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ORIGINAL ARTICLE

Phylogenetic diversity and the conservation biogeography of African primates

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ABSTRACT

Aim Phylogenetics has an important role in conservation biogeography. However, there are few data on the phylogenetic diversity of African primates. The phylogenetic diversity (PD) of a species is a measure of its taxonomic distinctness and can be estimated by looking at the phylogenetic relationships among taxa. Species-specific metrics on PD can then be used to determine conservation priorities at various biogeographical scales. We used PD metrics to rank 55 African primate species according to their conservation priorities at the country level and within six African biogeographical regions. We also addressed the following question: are there differences in conservation rankings between the IUCN Red List and our PD metrics?

Location Africa.

Methods We created a consensus phylogeny for all African primate clades based on genetic studies. Analyses of species distributions were determined using presence/absence scores at two levels: country and biogeographical region. A node-based method that standardizes for widespread taxa and endemicity was used to calculate PD indices. Hierarchical cluster analysis was used to convert one of the standardized, phylogenetic indices into three clusters that could be ranked and compared with the main IUCN conservation rankings of endangered, vulnerable, and lower risk.

Results At the country and region levels, the top-priority species in terms of PD are *Pan paniscus*, *Macaca sylvanus*, *Arctocebus calabarensis*, *Gorilla beringei*, *Arctocebus aureus*, *Allenopithecus nigroviridis*, *Gorilla gorilla*, *Procolobus verus*, *Cercopithecus solatus*, *Cercocebus galeritus, Colobus angolensis*, *Theropithecus gelada*, *Galagoides zanzibaricus, Galagoides granti,* and *Procolobus (Piliocolobus) badius*. Geographic rankings were highest for the Democratic Republic of the Congo (country level) and Central Africa (region level). Although there were no overall differences between IUCN conservation ranks and the PD rankings, there were significant differences between the two systems for vulnerable and endangered primate taxa.

Main conclusions There are few ecological and behavioural data on populations of some of the African primates that represent the highest levels of phylogenetic diversity. Studies of primate taxa with high PD rankings should focus on identifying sites suitable for intensive studies of population densities, feeding ecology, and reproductive behaviour. We suggest that PD metrics can serve as an important, complementary data set in the IUCN ranking system for primates.

Keywords

Africa, catarrhines, conservation biogeography, conservation rankings, endemism, phylogenetics, primates.

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INTRODUCTION

Conservation plans have typically focused on the preservation of biodiversity as measured by species richness and patterns of endemism (Wilson *et al.*, 2006). However, biodiversity indices that treat all taxa equally may be inadequate because studies show that phylogenetic relationships among taxa are an important component for determining conservation priorities (e.g. Vane-Wright *et al.*, 1991; Williams *et al.*, 1991; Faith *et al.*, 2004). The phylogenetic diversity (PD) of a species is a measure of its taxonomic distinctness and can be estimated by looking at the phylogenetic relationships among taxa (Vane-Wright *et al.*, 1991). In this approach, phylogenetically unique taxa are prioritized because their extinction would result in a larger loss of evolutionary history than species with numerous sister taxa. For example, Lehman (2006) found that *Daubentonia madagascariensis,* a basal species not closely related to any other extant primate taxa, ranked higher in terms of its PD than *Lepilemur edwardsi*, a lemur species with several sister taxa in Madagascar. Because the probability of extinction for sister taxa within a clade is higher than for taxa between clades (Heard & Mooers, 2000), information on PD can also help to evaluate the effects of extinction on community structure and dynamics. Furthermore, PD metrics can then be used to set priorities at various biogeographical scales in order to maximize future biodiversity and evolutionary distinctiveness (Posadas *et al.*, 2001). Despite the importance of incorporating phylogeny into studies of primate conservation biogeography (Sechrest *et al.*, 2002; Whittaker *et al.*, 2005), there are few data on PD priorities for African primates.

There has been a growing emphasis placed on determining the conservation status of and priorities for African primates, mainly owing to their rapidly declining numbers (Oates, 1996; Chapman *et al.*, 2006; Jha & Bawa, 2006; Laurance *et al.*, 2006; Lovett & Marshall, 2006). Primate populations in Africa are declining as a result of deforestation, hunting, disease, and climate change (Chapman *et al.*, 2006). Of the approximately 348 extant primate species in the world, 22% ($N = 79$ species) are endemic to Africa (Lehman & Fleagle, 2006). There are 13 endangered primate species in Africa (IUCN, 2006). Moreover, some endemic primate taxa, such as *Pan* spp., are important for understanding human evolution and zoonotic virus transmission (Ruvolo, 1997; Gao *et al.*, 1999; Chen & Li, 2001; Leroy *et al.*, 2004). It has, however, been difficult to set conservation priorities for many primates because of the size of the African continent (30 million km^2), low levels of species endemicity, and the complexity of political and economic instability at the country level (Cowlishaw, 1999; Chapman *et al.*, 2006).

Researchers have used various broad-scale indicators, such as rates of population decline, in the IUCN Red List of Threatened Species to study the conservation biogeography of African mammals (e.g. Gaston, 1994; Purvis *et al.*, 2000; Rondinini & Boitani, 2006). Despite the importance of these studies (Rodrigues *et al.*, 2006), there is little consensus among biogeographers on the accuracy and precision of broad-scale indicators listed by the IUCN (e.g. Harcourt *et al.*, 2005; Oates, 2006; Wolman, 2006). Specifically, there are few accurate data on population sizes or associated demographic processes for the primate species most in need of conservation attention (Harcourt, 2004; Lehman *et al.*, 2006; Roberts & Kitchener, 2006). For example, Oates (2006) and Walsh *et al.* (2003) presented differing insights on the conservation biogeography of *Pan troglodytes* in Africa. Although authors in both studies agreed on the importance of protecting remaining populations of *Pan troglodytes*, they differed markedly in their assessments of population viability and IUCN threat-ratings for this taxon. These differences resulted largely from how the authors interpreted survey data, model assumptions, and the value of protected areas for preserving isolated populations. Furthermore, several models show that it is changes in population dynamics (e.g. per capita death rate, efficiency of converting food to offspring) rather than reduced population size that are the key factors leading to species extinction (Abrams, 2002). In this study, we outline a different method of assessing conservation priorities for primate species based on phylogenetic diversity (PD). We compare the results obtained using our PD method with the IUCN conservation priorities for African primates. If there are no differences in conservation rankings between the two methods, PD rankings have more heuristic than conservation value. Conversely, any differences between the two methods may provide new insights into empirical measures for determining primate conservation priorities in Africa.

The objective of our study was to use PD metrics to rank African primate species according to their conservation priority. We analysed these priorities by subdividing the continent into two distinct types of operational geographic units (Crovello, 1981). First, we examined primate PD by country, and second we examined primate PD according to six African biogeographical regions. Finally, we addressed the following question: are there differences in conservation rankings between the IUCN listings and our PD metrics?

METHODS

We used a list of 74 of the 79 African primate species compiled by Grubb *et al.* (2003). The remaining five species are *sp. nov*. and of ambiguous taxonomic status; they were therefore omitted from our analysis. Using these 74 species, we created a consensus phylogeny for all African primate clades based on genetic studies (van der Kuyl *et al.*, 1995; Disotell, 1996; Goodman *et al.*, 1998; Harris & Disotell, 1998; Grubb, 1999; Page *et al.*, 1999; DelPero *et al.*, 2000a,b; Harris, 2000; Page & Goodman, 2001; Tosi *et al.*, 2002, 2003, 2004; Grubb *et al.*, 2003; Newman *et al.*, 2004; Roos *et al.*, 2004; Wildman & Goodman, 2004; Masters *et al.*, 2005; Xing *et al.*, 2005) (Fig. 1). The consensus phylogeny was constructed using a majority-rule approach to cladogram construction, choosing the phylogenetic relationships that were depicted in at least 50% of the genetic studies we investigated. We chose to omit from our analysis species for which we could not obtain

