are known from the southern bank of the Onilahy River, near Soalara (e.g. AMNH 412320) and Anakao (AMNH 412308-412313). The specimen FMNH 434452, which was obtained on the north bank of the Onilahy River, 8 km direct distance from Soalara, is genetically placed within Group E (Fig. 3). There are published records of *M. imerinus* further to the north and as far as the Mikea Forest (Projet ZICOMA 1999; Gardner *et al.*

Fig. 5 Views of the different forms of adult male *Monticola* from Madagascar within the *sharpei* group based on reference specimens (from the upper centre portion of the figure and following a clockwise direction): *M. sharpei* (FMNH 427384), Group A, Province de Fianarantsoa, Forêt de Vinanitelo au pied d'Ambodivohitra, 15.5 km au SE de Vohitrafeno, 1100 m; *M. sharpei* '*interioris*' [= *M. sharpei*] (FMNH 384724), Group A, Province d'Antananarivo, Montagne d'Ankaratra, Forêt de Nosiarivo, 2 km NNW (by air) Station de Manjakatompo, 2000 m; *M. erythronotus* [= *M. sharpei*] (FMNH 394798), Group D, Province d'Antsiranana, Parc National de la Montagne d'Ambre, 5.5 km SW Joffreville, 1000 m; *M. bensoni* [=*M. sharpei*] (FMNH 396194), Group E, Province de Fianarantsoa, Parc National de l'Isalo, 3.8 km NW Ranohira, 800 m; 'Bemaraha-form' [= *M. sharpei*] (FMNH 431254), Group B, Province de Toliara, Parc National de Bemaraha, S. bank Manambolo River, 3.5 km E. Bekopaka, 100 m. Illustration by Velizar Simeonovski.

2009). However, given the recent discovery of birds referable to the southern group (Group E) near St. Augustin, and the history of misidentified individuals of *sharpei/bensoni* mentioned above, these northern records of *M. imerinus* may actually be of birds falling within Group E.

Phylogeographic and biogeographic patterns

While standard phylogenetic and phylogeographic approaches indicate little significant historical structure, AMOVA revealed clear phylogeographic structure between the different geographical populations of *Monticola*. The molecular results show no evidence of the sympatric occurrence between members of the different recovered clades. As previously reported, the species *M. imerinus*, falling within the basal Group F, is notably divergent (3.4%) from the balance of the sequenced individuals associated with the *sharpei* complex (Goodman & Weigt 2002; Zuccon & Ericson 2010). The *sharpei* complex is composed of five clades and with notably lower levels of sequence divergence (0.1–0.7%).

1 Group A is composed of individuals from different areas of the Central Highlands and is associated with the name *sharpei*.
2 Group B contains only birds obtained in the limestone wooded canyon areas of Bemaraha in lowland central western Madagascar. These individuals are nested between Group A and Group C (Fig. 3). No taxonomic name has been previously proposed for this clade.
3 Group C contains a series of specimens obtained from different massifs (Marojejy, Anjanaharibe-Sud and Manongarivo) in the Northern Highlands (Carleton & Goodman 1998). No taxonomic name has been previously proposed for this clade.
4 Group D is composed of a single bird from Montagne d'Ambre in the far north, associated with the name *erythronotus*, and based on limited current data shows shallow molecular divergence from adjacent Group C and Group E (Fig. 3). Members of Group D have some discrete and fixed morphological differences from the other members of the *sharpei* complex (Table 4).
5 Group E is composed of birds collected in southern and southwestern Madagascar and is associated with the name *bensoni*.

At the western edge of the Anosyenne Mountains is a dramatic ecotone between humid forest to the east (Andohahela) and dry forest to the west (the extensive spiny bush). Direct evidence from subfossils collected in a cave located close to the modern ecotone (Burney *et al.* 2008) indicates that during periods of the Quaternary, this zone experience waning and waxing of climatic conditions and associated faunistic shifts. A number of land vertebrates that are more typical of dry forests, such as birds (e.g. Fuchs *et al.* 2007) and lemurs (e.g. Hapke *et al.* 2005; Gligor *et al.* 2009), occur on the modern humid forest side of this divide. A similar pattern is observed here with respect to Group E (Southwestern, *bensoni*), showing that individuals collected in the humid forests of Andohahela are part of a widespread dry habitat group. Further, within Group E there appears to be

little in the way of geographical structure, with birds from Vohimena within the Zombitse-Vohibasia National Park present within two different subclades (Fig. 3).