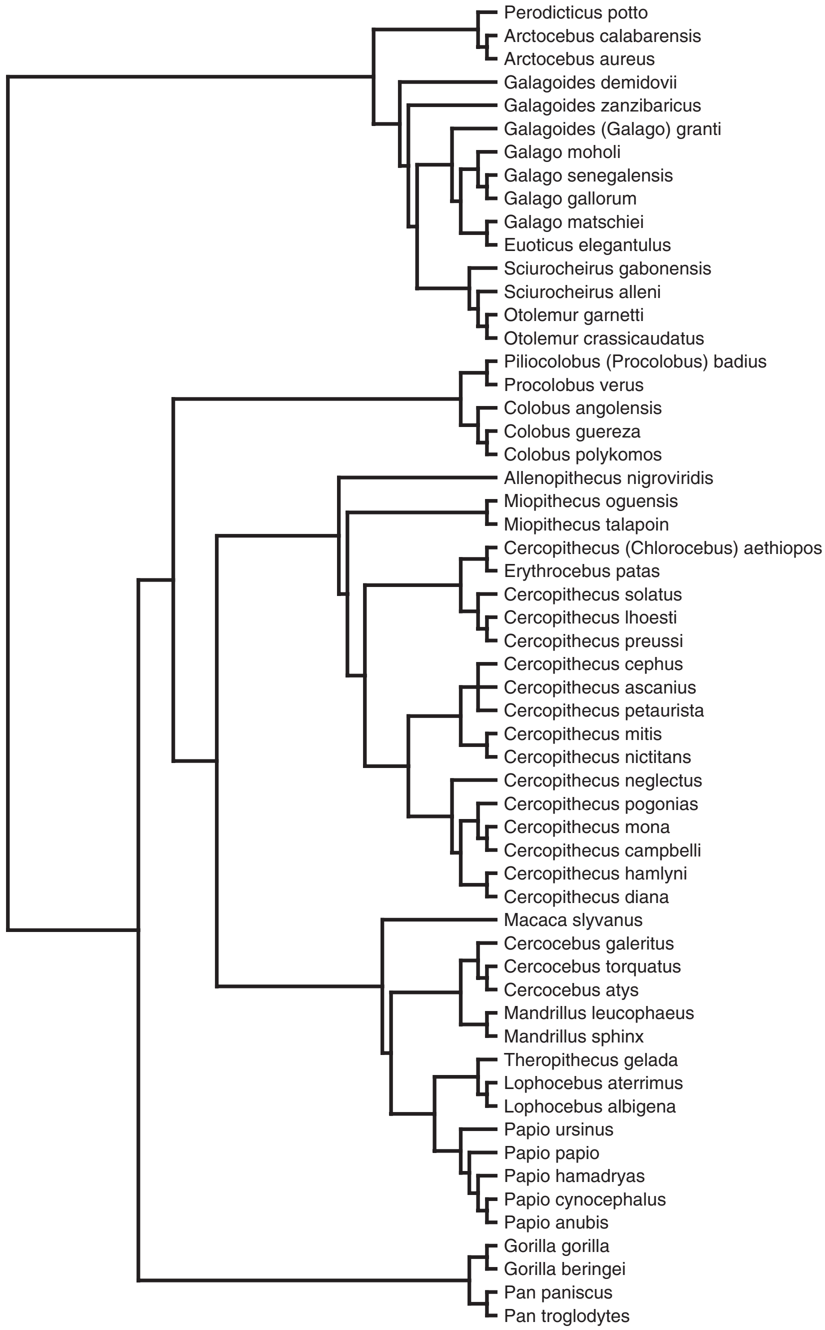


Figure 1 Consensus phylogeny of the African primates used in this study, based on genetic studies. The phylogeny was constructed using a majority-rule approach to cladogram construction, choosing the phylogenetic relationships that were depicted in at least 50% of the genetic studies we investigated

molecular phylogenetic data (primarily species attributed to the Galaginae and Colobinae) in preference to estimating species relationships from phylogenetic data derived from morphology-based studies. Resolved molecular cladograms were available for 54 of our 74 recognized species (Table 1). One trichotomy among three species of the Cercopithecinae could not be resolved, and therefore analyses were conducted by manually resolving this polytomy in all possible phylogenetic solutions. In total, analyses could be run on 57 African primate species; however, based on the information available for species distribution, only 55 of these 57 primate species were analysed in this study. We chose to limit our analysis to the species level for the following reasons: (1) consistency within our analysis, because not all species have subspecies distinctions (e.g. *Macaca sylvanus*) or have been studied thoroughly enough to recognize such intraspecific distinctions (e.g. *Gorilla beringei*), (2) consistency with similar studies that are usually completed at the specific level (Lehman, 2006), and (3) the taxonomic uncertainty of subspecies distinctions, and debates surrounding the evolutionary significance of subspecies in extant primates (Kimbel & Rak, 1993).

Analyses of species distributions were determined using presence/absence scores and were conducted at two levels: country and biogeographical region. Although biogeographical studies typically focus on biogeographical regions, we included countries as an operational unit because conservation

Table 1 Phylogenetic diversity metrics for 57 primate species by country and biogeographical region in Africa.

		Country		Region	
Taxa	W_s	I_{es}	W_{es}	I_{es}	W_{es}
Allenopithecus nigroviridis	0.10	0.17	0.25	0.25	0.05
Arctocebus aureus	0.30	0.05	0.03	0.13	0.15
Arctocebus calabarensis	0.30	0.13	0.06	0.13	0.15
Cercocebus atys	0.07	0.00	0.15	0.02	0.07
Cercocebus galeritus	0.08	0.02	0.01	0.04	0.08
Cercocebus torquatus	0.07	0.00	0.04	0.01	0.03
Cercopithecus aethiops	0.06	0.00	0.01	0.00	0.01
Cercopithecus ascanius	0.05	0.00	0.00	0.00	0.02
Cercopithecus campbelli	0.04	0.00	0.00	0.01	0.04
Cercopithecus cephus	0.05	0.00	0.01	0.01	0.02
Cercopithecus diana	0.05	0.00	0.01	0.01	0.05
Cercopithecus hamlyni	0.05	0.00	0.01	0.01	0.05
Cercopithecus lhoesti	0.05	0.00	0.02	0.01	0.05
Cercopithecus mitis	0.05	0.00	0.01	0.00	0.02
Cercopithecus mona	0.04	0.00	0.00	0.01	0.02
Cercopithecus neglectus	0.06	0.01	0.01	0.02	0.02
Cercopithecus nictitans	0.05	0.00	0.01	0.00	0.02
Cercopithecus petaurista	0.05	0.00	0.01	0.01	0.03
Cercopithecus pogonias	0.05	0.00	0.01	0.01	0.02
Cercopithecus preussi	0.05	0.00	0.01	0.01	0.05
Cercopithecus solatus	0.06	0.02	0.02	0.02	0.06
Colobus angolensis	0.21	0.04	0.06	0.17	0.11
Colobus guereza	0.18	0.01	0.02	0.04	0.04
Colobus polykomos	0.18	0.02	0.01	0.08	0.09
Erythrocebus patas	0.06	0.00	0.02	0.00	0.01
Euoticus elegantulus	0.07	0.00	0.00	0.01	0.03
Galago gallarum	0.06	0.01	0.01	0.02	0.06
Galago matschiei	0.07	0.01	0.02	0.02	0.07
Galago moholi	0.07	0.00	0.02	0.01	0.02
Galago senegalensis	0.06	0.00	0.01	0.00	0.01
Galagoides demidovii	0.19	0.02	0.00	0.10	0.04
Galagoides granti	0.09	0.02	0.01	0.09	0.09
Galagoides zanzibaricus	0.14	0.04	0.02	0.25	0.14
Gorilla beringei	0.25	0.08	0.02	0.25	0.25
Gorilla gorilla	0.25	0.04	0.08	0.13	0.13
Lophocebus albigenia	0.07	0.00	0.04	0.01	0.02
Lophocebus aterrimus	0.07	0.01	0.01	0.02	0.07
Macaca sylvannus	0.12	0.25	0.03	0.50	0.12
Mandrillus leucophaeus	0.08	0.01	0.06	0.02	0.08
Mandrillus sphinx	0.08	0.00	0.03	0.02	0.08
Miopithecus talapoin	0.09	0.04	0.02	0.13	0.04
Otolemur crassicaudatus	0.08	0.00	0.01	0.01	0.03
Otolemur garnetti	0.08	0.01	0.01	0.02	0.08
Pan paniscus	0.25	0.25	0.03	0.25	0.25
Pan troglodytes	0.25	0.01	0.01	0.05	0.05
Papio anubis	0.05	0.00	0.00	0.00	0.01
Papio cynocephalus	0.05	0.00	0.01	0.01	0.02
Papio hamadryas	0.06	0.01	0.01	0.02	0.03
Papio papio	0.07	0.01	0.01	0.04	0.03
Papio ursinus	0.08	0.02	0.01	0.05	0.03
Perodicticus potto	0.40	0.02	0.02	0.10	0.08
Procolobus (P.) badius	0.21	0.02	0.02	0.08	0.11
Procolobus verus	0.21	0.03	0.04	0.08	0.11
Sciurocheirus alleni	0.09	0.00	0.01	0.02	0.05
Theropithecus gelada	0.08	0.02	0.04	0.04	0.08

measures and actions are typically conducted at the national level in Africa (Olson & Dinerstein, 1998). All data on the presence and absence of species by country and biogeographical region were obtained from the World Conservation Union online data base (IUCN, 2006). We took a conservative approach in that a species was not included in a particular country or region if its presence was questionable (e.g. thought to be locally extinct, or had been introduced). Furthermore, those species that were not listed by the IUCN ($N = 2$) were omitted from this study.

Continental and island African countries with primates were included in the analysis ($N = 47$) with the following two exceptions: (1) Madagascar was excluded because it required its own, endemic analysis given its unique primate and ecological characteristics (Lehman, 2006), and (2) Mauritius was excluded because it is an island country east of Madagascar and geographically far removed from continental Africa. The boundaries for the regional communities are based on the geographic areas defined by Cowlishaw (1999). Cowlishaw (1999) divided African countries along political boundaries into four biogeographical categories (regions 1–4), based on primary vegetation types identified by Oates (1996). Two additional regions were added to delineate Southern Africa and Northern Africa (Fig. 2).

We used a node-based method to calculate phylogenetic diversity indices I and W (Vane-Wright *et al.*, 1991). Index I assigns a value of 1 to each terminal taxon that belongs to a pair of terminal sister taxa. The taxon that constitutes the sister group of this pair receives a value of 2 (equal to the sum of its sister group). Each successive taxon receives a value equal to

Figure 2 Locations of six biogeographical regions in Africa. Boundaries are based on the geographic areas divided along political boundaries defined by Cowlishaw (1999).

that of the total sister group. The phylogenetic diversity index W measures the proportion that each taxon contributes to the total diversity of the group. Specifically, index W assigns an information value (i) to each terminal taxon. This value is calculated as the number of groups (nodes) to which each taxon belongs. A basic phylogenetic weight (Q) was calculated using the following formula:

$$Q_j = \sum i/i_j,$$

where j is equal to each specific taxon in the cladogram. The Q-value for each taxon refers to the proportion of the total diversity of the group that is contributed by this taxon. The phylogenetic diversity measure (W) was calculated using the following formula:

$$W = Q_j/Q_{\min},$$

where $Q_{\min}$ refers to the lowest Q-value for the entire group. Following Posadas *et al.* (2001), the phylogenetic diversity indices I and W for primate species in each country and region were standardized for widespread taxa and endemicity to produce total endemicity standardized weights (TESW). This standardization is necessary to control for differences in species diversity between different clades, and was achieved by dividing the taxon value in each clade by the sum of all index values in the clade (I_s and W_s). Variations in levels of endemism between countries and regions were determined by dividing the index value by all countries or regions where a primate species was present (I_e and W_e). Both standardization and endemicity were then incorporated into I and W (I_{es} and W_{es}). These indices control for over-weighting of clades that have a large number of taxa and/or one country or region because of widespread taxa.

For example, phylogenetic and biogeographical data for five hypothetical species in four regions are presented in Fig. 3. The first step in the process is to determine the unweighted metrics for phylogenetic diversity (I and W). The measures are then standardized for cladistic relationships and biogeographical data (I_{es} and W_{es}). Species 1 has the highest priority in terms of TESW measures of phylogenetic diversity. TESW metrics for each taxon in a particular region are summed to produce regional measures of phylogenetic diversity. For example, region C contains species 1 ($W_{es} = 0.21$) and species 5 ($W_{es} = 0.04$). Thus, the W_{es} score for region C is 0.21 + 0.04 = 0.25. Each region is then ranked from lowest to highest, controlling for any ties. Results indicate that region D should be prioritized for conservation attention.

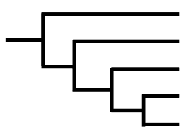
Biogeographical definitions and associated computations follow those used by Posadas *et al.* (2001). Richness was defined as the total number of primate species in each country and region. An endemicity index was calculated for each country and region as the quotient between the number of endemic species and the total species in that region.

Hierarchical cluster analysis was used to convert the standardized, phylogenetic index W_s for each species into three clusters that could be ranked and compared with the main IUCN conservation rankings of endangered, vulnerable, and lower risk. Species-scores for the PD indices were differentiated using squared Euclidean distance methods, and a dendrogram was selected to produce three clusters based on within-group linkages. Phylogenetic rankings (1–3) were then assigned to the three main clusters. Wilcoxon signed ranks tests were used to determine if there were differences between the IUCN conservation rankings and our PD rankings. Only congruent species and associated rankings/scores were used in the tests.

RESULTS

Table 1 shows the main PD metrics for 57 primate species in Africa (W_s, I_{es}, and W_{es}). The species with the highest W_s scores are *Perodicticus potto* (0.40), *Arctocebus aureus* (0.30), *Arctocebus calabarensis* (0.30), *Gorilla gorilla* (0.25), *Gorilla beringei* (0.25), *Pan paniscus* (0.25), and *Pan troglodytes* (0.25). This score is purely phylogenetic in origin and is not influenced by selection of operational geographic units.

At the country level (Table 1), standardizing for endemicity (I_{es}) resulted in high priorities for *Macaca sylvanus* (0.25), *Pan paniscus* (0.25), *Allenopithecus nigroviridis* (0.17), *Arctocebus calabarensis* (0.13), and *Gorilla beringei* (0.08). The W_{es} metrics are highest for *Pan paniscus* (0.25), *Arctocebus calabarensis* (0.15), *Gorilla beringei* (0.08), *Arctocebus aureus* (0.06), *Macaca sylvanus* (0.06), and *Cercopithecus solatus* (0.06). Based on the data analysed at the country level, the combined I_{es} and W_{es} rankings indicate that the species with the highest phylogenetic importance for conservation at the country level are (highest priority to lowest priority): *Pan paniscus*, *Macaca sylvanus*, *Arctocebus calabarensis*, *Gorilla beringei*, *Arctocebus aureus*, *Allenopithecus nigroviridis*, *Gorilla gorilla*, *Procolobus verus*,



Species	Region A	B	C	D	Σ	TESW Metrics I	I_e	I_s	I_{es}	i	Q	W	W_e	W_s	W_{es}
1	-	-	x	x	2	8	4.00	0.50	0.25	1	14.00	4.00	2.00	0.43	0.21
2	x	x	-	-	2	4	2.00	0.25	0.13	2	7.00	2.00	1.00	0.21	0.11
3	x	x	-	-	2	2	1.00	0.13	0.06	3	4.67	1.33	0.67	0.14	0.07
4	-	x	-	x	2	1	0.50	0.06	0.03	4	3.50	1.00	0.50	0.11	0.05
5	x	x	x	-	3	1	0.33	0.06	0.02	4	3.50	1.00	0.33	0.11	0.04
Σ	3	4	2	2		16				14		9.3			

Region	Regional Phylogenetic Diversity Metrics Σ I_{es}	Rank	Σ W_{es}	Rank
A	0.21	1	0.21	1
B	0.24	2	0.27	3.5
C	0.27	3	0.25	2
D	0.28	4	0.27	3.5

Combined Ranks	= I_{es} Rank	+ W_{es} Rank
2.0	1	1
5.5	2	3.5
5.0	3	2
7.5	4	3.5

Figure 3 Hypothetical example of the process for determining phylogenetic diversity metrics at the species and regional levels (based on Lehman, 2006).

Table 2 Total combined ranked scores for TESW primate measures of I_{es} and W_{es} in 46 African countries.

Country	I_{es}	Rank	W_{es}	Rank	Combined I_{es} and W_{es} ranks
Democratic Republic of the Congo	0.12	1.0	0.09	1.0	2.0
Cameroon	0.11	2.5	0.08	2.0	4.5
Congo	0.11	2.5	0.05	4.5	7.0
Equatorial Guinea	0.04	7.5	0.05	4.5	12.0
Gabon	0.04	7.5	0.05	4.5	12.0
Angola	0.04	7.5	0.04	8.5	16.0
Tanzania	0.04	7.5	0.04	8.5	16.0
Kenya	0.03	10.0	0.04	8.5	18.5
Nigeria	0.02	15.5	0.05	4.5	20.0
Uganda	0.02	15.5	0.04	8.5	24.0
Central African Republic	0.02	15.5	0.03	13.0	28.5
Rwanda	0.02	15.5	0.03	13.0	28.5
Sierra Lione	0.02	15.5	0.03	13.0	28.5
Algeria	0.06	4.5	0.01	30.5	35.0
Guinea	0.02	15.5	0.02	19.5	35.0
Malawi	0.02	15.5	0.02	19.5	35.0
Morocco	0.06	4.5	0.01	30.5	35.0
Mozambique	0.02	15.5	0.02	19.5	35.0
Somalia	0.02	15.5	0.02	19.5	35.0
Zimbabwe	0.02	15.5	0.02	19.5	35.0
Cote d'Ivoire	0.01	27.5	0.03	13.0	40.5
Ghana	0.01	27.5	0.03	13.0	40.5
Burundi	0.01	27.5	0.02	19.5	47.0
Ethiopia	0.01	27.5	0.02	19.5	47.0
Liberia	0.01	27.5	0.02	19.5	47.0
Benin	0.01	27.5	0.01	30.5	58.0
Burkina Faso	0.01	27.5	0.01	30.5	58.0
Eritrea	0.01	27.5	0.01	30.5	58.0
Guinea Bissau	0.01	27.5	0.01	30.5	58.0
Mali	0.01	27.5	0.01	30.5	58.0
Senegal	0.01	27.5	0.01	30.5	58.0
Sudan	0.01	27.5	0.01	30.5	58.0
Togo	0.01	27.5	0.01	30.5	58.0
Zambia	0.01	27.5	0.01	30.5	58.0
Gambia	0.00	40.5	0.01	30.5	71.0
South Africa	0.00	40.5	0.01	30.5	71.0
Swaziland	0.00	40.5	0.01	30.5	71.0
Botswana	0.00	40.5	0.00	42.0	82.5
Chad	0.00	40.5	0.00	42.0	82.5
Djibouti	0.00	40.5	0.00	42.0	82.5
Lesotho	0.00	40.5	0.00	42.0	82.5
Libya	0.00	40.5	0.00	42.0	82.5
Mauritania	0.00	40.5	0.00	42.0	82.5
Namibia	0.00	40.5	0.00	42.0	82.5
Niger	0.00	40.5	0.00	42.0	82.5
Sao Tome and Principe	0.00	40.5	0.00	42.0	82.5