Taxonomic conclusions

1 *Monticola imerinus* is a distinct species based on genetic and morphological characters. It occurs in the coastal scrub habitat in the southern portion of the island from at least the Onilahy River south and then east to near Tolagnaro.
2 The form *Monticola imerina interioris* Salomonsen 1934 is a synonym of *M. sharpei*.
3 *Monticola sharpei* is composed of different groups, several with proposed names, which show fixed morphological characters but relatively low levels of genetic sequence divergence. On the basis of the analyses presented herein, while some of the different groups within the *sharpei* complex show phylogeographic structure and in some cases discrete morphological characters, the level of sequence divergence is sufficiently low that these populations do not warrant distinct specific recognition. Hence, we consider the named forms *bensoni* and *erythronotus* to be synonyms of *sharpei*. Further, there is no evidence that the population of *Monticola* within the Bemaraha Massif is genetically or morphologically well differentiated from typical *sharpei* occurring in the eastern forests. These different populations are best considered part of *M. sharpei* and populations that are undergoing differentiation and may represent lineages of incipient speciation.

Acknowledgements

We are grateful to the Malagasy Government, specifically the Direction du Système des Aires Protégées, Direction Générale de l'Environnement et des Forêts and the Département de Biologie Animale, Université d'Antananarivo, for permits to conduct research and collect specimens. For access to specimens under their care, we acknowledge the curators of the American Museum of Natural History, New York; Muséum national d'Histoire naturelle, Paris; The Natural History Museum, London [formerly British Museum (Natural History)]; and Université d'Antananarivo, Département de Biologie Animale. We thank Tom Gnoske, Achille Raselimanana, Voahangy Soarimalala and David Willard for assistance in the field and the collection of specimens and Jérôme Fuchs, Arnaud Couloux and Corinne Curaud (Génoscope), and Annie Tillier and Céline Bonillo from the Service de Systématique Moléculaire UMS2700-CNRS of the Muséum national d'Histoire naturelle. Astrid Cruaud thanks Carole Kerdelhué (CBGP, Montferrier-sur-Lez) for her advice on phylogeographic analyses. Fig. 1 was created by Herivololona Mbola Rakotondratsimba. The fieldwork of Marie Jeanne Raherilalao and Steven M. Goodman in Madagascar has been supported by grants from the John D. and Catherine T. MacArthur Foundation, National Geographic Society and Volkswagen Foundation. Two anonymous reviewers provided very helpful comments on an earlier version of this paper.

References

Baldwin, S. P., Oberholser, H. C. & Worley, L. G. (1931). Measurements of birds. *Scientific Publications of the Cleveland Museum of Natural History*, *2*, 1–165.

Bandelt, H.-J., Forster, P. & Röhl, A. (1999). Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, *16*, 37–48.

Burney, D. A., Vasey, N., Godfrey, L. R., Ramilisonina, Jungers, W. L., Ramarolahy, M. & Raharivony, L. (2008). New findings at Andrahomana Cave, southeastern Madagascar. *Journal of Cave and Karst Studies*, *70*, 13–24.

Carleton, M. D. & Goodman, S. M. (1998). New taxa of nesomyine rodents (Muroidea: Muridae) from Madagascar's northern highlands, with taxonomic comments on previously described forms. In S. M. Goodman (Ed.) *A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With Reference to Elevational Variation*, *Fieldiana: Zoology*, new series, *90*, 163–200.

Cibois, A., Slikas, B., Schulenberg, T. S. & Pasquet, E. (2001). An endemic radiation of Malagasy songbirds is revealed by mitochondrial DNA sequence data. *Evolution*, *55*, 1198–1206.