Cercopithecus solatus, *Cercocebus galeritus*, *Colobus angolensis*, and *Theropithecus gelada*.

I_{es} metrics are highest for primate species in the Democratic Republic of the Congo (0.12), Cameroon (0.11), Congo (0.11), Algeria (0.06) and Morocco (0.06) (Table 2). The W_{es} values are highest in the Democratic Republic of the Congo (0.09) and Cameroon (0.08). Species richness scores are highest for the Democratic Republic of the Congo (27) and Cameroon (27). By country, scores for endemicity are low, with only two countries having a score above zero: the Democratic Republic of the Congo and Gabon each had one endemic taxon. Based on the combined I_{es} and W_{es} rankings, the countries that should be considered the highest priority for conservation are (in decreasing order): the Democratic Republic of the Congo, Cameroon, and Congo.

At the level of biogeographical region (Table 1), the species with the highest I_{es} scores are *Macaca sylvanus* (0.50), *Galagoides zanzibaricus* (0.25), *Allenopithecus nigroviridis* (0.25), *Gorilla beringei* (0.25), and *Pan paniscus* (0.25). The W_{es} metrics are highest for *Pan paniscus* (0.25), *Gorilla beringei* (0.25), *Arctocebus aureus* (0.15), *Arctocebus calabarensis* (0.15), *Galagoides zanzibaricus* (0.14), and *Gorilla gorilla* (0.13). The combined I_{es} and W_{es} rankings indicated that the species with the highest phylogenetic importance for conservation at the region level are (highest priority to lowest priority): *Gorilla beringei, Pan paniscus, Macaca sylvanus, Galagoides zanzibaricus, Arctocebus aureus, Arctocebus calabarensis, Gorilla gorilla, Colobus angolensis, Galagoides granti, Procolobus (Piliocolobus) badius*, and *Procolobus verus*.

Phylogenetic diversity is highest for the I_{es} rankings in Central Africa (0.28), West Central Africa (0.27), and East Africa (0.20) (Table 3). The highest W_{es} rankings are also for Central Africa (0.29), West Central Africa (0.28), and East Africa (0.21). Species richness scores are highest for Central Africa (33 taxa) and West Central Africa (31 taxa). The regions with the highest number of endemic species are Central Africa and East Africa, each with six endemic species. When we combine the I_{es} and W_{es} rankings with regional primate species richness, the highest-priority regional communities are Central Africa, West Central Africa, and East Africa.

The IUCN conservation rankings did not differ significantly from the PD measure W_s for congruent primate species ($z = -9.20$, $n = 54$, $P = 0.358$; Fig. 4). However, there were significant differences between studies in species rankings for taxa with an IUCN ranking above lower risk ($z = -3.07$, $n = 10$, $P = 0.001$). Of the 10 African primate taxa listed by the IUCN as vulnerable or endangered, all received a lower W_s ranking than IUCN ranking (*Cercopithecus diana, Cercopithecus preussi, Cercopithecus solatus, Gorilla beringei, Gorilla gorilla, Mandrillus leucophaeus, Mandrillus sphinx, Pan paniscus, Pan troglodytes*, and *Procolobus (Piliocolobus) badius*).

DISCUSSION

Highest-priority primates

Our objective was to use PD metrics to rank African primate species according to their conservation priority. For pure PD metrics (I_s and W_s), the highest rankings were for *Perodicticus potto*, *Galagoides demidovii*, *Allenopithecus nigroviridis*, *Macaca sylvanus*, *Colobus angolensis*, *Arctocebus aureus*, *Arctocebus*

Table 3 Phylogenetic values, species richness, and endemicity for primates in six biogeographical regions in Africa.

Region	I_{es}	Rank	W_{es}	Rank	Sum of ranks	Richness (% richness)	Endemicity (% endemicity)
Central Africa	0.28	1	0.29	1	2	33 (60.00)	6 (10.91)
West Central Africa	0.27	2	0.28	2	4	31 (56.36)	5 (9.09)
East Africa	0.20	3	0.21	3	6	24 (43.64)	6 (10.91)
West Africa	0.07	5	0.13	4	9	18 (32.73)	3 (5.45)
North Africa	0.16	4	0.07	5	9	11 (20.00)	1 (1.82)
South Africa	0.02	6	0.02	6	12	5 (9.09)	0 (0.00)

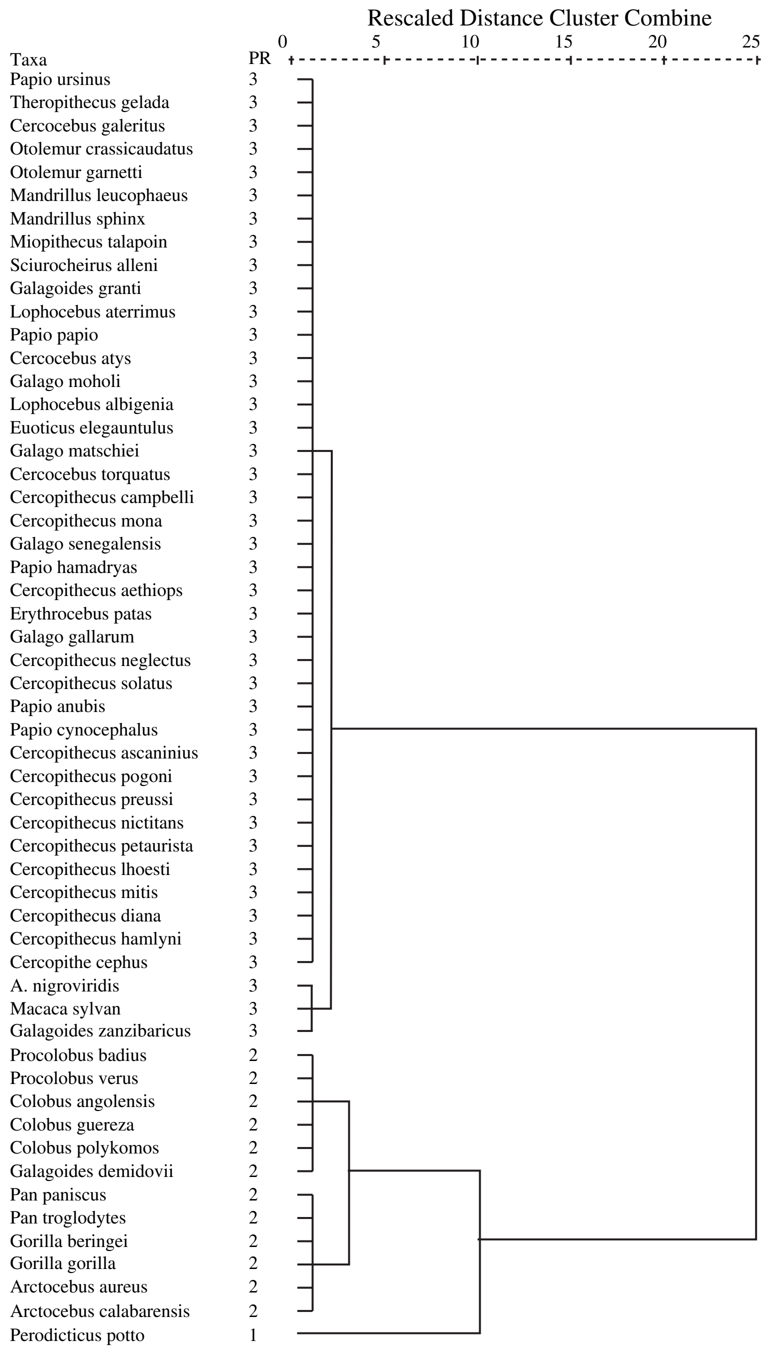


Figure 4 Hierarchical cluster dendogram reflecting analyses of the phylogenetic idex W_s for 57 primate species in six biogeographical regions in Africa. PR refers to a three-point phylogenetic ranking for taxa in each cluster.

calabarensis, *Gorilla gorilla*, *Gorilla beringei*, *Pan paniscus*, and *Pan troglodytes*. The primate taxa within the top five rankings for conservation priority remained fairly consistent irrespective of operational geographic unit (i.e., country or region). Two species of Homininae are among the highest priority for conservation owing to the limited number of sister taxa within this clade. Using combined I_{es} and W_{es} rankings, *Pan paniscus* ranked first at the country level, and was tied with *Gorilla beringei* for the highest ranking at the regional level. This species has an extremely limited biogeographical distribution, being found only in the Democratic Republic of the Congo (Butynski, 2003). *Gorilla beringei* ranked fourth at the country level and was tied for first at the region level. *Gorilla beringei* ranges into the Democratic Republic of the Congo, Rwanda, and Uganda (Goldsmith, 2003). Both hominine taxa are listed by the IUCN as endangered, and they are endemic to Central Africa (Region 3). Interestingly, *Pan troglodytes* has PD rankings that are relatively lower than those for *Pan paniscus* and *Gorilla beringei* at the country and region levels. Although *Pan troglodytes* has been decimated by infectious disease and hunting (Fa *et al.*, 2005; Leendertz *et al.*, 2006), it is one of the most geographically widespread of the forest-zoned anthropoid species in Africa and has an estimated population size of 300,000 individuals (Oates, 2006). Furthermore, Oates (2006) noted that *Pan troglodytes* ranges into 51 national parks in at least 19 countries. Despite similarities in IUCN conservation rankings for the extant African hominins, our PD approach would place greater emphasis on conserving *Pan paniscus* and *Gorilla beringei*.

Macaca sylvanus should be considered of high conservation priority because it is the only representative of the speciose *Macaca* clade in Africa and because of its limited distribution on this continent (Algeria and Morocco; Region 6). These phylogenetic and biogeographical characteristics indicate that this species should be considered a conservation priority, and this assessment is supported by our PD metrics. However, *Macaca* is the most widely distributed, extant primate genus, with approximately 21 other species of *Macaca* ranging throughout Southeast Asia (Brandon-Jones *et al.*, 2004). Based on these considerations, it is clear that this species is considered a conservation priority in our study because it is the only member of this genus found in Africa. If we were to examine *Macaca sylvanus* at a broader scale (e.g. Africa and Asia), it might not be considered to be a high priority.

Four nocturnal primate taxa received high TESW rankings at the country and region levels (*Arctocebus calabarensis*, *Arctocebus aureus, Galagoides zanzibaricus,* and *Galagoides granti*). These high rankings are a result of the phylogenetic uniqueness and limited distributions of these species. For example, *Arctocebus calabarensis* is endemic to Cameroon and Nigeria (Region 2), and *Arctocebus aureus* is found only in Angola, Cameroon, Congo, Equatorial Guinea, and Gabon (Regions 2 and 3). Although some phylogenetically important primate species have been well studied in the wild (e.g. *Pan troglodytes*, *Gorilla beringei)*, there are few conservation data for many nocturnal primate taxa (Nekaris & Bearder, 2007). It has generally been assumed that nocturnal primates are of lower conservation risk because of their small body size, faunivorous diet, and reduced vulnerability to hunting in Africa (Jernvall & Wright, 1998; Chapman *et al.*, 2006). However, recent studies on the effects of forest-landscape patterns on primate biogeography indicate that more conservation attention is warranted for nocturnal primates (Lehman *et al.*, 2006). Therefore, we suggest that greater effort be made to collect data that can be used to set conservation priorities for nocturnal African taxa (e.g. population dynamics, biogeography, and behavioural ecology).

Highest-priority countries

The country with the highest PD rankings is the Democratic Republic of the Congo. Of the 30 primate species in the Democratic Republic of the Congo, four are among the top ten priority species for PD: *Pan paniscus*, *Gorilla beringei*, *Allenopithecus nigroviridis* and *Colobus angolensis*. Cameroon is ranked second and contains 28 primate species, three of which are among the top ten species for PD: *Arctocebus aureus*, *Arctocebus calabarensis,* and *Allenopithecus nigroviridis*. The Congo was ranked third and is also home to the following high-ranking primate species: *Arctocebus aureus, Peridicticus potto*, and *Allenopithecus nigroviridus*. These PD rankings bring attention to some countries in Africa that are not commonly recognized as top conservation priorities. For example, Myers *et al.* (2000) listed 25 hotspots for biodiversity, which they defined as areas that contain a high number of endemic species and are experiencing high rates of habitat loss. Although Myers *et al.* (2000) included Tanzania and Kenya (PD rankings of 7th and 8th) in their list, they did not prioritize any of the highest-ranked countries according to PD analyses (i.e., Democratic Republic of the Congo, Cameroon, and Congo). These differences between hotspot and PD rankings largely reflect methodological variations in taxa and scale. Myers *et al.* (2000) focused on multiple plant and vertebrate species at the global level, whereas our PD focus is only on primates endemic to the African continent. Despite these methodological differences, we suggest that PD metrics provide important data for conservation biogeographers to consider when suggesting conservation priorities in Africa.

Highest-priority regions

Our TESW metrics indicate that the following three regions are of highest conservation priority for primates: Central Africa, West Central Africa, and East Africa. Concomitantly, these regions contain many of the top-ranked species in terms of PD values (e.g. *Perodicticus potto*, *Galagoides demidovii*, and *Allenopithecus nigroviridis*). It is interesting to note that our PD rankings for biogeographical regions are concordant with the hotspot classifications (Harcourt, 2000a; Myers *et al.*, 2000). The East African region (Region 4) in our study overlaps with Myers *et al.*'s (2000) 'Eastern Afromontane' hotspot, and the regional communities of Central and West

Central Africa (Regions 4 and 5) overlap with Myers *et al.*'s (2000) 'West African Forest' hotspot.

Congruent patterns of PD and endemicity for central African regions probably reflect complex biogeographical patterns of latitudinal gradients, rainfall, and cladogenesis (Grubb, 2001). For example, latitudinal gradients have been suggested to influence species richness and diversity in African primates (Cowlishaw & Hacker, 1997; Harcourt, 2000b; Böhm & Mayhew, 2005; Fernandez & Vrba, 2005). Latitude appears to be a particularly strong correlate of the geographical range of African primates south of the equator. However, rainfall may be a better predictor of the geographic range of African primates both north and south of the equator (Cowlishaw & Hacker, 1997). Emmons (1999) noted that regions such as Central Africa are close to the equator and are characterized by increased rainfall and habitat heterogeneity, which result in more niches and higher mammalian species richness. Conversely, the historical biogeography of species richness for papionin taxa (Böhm & Mayhew, 2005) and other mammal species (Grubb, 1999) in Africa may have resulted from rates of cladogenesis rather than latitude. Specifically, Grubb (1999) hypothesized that the expansion and contraction of African biomes led to changes in dispersal rates for many primate species. Although there is little consensus on the specific biogeographical patterns influencing primate evolution in Central Africa, this region is clearly important in terms of conservation attention.

PD and IUCN rankings

Our aim was to determine if differences exist in conservation rankings between the IUCN listings and W_s metrics. Although there were no overall differences between PD and IUCN rankings, we found that there were significant differences in conservation rankings between the two systems for vulnerable and endangered taxa. The greatest disparities exist for *Cercopithecus diana*, *Cercopithecus preussi*, and *Mandrillus leucophaeus*, which are listed as endangered by the IUCN but are of lowest PD priority in our study, and for one species with the highest PD ranking but low IUCN priority (*Perodicticus potto*). The low PD rankings for *Cercopithecus diana*, *Cercopithecus preussi*, and *Mandrillus leucophaeus* are indicative of the overall low PD rankings, high species diversity, and relatively low levels of endemism at the country and region levels for all *Cercopithecinae*. In contrast, the higher PD ranking for *Perodicticus potto* reflects its basal placement within the African Catarrhini clade.