Cibois, A., David, N., Gregory, S. M. S. & Pasquet, E. (2010). Bernieridae (Aves: Passeriformes): a family-group name for the Malagasy sylvioid radiation. *Zootaxa*, *2554*, 65–68.

Collar, N. J. & Tattersall, I. (1987). J. T. Last and the type-locality of Benson's Rockthrush *Monticola bensoni*. *Bulletin of the British Ornithologists' Club*, *107*, 55–59.

Drummond, A. J., Ashton, B., Cheung, M., Heled, J., Kearse, M., Moir, R., Stones-Havas, S., Thierer, T. & Wilson, A. (2007). Geneious v3.7. Available at http://www.geneious.com/. Accessed 20 September 2011.

Excoffier, L., Smouse, P. E. & Quattro, J. M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics*, *131*, 479–491.

Excoffier, L., Laval, G. & Schneider, S. (2005). Arlequin ver 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, *1*, 47–50.

Farkas, T. (1971). *Monticola bensoni*, a new species from south-western Madagascar. *Ostrich*, *9*(Suppl.), 83–90.

Farkas, T. (1973). The biology and a new subspecies of *Monticola sharpei*. *Bulletin British Ornithologists' Club*, *93*, 145–155.

Fuchs, J., Pons, J.-M., Pasquet, E., Raherilalao, M. J. & Goodman, S. M. (2007). Geographical structure of the genetic variation in the Malagasy Scops-owl inferred from mitochondrial sequence data. *Condor*, *109*, 408–418.

Gardner, C. J., Kidney, D. & Thomas, H. (2009). First comprehensive avifaunal survey of PK32-Ranobe, a new protected area in south-western Madagascar. *Phelsuma*, *17*, 20–39.

Gligor, M., Ganzhorn, J. U., Rakotondravony, D., Ramilijaona, O. R., Razafimahatratra, E., Zischler, H. & Hapke, A. (2009).

Hybridization between mouse lemurs in an ecological transition zone in southern Madagascar. *Molecular Ecology*, *18*, 520–533.

Goloboff, P. A., Farris, J. S. & Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics*, *24*, 1–13.

Goodman, S. M. & Hawkins, A. F. A. (2008). Les oiseaux. In S. M. Goodman (Ed.) *Paysages Naturels et Biodiversité de Madagascar*. (pp. 383–434). Paris: Muséum national d'Histoire naturelle.

Goodman, S. M. & Weigt, L. A. (2002). The generic and species relationships of the reputed endemic Malagasy genus *Pseudocossyphus* (Family Turdidae). *Ostrich*, *73*, 26–35.

Goodman, S. M., Tello, J. G. & Langrand, O. (2001). Patterns of morphological and molecular variation in *Acrocephalus newtoni* on Madagascar. *Ostrich*, *71*, 367–370.

Goodman, S. M., Raherilalao, M. J. & Block, N. L. (2011). Patterns of morphological and genetic variation in the *Mentocrex kioloides* complex (Aves: Gruiformes: Rallidae) from Madagascar, with the description of a new species. *Zootaxa*, *2776*, 49–60.

Goodwin, D. (1956). Note on the genus *Pseudocossyphus* Sharpe. *Bulletin of the British Ornithologists' Club*, *76*, 143–144.

Grandidier, A. (1879). *Histoire Physique, Naturelle et Politique de Madagascar: Histoire Naturelle des Oiseaux.Volume I—texte*. Paris: Imprimerie Nationale.

Groombridge, J. J., Jones, C. G., Bayes, M. K., van Zyl, A. J., Carrillo, J., Nichols, R. A. & Bruford, M. W. (2002). A molecular phylogeny of African kestrels with reference to divergence across the Indian Ocean. *Molecular Phylogenetics and Evolution*, *25*, 267–277.

Hajibabaei, M., Janzen, D. H., Burns, J. M., Hallwachs, W. & Hebert, P. D. N. (2006). NA barcodes distinguish species of tropical Lepidoptera. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 968–971.

Hapke, A., Fietz, J., Nash, S. D., Rakotondravony, D., Rakotosamimanana, B., Ramanamanjato, J.-B., Randria, H. F. N. & Zischler, H. (2005). Biogeography of dwarf lemurs: genetic evidence for unexpected patterns in southeastern Madagascar. *International Journal of Primatology*, *26*, 873–901.