There is considerable scientific debate regarding the use of PD metrics for setting conservation priorities (e.g. Owens & Bennett, 2000; Faith *et al.*, 2004; Posadas *et al.*, 2004). Specifically, Faith (1992, 1994a,b) has been critical of TESW metrics and is a strong proponent of the feature-based method for estimating phylogenetic diversity. The feature-based method focuses on the relative feature diversity of any nominated set of species rather than on nodes separating various taxa between clades. As a result, feature-based methods produce PD metrics by summing the lengths of all those phylogenetic branches spanned by a data set (Faith, 1994b). Branch lengths represent inferred evolutionary steps for the character(s) being considered. It is interesting to note that, in a series of published debates on node-based versus feature-based methods, both phylogenetic methods returned remarkably similar regional conservation rankings based only on phylogenetic diversity metrics (Faith *et al.*, 2004; Posadas *et al.*, 2004). However, differences in final regional rankings occurred as the result of how the two methods incorporated biogeographical data. In the node-based method, richness and endemism are properties of a specifically defined region. In contrast, in the feature-based method, richness and endemism are defined as properties of a set of species, and regions are only arbitrarily defined. Rigorously defined regions are critical in biogeography and conservation biology (Morrone, 1994; Morrone & Crisci, 1995; Crisci *et al.*, 2003). Moreover, as noted by Faith *et al.* (2004), there are a variety of methods for calculating branch lengths and there are few reliable data on branch lengths for many taxa, including primates. For example, Coddington & Scharff (1994) found that morphological and molecular data sets for the same taxa often result in different estimates for the same branch. These issues have led many researchers to assume that all branch lengths are equal (Owens & Bennett, 2000; Faith *et al.*, 2004), which seems contrary to the theoretical core of feature-based methods. Finally, one of the strengths of the TESW approach is that it allows information from diverse taxa to be combined (i.e. from different cladograms). Thus, phylogenetic and biogeographical data for multiple taxa (e.g. primates, ungulates, reptiles, amphibians, etc.) can be combined to formulate regional conservation priorities. Feature-based methods are not amenable to multispecies comparisons, largely because of issues related to determining branch lengths between different cladograms. Therefore, TESW metrics provide a more expandable measure than feature-based methods for prioritizing regional conservation plans for African primates.

It is important to note that the most basal taxa will not always achieve the highest-priority rankings when using TESW metrics. Although this is an issue with I and W metrics, standardization in the I_{es} and W_{es} indices controls for overweighting of only basal taxa in determining phylogenetic diversity. For example, use of I and W metrics would result in *Perodicticus potto* being considered a top-ranked species at the country level based on its basal placement within the highly speciose Lorisoid clade. However, the combined I_{es} and W_{es} rankings (after controlling for ties) result in *Perodicticus potto* being ranked 14th out of the total of 55 primate taxa at the country level. High country rankings are achieved if a taxon represents high levels of phylogenetic diversity and it is endemic to a particular region.

Although some researchers have reported relationships between the loss of evolutionary history and the loss of species richness (e.g. Heard & Mooers, 2000; Purvis *et al.*, 2000; Lockwood *et al.*, 2002), it has also been suggested that loss in species richness should automatically covary with loss in evolutionary history because of the intrinsic correlation between PD and species richness in a clade (Nee & May, 1997; Diniz-Filho, 2004b). For example, Diniz-Filho (2004b) modelled patterns of the loss of evolutionary history in the Felidae and found that extinction threats are randomly distributed across the phylogeny and are not a result of phylogenetic autocorrelation. Furthermore, some researchers have raised an interesting question concerning the importance of prioritizing basal taxa in PD metrics rather than those taxa that are experiencing high evolutionary rates (Owens & Bennett, 2000; Diniz-Filho, 2004a). In other words, the question arises whether the TESW metrics used here are prioritizing the primate taxa that are unlikely to contribute to new adaptive peaks. It is important to note, however, that comparative models of PD tend to suffer from analytical issues owing to the use of phylogenies with numerous polytomies and the fact that there are few reliable data on branch lengths for many mammalian taxa (Purvis *et al.*, 1994; Faith & Trueman, 2001).

CONCLUSIONS

There are few ecological and behavioural data on populations of some of the African primates that represent the highest levels of phylogenetic diversity (e.g. *Cercopithecus solatus*, *Arctocebus calabarensis, Colobus angolensis*). For example, *Cercopithecus solatus* has been the subject of only one longitudinal study using radio-collars (Brugiere *et al.*, 1998). Although some primate taxa with high PD priorities, such as *Pan paniscus* and *Gorilla beringei*, have been well studied (McGrew *et al.*, 1996; Caldecott & Miles, 2005), many of the nocturnal taxa that received high PD rankings are amongst the least-studied of all extant primates (Nekaris & Bearder, 2007). Studies of primate taxa with high PD rankings should focus on identifying sites suitable for intensive studies of population dynamics, feeding ecology, and reproductive behaviour.

Although the biogeographical regions in Central and West Central Africa are the top priorities in terms of primate PD, countries in these regions also suffer from considerable political instability and corruption (Barrett *et al.*, 2006; Chapman *et al.*, 2006). These socio-economic issues have led to the failure of numerous conservation initiatives (Oates, 1999; Smith *et al.*, 2003; West & Brockington, 2006). Moreover, primates in these regions experience intense hunting pressures (Pearce, 2005). Most hunting is not for personal consumption but rather for sale as part of an unsustainable commercial venture known as the bushmeat trade (Fa *et al.*, 2005; de Merode & Cowlishaw, 2006). Despite these serious issues, forest cover in parts of the Congo Basin remained remarkably intact through the 1990s (Mayaux *et al.*, 2005). Furthermore, various development programs and countries are working together closely to implement and hopefully sustain conservation projects and the formation of new protected areas (Hackel, 1999; Knight *et al.*, 2006).

Finally, we suggest that PD metrics should be included in the IUCN ranking system. Specifically, the TESW metrics could serve as an important empirical metric that balances the necessity to use conservation criteria and subcriteria derived from inferred or projected data (e.g. levels of exploitation, changes in population size). One of the strengths of the TESW approach that we used is that it allows information from diverse taxa to be combined and analysed at various biogeographical scales (Posadas *et al.*, 2001, 2004). Thus, phylogenetic and biogeographical data for multiple taxa (e.g. primates, ungulates, plants, etc.) can be combined to formulate regional conservation priorities. The advent of molecular techniques in conservation biogeography has provided valuable data for understanding population dynamics in many endangered species (e.g. Soulé & Simberloff, 1986; Mech & Hallett, 2001; Frankham *et al.*, 2002). Population data are often difficult to collect in standard observational studies of endangered primates, which has led some researchers to suggest that IUCN priorities are based on circularity of biological traits (Harcourt *et al.*, 2005).

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REFERENCES

Abrams, P.A. (2002) Will small population sizes warn us of impending extinctions? *The American Naturalist*, **160,** 293–305.

Barrett, C.B., Gibson, C.C., Hoffman, B. & McCubbins, M.D. (2006) The complex links between governance and biodiversity. *Conservation Biology*, **20,** 1358–1366.

Böhm, M. & Mayhew, P.J. (2005) Historical biogeography and the evolution of the latitudinal gradient of species richness in the Papionini (Primata: Cercopithecidae). *Biological Journal of the Linnean Society*, **85,** 235–246.

Brandon-Jones, D., Eudey, A.A., Geissmann, T., Groves, C.P., Melnick, D.J., Morales, J.C., Shekelle, M. & Stewart, C.B. (2004) Asian primate classification. *International Journal of Primatology*, **25,** 97–164.

Brugiere, D., Gautier, J.P. & Lahm, S.A. (1998) Additional data on the distribution of *Cercopithecus* (*lhoesti*) *solatus*. *Folia Primatologica*, **69,** 331–336.

Butynski, T.M. (2003) The robust chimpanzee *Pan troglodytes*: taxonomy, distribution, abundance, and conservation status. *West African Chimpanzees: status, survey, and conservation action plan* (ed. by R. Kormos, C. Boesch, M.I. Bakarr and T.M. Butynski), pp. 5–12. IUCN – World Conservation Union, Gland, Switzerland.

Caldecott, J. & Miles, L. (Eds) (2005) *World Atlas of Great Apes and their Conservation*. University of California Press, Berkeley, CA/UNEP WCMC.

Chapman, C.A., Lawes, M.J. & Eeley, H.A.C. (2006) What hope for African primate diversity? *African Journal of Ecology*, **44,** 116–133.

Chen, F.C. & Li, W.H. (2001) Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees. *The American Journal of Human Genetics*, **68,** 444–456.

Coddington, J. & Scharff, N. (1994) Problems with zero length branches. *Cladistics*, **10,** 415–423.

Cowlishaw, G. (1999) Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. *Conservation Biology*, **13,** 1183–1193.

Cowlishaw, G. & Hacker, J.E. (1997) Distribution, diversity, and latitude in African primates. *The American Naturalist*, **150,** 505–512.

Crisci, J.V., Katinas, L. & Posadas, P. (2003) *Historical biogeography: an introduction*. Harvard University Press, Boston, MA.

Crovello, T.J. (1981) Quantitative biogeography: an overview. *Taxon*, **30,** 563–575.

DelPero, M., Masters, J.C. & Ardito, G. (2000a) Phylogenetic relationships among the African galagos as indicated by mitochondrial sequence data. *Folia Primatologica*, **71,** 288–289.

DelPero, M., Masters, J.C., Zuccon, D., Cervella, P., Crovella, S. & Ardito, G. (2000b) Mitochondrial sequences as indicators of generic classification in bush babies. *International Journal of Primatology*, **21,** 889–904.

Diniz-Filho, A.J.F. (2004a) Phylogenetic diversity and conservation priorities under distinct models of phenotypic evolution. *Conservation Biology*, **18,** 698–704.

Diniz-Filho, J.A.F. (2004b) Phylogenetic autocorrelation analysis of extinction risks and the loss of evolutionary history in Felidae (Carnivora: Mammalia). *Evolutionary Ecology*, **18,** 273–282.

Disotell, T.R. (1996) The phylogeny of Old World monkeys. *Evolutionary Anthropology*, **5,** 18–24.

Emmons, L.H. (1999) Of mice and monkeys: Primates as predictors of mammal community richness. *Primate communities* (ed. by J.G. Fleagle, C.H. Janson and K. Reed), pp. 75–89. Cambridge University Press, Cambridge.

Fa, J.E., Ryan, S.F. & Bell, D.J. (2005) Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. *Biological Conservation*, **121,** 167–176.

Faith, D.P. (1992) Systematics and conservation: on predicting the feature diversity of subsets of taxa. *Cladistics*, **8,** 361–373.

Faith, D.P. (1994a) Genetic diversity and taxonomic priorities for conservation. *Biological Conservation*, **68,** 69–74.

Faith, D.P. (1994b) Phylogenetic diversity: a general framework for the prediction of feature diversity. *Systematics and conservation evaluation* (ed. by P.L. Forey, C.J. Humphries and R.I. Vane-Wright), pp. 251–268. Clarendon Press, Oxford.

Faith, D.P. & Trueman, J.W.H. (2001) Towards an inclusive philosophy for phylogenetic inference. *Systematic Biology*, **50,** 331–350.

Faith, D.P., Reid, C.A.M. & Hunter, J. (2004) Integrating phylogenetic diversity, complementarity, and endemism for conservation assessment. *Conservation Biology*, **18,** 255–261.

Fernandez, M.H. & Vrba, E.S. (2005) Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis. *Journal of Biogeography*, **32,** 903–918.

Frankham, R., Ballou, J.D. & Briscoe, D.A. (2002) *Introduction to conservation genetics*. Cambridge University Press, Cambridge.

Gao, F., Bailes, E., Robertson, D.L., Chen, Y., Rodenburg, C.M., Michael, S.F., Cummins, L.B., Arthur, L.O., Peeters, M., Shaw, G.M., Sharp, P.M. & Hahn, B.H. (1999) Origin of HIV-1 in the chimpanzee *Pan troglodytes troglodytes*. *Nature*, **397,** 436–441.

Gaston, K.J. (1994) *Rarity*. Chapman Hall, New York, NY.

Goldsmith, M.L. (2003) Comparative behavioral ecology of a lowland and highland gorilla population: Where do Bwindi gorillas fit? *Gorilla biology: a multidisciplinary perspective* (ed. by A.B. Taylor and M.L. Goldsmith), pp. 358–384. Cambridge University Press, New York, NY.

Goodman, M., Porter, C., Czelusniak, J., Page, S., Schneider, H., Shoshani, J., Gunnell, G. & Groves, C. (1998) Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. *Molecular Phylogenetics and Evolution*, **9,** 585–598.

Grubb, P. (1999) Evolutionary processes implicit in distribution patterns of modern African mammals. *African biogeography, climate change, and human evolution* (ed. by T.G. Bromage and F. Schrenk), pp. 150–164. Oxford University Press, New York, NY.

Grubb, P. (2001) Endemism in African rain forest mammals. *African rain forest ecology and conservation: an interdisciplinary perspective* (ed. by W. Weber, L.J.T. White, A. Vedder and L. Naughton-Treves), pp. 88–100. Yale University Press, New Haven.

Grubb, P., Butynski, T.M., Oates, J.F., Bearder, S.K., Disotell, T.R., Groves, C.P. & Struhsaker, T.T. (2003) Assessment of the diversity of African primates. *International Journal of Primatology*, **24,** 1301–1357.

Hackel, J.D. (1999) Community conservation and the future of Africa's wildlife. *Conservation Biology*, **13,** 726–734.

Harcourt, A.H. (2000a) Coincidence and mismatch of biodiversity hotspots: a global survey for the order, Primates. *Biological Conservation*, **93,** 163–175.

Harcourt, A.H. (2000b) Latitude and latitudinal extent: a global analysis of the Rapoport effect in a tropical mammalian taxon: primates. *Journal of Biogeography*, **27,** 1169–1182.

Harcourt, A.H. (2004) Are rare primate taxa specialists or simply less studied? *Journal of Biogeography*, **31,** 57–61.

Harcourt, A.H., Putland, D., Cardillo, M., Mace, G. & Purvis, A. (2005) Problems of studying extinction risks. *Science*, **310,** 1276–1278.

Harris, E.E. (2000) Molecular systematics of the Old World monkey tribe Papionini: analysis of the total available genetic sequences. *Journal of Human Evolution*, **38,** 235–256.

Harris, E.E. & Disotell, T.R. (1998) Nuclear gene trees and the phylogenetic relationships of the mangabeys (Primates: Papionini). *Molecular Biology and Evolution*, **15,** 892–900.

Heard, S.B. & Mooers, A.Ø. (2000) Measuring the loss of evolutionary history from extinction: phylogenetically patterned speciation rates and extinction risks change the loss of evolutionary history during extinctions. *Proceedings of the Royal Society B: Biological Sciences*, **267,** 613–620.

IUCN (2006) *IUCN Red List of Threatened Species*. IUCN Species Survival Commission, Gland, Switzerland.

Jernvall, J. & Wright, P.C. (1998) Diversity components of impending primate extinctions. *Proceedings of the National Academy of Sciences USA*, **95,** 11279–11283.

Jha, S. & Bawa, K.S. (2006) Population growth, human development, and deforestation in biodiversity hotspots. *Conservation Biology*, **20,** 906–912.

Kimbel, W.H. & Rak, Y. (1993) The importance of species taxa in paleoanthropology and an argument for the phylogenetic concept of the species category. *Species, species concepts, and primate evolution* (ed. by W.H. Kimbel and L.B. Martin), pp. 461–484. Plenum Press, New York, NY.

Knight, A.T., Driver, A., Cowling, R.M., Maze, K., Desmet, P.G., Lombard, A.T., Rouget, M., Botha, M.A., Boshoff, A.F., Castley, J.G., Goodman, P.S., Mackinnon, K., Pierce, S.M., Sims-Castley, R., Stewart, W.I. & von Hase, A. (2006) Designing systematic conservation assessments that promote effective implementation: best practice from South Africa. *Conservation Biology*, **20,** 739–750.

van der Kuyl, A.C., Kuiken, C.L., Dekker, J.T. & Goudsmit, J. (1995) Phylogeny of African monkeys based upon mitochondrial 12S rRNA sequences. *Journal of Molecular Evolution*, **40,** 173–180.

Laurance, M.F., Croes, B.M., Tchignoumba, L., Lahm, S.A., Alonso, A., Lee, M.E., Campbell, P. & Ondzeano, C. (2006) Impacts of roads and hunting on Central African rainforest mammals. *Conservation Biology*, **20,** 1251–1261.

Leendertz, F.H., Pauli, G., Maetz-Rensing, K., Boardman, W., Nunn, C.L., Ellerbrok, H., Jensen, S.A., Junglen, S. & Boesch, C. (2006) Pathogens as drivers of population declines: the importance of systematic monitoring in great apes and other threatened mammals. *Biological Conservation*, **131,** 325–337.

Lehman, S.M. (2006) Conservation biology of Malagasy Strepsirhines: a phylogenetic approach. *American Journal of Physical Anthropology*, **130,** 238–253.

Lehman, S.M. & Fleagle, J.G. (2006) Primate biogeography: a review. *Primate biogeography* (ed. by S.M. Lehman and J.G. Fleagle), pp. 1–58. Plenum/Kluwer Press, New York, NY.

Lehman, S.M., Rajoanson, A. & Day, S. (2006) Edge effects on the density of *Cheirogaleus major*. *International Journal of Primatology*, **27,** 1569–1588.