Hawkins, A. F. A. & Goodman, S. M. (1999). Bird community variation with elevation and habitat in parcels 1 and 2 of the Réserve Naturelle Intégrale d'Andohahela, Madagascar. In S. M. Goodman (Ed.) *A Floral and Faunal Inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: with Reference to Elevational Variation*. *Fieldiana: Zoology*, new series, *94*, 175–186.

Hawkins, A. F. A., Thiollay, J.-M. & Goodman, S. M. (1998). The birds of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar. In S. M. Goodman (Ed.) *A Floral and Faunal Inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: with Reference to Elevational Variation*. *Fieldiana: Zoology*, new series, *90*, 93–127.

Helbig, A. J. & Seibold, I. (1999). Molecular phylogeny of Palearctic-African *Acrocephalus* and *Hippolais* warblers (Aves: Sylviidae). *Molecular Phylogenetics and Evolution*, *11*, 246–260.

Houde, P., Cooper, A., Leslie, E., Strand, E. & Montaño, G. A. (1997). Phylogeny and evolution of 12S rDNA in Gruiformes (Aves). In D. P. Mindell (Ed.) *Avian Molecular Evolution and Systematics* (pp. 121–158). San Diego: Academic.

IUCN. (2010) IUCN Red List of Threatened Species. Version 2010.4. Available via http://www.iucnredlist.org. Downloaded on 17 February 2011.

Johnson, K. P., Goodman, S. M. & Lanyon, S. M. (2000). A phylogenetic study of the Malagasy couas with insights into cuckoo relationships. *Molecular Phylogenetic & Evolution*, *14*, 436–444.

Jones, C. G. & Swinnerton, K. J. (2000). A possible new taxon of rock thrush *Monticola* sp. from the limestone karst region of western Madagascar. *Bulletin of the African Bird Club*, 7, 52–53.

Kirchman, J. J., Hackett, S. J., Goodman, S. M. & Bates, J. M. (2001). Phylogeny and systematics of the ground rollers (Brachypteraciidae) of Madagascar. *Auk*, *118*, 849–863.

Kremen, C., Cameron, A., Moilanen, A., Phillips, S. J., Thomas, C. D., Beentje, H., Dransfield, J., Fisher, B. L., Glaw, F., Good, T. C., Harper, G. J., Hijmans, R. J., Lees, D. C., Louis., E., Jr, Nussbaum, R. A., Raxworthy, C. J., Razafimpahanana, A., Schatz, G. E., Vences, M., Vieites, D. R. & Zjhra, M. L. (2008). Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science*, *320*, 222–226.

Kruckenhauser, L., Haring, E., Pinsker, W., Riesing, M. J., Winkler, H., Wink, M. & Gamauf, A. (2004). Genetic vs. morphological differentiation of Old World buzzards (genus *Buteo*, Accipitridae). *Zoologica Scripta*, *33*, 197–211.

Langrand, O. (1990). *Guide to the Birds of Madagascar*. New Haven: Yale University Press.

Langrand, O. & Goodman, S. M. (1996). Current distribution and status of Benson's Rockthrush, *Pseudocossyphus bensoni*, a Madagascar endemic. *Ostrich*, *67*, 49–54.

Lavauden, L. (1929). Description de quelques oiseaux nouveaux de Madagascar. *Alauda*, *4*, 231–234.

Lehtonen, P. K., Laaksonen, T., Artemyev, A. V., Belskii, E., Both, C., Bureš, S., Bushuev, A. V., Krams, I., Moreno, J., Mägi, M., Nord, A., Potti, J., Ravussin, P.-A., Sirkiä, P. M., Sætre, G.-P. & Primmer, C. R. (2009). Geographic patterns of genetic differentiation and plumage colour variation are different in the pied flycatcher (*Ficedula hypoleuca*). *Molecular Ecology*, *18*, 4463–4476.

Milon, P., Petter, J.-J. & Randrianasolo, G. (1973). *Faune de Madagascar. XXXV. Oiseaux*. Tananarive and Paris: ORSTOM & CNRS.

Morris, P. & Hawkins, F. (1998). *Birds of Madagascar: A Photographic Guide*. New Haven: Yale University Press.

Nylander, J. A. A. (2004). *MrAIC.pl*. Sweden: Evolutionary Biology Centre, Uppsala University. Available at http://www.abc.se/~nylander/. Accessed 20 September 2011.

Outlaw, R. K., Voelker, G. & Outlaw, D. C. (2007). Molecular systematics and historical biogeography of the rock-thrushes (Muscicapidae: *Monticola*). *The Auk*, *124*, 561–577.

Posada, D. & Crandall, K. A. (2001). Infraspecific gene genealogies: trees grafting into networks. *Trends in Ecology and Evolution*, *16*, 37–45.

Projet ZICOMA. (1999). *Les Zones d'Importance Pour la Conservation des Oiseaux à Madagascar*. Antananarivo: Projet ZICOMA.

Renoult, J. P. (2009). The Sooty Gull, *Larus hemprichii* (Aves: Laridae), on Nosy Ve: first records for Madagascar. *Malagasy Nature*, *2*, 174–176.

Ripley, S. D. (1964). Subfamily Turdinae, thrushes. In E. Mayr & R. A. Paynter Jr. (Eds) *Check-List of Birds of the World, vol. 10* (pp. 13–227). Cambridge, Massachusetts: Museum of Comparative Zoology.

Salomonsen, F. (1934). Four new birds and a new genus from Madagascar. *Ibis*, *1934*, 382–390.

Sheldon, F. H., Whittingham, L. A., Moyle, R. G., Slikas, B. & Winkler, D. W. (2005). Phylogeny of swallows (Aves: Hirundinidae) estimated from nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, *35*, 254–270.

Sinclair, I. & Langrand, O. (1998). *Birds of the Indian Ocean islands*. Cape Town: Struik Publishers.

Sorensen, M. D. & Payne, R. B. (2005). A molecular genetic analysis of cuckoo phylogeny. In R. B. Payne (Ed.) *The Cuckoos* (pp. 68–94). Oxford: Oxford University Press.

Sorenson, M. D., Ast, J. C., Dimcheff, D. E., Yuri, T. & Mindell, D. P. (1999). Primers for a PCR-based approach to mitochondrial genome sequences in birds and other vertebrates. *Molecular Phylogenetics and Evolution*, *12*, 105–114.

Stamatakis, A. (2006a). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, *22*, 2688–2690.

Stamatakis, A. (2006b). *Phylogenetic Models of Rate Heterogeneity: A High Performance Computing Perspective*. Rhodes Island, Greece: International Parallel and Distributed Processing Symposium (IPDPS 2006).

Tamura, K., Dudley, J., Nei, M. & Kumar, S. (2007). MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution*, *24*, 1596–1599.

Thompson, J. D., Higgins, D. G. & Gibson, J. T. (1994). CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. *Nucleic Acids Research*, *22*, 4673–4680.

Voelker, G. (2002). Systematics and historical biogeography of wagtails: dispersal versus vicariance revisited. *The Condor*, *104*, 725–739.

Winnepenninckx, B., Backeljau, T. & De Wachter, R. (1993). Extraction of high molecular weight DNA from mollusks. *Trends in Genetics*, *9*, 407.

de Wit, M. J. (2003). Madagascar: heads it's a continent, tails its an island. *Annual Review of Earth Planetary Science*, *31*, 213–248.

Yamagishi, S., Honda, M., Eguchi, K. & Thorstrom, R. (2001). Extreme endemic radiation of the Malagasy vangas (Aves: Passeriformes). *Journal of Molecular Evolution*, *53*, 39–46.

Zuccon, D. & Ericson, P. G. P. (2010). The *Monticola* rock-thrushes: phylogeny and biogeography revisited. *Molecular Phylogenetics and Evolution*, *55*, 901–910.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Specimens of *Monticola* spp. used in the molecular portion of the study.

Appendix S2. Measurements in mm of adult *Monticola* from Madagascar and segregated by phylogroups.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.