Leroy, E.M., Rouquet, P., Formenty, P., Souquiere, S., Kilbourne, A., Froment, J.-M., Bermejo, M., Smit, S., Karesh, W., Swanepoel, R., Zaki, S.R. & Rollin, P.E. (2004) Multiple ebola virus transmission events and rapid decline of Central African wildlife. *Science*, **303,** 387–390.

Lockwood, J.L., Russell, G.J., Gittleman, J.L., Daehler, C.C., McKinney, M.L. & Purvis, A. (2002) A metric for analyzing taxonomic patterns of extinction risk. *Conservation Biology*, **16,** 1137–1142.

Lovett, J.C. & Marshall, A.R. (2006) Why should we conserve primates? *African Journal of Ecology*, **44,** 113–115.

Masters, J.C., Anthony, N.M., de Wit, M.J. & Mitchell, A. (2005) Reconstructing the evolutionary history of the Lorisidae using morphological, molecular, and geological data. *American Journal of Physical Anthropology*, **127,** 465–480.

Mayaux, P., Holmgren, P., Achard, F., Eva, H., Stibig, H. & Branthomme, A. (2005) Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360,** 373–384.

McGrew, W.C., Marchant, L.F. & Nishida, T. Eds. (1996) *Great Ape Societies*. Cambridge University Press, Cambridge.

Mech, S.G. & Hallett, J.G. (2001) Evaluating the effectiveness of corridors: a genetic approach. *Conservation Biology*, **15,** 467–474.

de Merode, E. & Cowlishaw, G. (2006) Species protection, the changing informal economy, and the politics of access to the bushmeat trade in the Democratic Republic of Congo. *Conservation Biology*, **20,** 1262–1271.

Morrone, J.J. (1994) On the identification of areas of endemism. *Systematic Biology*, **43,** 373–401.

Morrone, J.J. & Crisci, J.V. (1995) Historical biogeography: introduction to methods. *Annual Review of Ecology and Systematics*, **26,** 373–401.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403,** 853–858.

Nee, S. & May, R.M. (1997) Extinction and the loss of evolutionary history. *Science*, **278,** 692–694.

Nekaris, A. & Bearder, S.K. (2007) The Lorisiform primates of Asia and mainland Africa: diversity shrouded in darkness. *Primate in perspective* (ed. by C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger and S.K. Bearder), pp. 24–45. Oxford University Press, New York, NY.

Newman, T.K., Jolly, C.J. & Rogers, J. (2004) Mitochrondrial phylogeny and systematics of baboons (*Papio*). *American Journal of Physical Anthropology*, **124,** 17–27.

Oates, J.F. (1996) *African primates: status survey and conservation action plan*, revised edn. IUCN, Cambridge.

Oates, J.F. (1999) *Myth and reality in the rain forest: how conservation strategies are failing in West Africa*. University of California Press, Berkeley, CA.

Oates, J.F. (2006) Is the chimpanzee, *Pan troglodytes*, an endangered species? It depends on what "endangered" means. *Primates*, **47,** 102–112.

Olson, D.M. & Dinerstein, E. (1998) The Global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. *Conservation Biology*, **12,** 502–515.

Owens, I.P.F. & Bennett, P.M. (2000) Quantifying biodiversity: a phenotypic perspective. *Conservation Biology*, **14,** 1014–1022.

Page, S.L. & Goodman, M. (2001) Catarrhine phylogeny: noncoding DNA evidence for a diphyletic origin of the

mangabeys and for a human-chimpanzee clade. *Molecular Phylogenetics and Evolution*, **18,** 14–25.
Page, S.L., Chiu, C.-H. & Goodman, M. (1999) Molecular phylogeny of Old World monkeys (Cercopithecidae) as inferred from gamma-globin DNA sequences. *Molecular Phylogenetics and Evolution*, **13,** 348–359.
Pearce, F. (2005) The protein gap. *Conservation in Practice*, **6,** 21–27.
Posadas, P., Esquivel, D.R.M. & Crisci, J.V. (2001) Using phylogenetic diversity measures to set priorities in conservation: an example from southern South America. *Conservation Biology*, **15,** 1325–1334.
Posadas, P., Esquivel, D.R.M. & Crisci, J.V. (2004) On words, tests, and applications: Reply to Faith *et al.*. *Conservation Biology*, **18,** 262–266.
Purvis, A., Gittleman, J.L. & Luh, H.-K. (1994) Truth or consequences: effects of phylogenetic accuracy on 2 comparative methods. *Journal of Theoretical Biology*, **167,** 293–300.
Purvis, A., Agapow, P.-M., Gittleman, J.L. & Mace, G.M. (2000) Nonrandom extinction and the loss of evolutionary history. *Science*, **288,** 328–330.
Roberts, D.L. & Kitchener, A.C. (2006) Inferring extinction from biological records: were we too quick to write off Miss Waldron's red colobus monkey (*Piliocolobus badius waldronae*)? *Biological Conservation*, **128,** 285–287.
Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M. & Brooks, T.M. (2006) The value of the IUCN Red List for conservation. *Trends in Ecology & Evolution*, **21,** 71–76.
Rondinini, C. & Boitani, L. (2006) Differences in the umbrella effects of African amphibians and mammals based on two estimators of the area of occupancy. *Conservation Biology*, **20,** 170–179.
Roos, C., Schmitz, J. & Zischler, H. (2004) Primate jumping genes elucidate strepsirrhine phylogeny. *Proceedings of the National Academy of Sciences USA*, **101,** 10650–10654.
Ruvolo, M. (1997) Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets. *Molecular Biology and Evolution*, **14,** 248–265.
Sechrest, S., Brooks, T.M., da Fonseca, G.A.B., Konstant, W.R., Mittermeier, R.A., Purvis, A., Rylands, A.B. & Gittleman, J.L. (2002) Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences USA*, **99,** 2067–2071.
Smith, R.J., Muir, R.D.J., Walpole, M.J., Balmford, A. & Leader-Williams, N. (2003) Governance and the loss of biodiversity. *Nature*, **426,** 67–70.
Soulé, M.E. & Simberloff, D. (1986) What do genetics and ecology tell us about the design of nature reserves? *Biological Conservation*, **35,** 19–40.
Tosi, A.J., Buzzard, P.J., Morales, J.C. & Melnick, D.J. (2002) Y-chromosome data and tribal affiliations of *Allenopithecus* and *Miopithecus*. *International Journal of Primatology*, **23,** 1287–1299.
Tosi, A.J., Disotell, T.R., Morales, J.C. & Melnick, D.J. (2003) Cercopithecine Y-chromsome data provide a test of competing morphological evolutionary hypotheses. *Molecular Phylogenetics and Evolution*, **27,** 510–521.
Tosi, A.J., Melnick, D.J. & Disotell, T.R. (2004) Sex chromosome phylogenetics indicate a single transition to terrestriality in the guenons (tribe Cercopithecini). *Journal of Human Evolution*, **46,** 223–237.
Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991) What to protect? Systematics and the agony of choice. *Biological Conservation*, **55,** 235–254.
Walsh, P.D., Abernethy, K., Bermejo, M., Beyers, R., De, W.P., Akou, M., Huijbregts, B., Mambounga, D., Toham, A., Kilbourn, A., Lahm, S., Latour, S., Maisels, F., Mbina, C., Mihindou, Y., Obiang, S., Effa, E., Starkey, M., Telfer, P., Thibault, M., Tutin, C., White, L. & Wilkie, D. (2003) Catastrophic ape decline in western equatorial Africa. *Nature*, **422,** 611–614.
West, P. & Brockington, D. (2006) An anthropological perspective on some unexpected consequences of protected areas. *Conservation Biology*, **20,** 609–616.
Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. (2005) Conservation biogeography: assessment and prospect. *Diversity and Distributions*, **11,** 3–23.
Wildman, D.E. & Goodman, M. (2004) Humankind's place in a phylogenetic classification of living primates. *Evolutionary theory and processes: modern horizons, papers in honour of Eviatar Nevo* (ed. by S.P. Wasser), pp. 293–311. Kluwer Academic Publishers, Dordrecht.
Williams, P.H., Humphries, C.J. & Vane-Wright, R.I. (1991) Measuring biodiversity: Taxonomic relatedness for conservation priorities. *Australian Journal of Systematics and Botany*, **4,** 665–679.
Wilson, K.A., McBride, M.F., Bode, M. & Possingham, H.P. (2006) Prioritizing global conservation efforts. *Nature*, **440,** 337–340.
Wolman, A.G. (2006) Measurement and meaningfulness in conservation science. *Conservation Biology*, **20,** 1626–1634.
Xing, J., Wang, H., Han, K., Ray, D.A., Huang, C.H., Chemnick, L.G., Stewart, C.-B., Disotell, T.R., Ryder, O.A. & Batzer, M.A. (2005) A mobile element based phylogeny of Old World monkeys. *Molecular Phylogenetics and Evolution*, **37,** 872–880.

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