

## Short communication

# Seeing the woodhoopoe for the trees: should we abandon Namibia's Violet Woodhoopoe *Phoeniculus damarensis* as a species?

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Opening the pages of *Ibis* to find that one of the near-endemic species of most concern in your country has been subsumed into another commoner species (Cooper *et al.* 2001) is a little disconcerting. Cooper *et al.*'s study of the mitochondrial oxidase gene concludes that the divergence of 1.06–1.21% between Namibia's Violet Woodhoopoe *Phoeniculus damarensis* and the commoner Green Woodhoopoe *Phoeniculus purpureus* is too small to consider them separate species and that the two should be synonymized.

We view this with some concern given that the Violet Woodhoopoe has been treated by conservation authorities in Namibia, Angola and elsewhere as a recognizable taxonomic unit for many years (Pinto 1983, Clancey 1986, Howard & Moore 1991, du Plessis 1997), and since 1992 has been the subject of Namibia-wide scrutiny of its population status (Robertson *et al.* 1995, 1998, Jarvis & Robertson 1999) and occurrence in conservation areas (Brown *et al.* 1998, Simmons *et al.* 2001).

There are several responses one can have to learning of the apparent demise of a near-endemic – one can ignore the results, challenge them, carry on regardless, or as we do here, state our conservation response and re-evaluate the likelihood that the two species really are genetically synonymous. In particular, we set out our reasons for believing that it is premature to regard *P. purpureus* and *P. damarensis* as being synonymous. We then discuss some philosophical issues surrounding conservation in the face of taxonomic ambiguity.

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## SAMPLING PROCEDURES AND PHYLOGENIES

Violet and Green Woodhoopoes overlap in Namibia's western ephemeral rivers (du Plessis 1997) and are found in mixed groups and probably interbreed in these areas of sympatry (M.A. du Plessis & R.E. Simmons unpubl. data). It is therefore surprising to note that the genetic samples used by Cooper *et al.* were obtained from regions (Omaruru and Hobatere) where mixed groups have previously been reported. This is the single greatest concern regarding Cooper *et al.*'s study, and one that undermines their main assumption that they in fact sampled pure Violet Woodhoopoes. By sampling in more extreme western (arid) parts, the likelihood of finding Red-billed Woodhoopoes among Violet Woodhoopoe groups (and hybrids between the two) would have been much lower. Our prediction that interbreeding is occurring (M.A. du Plessis & R.E. Simmons unpubl. data) is supported by Cooper *et al.*'s single comparison with a Namibian Green Woodhoopoe (*Phoeniculus purpureus angolensis*) taken from a mixed flock of Violet and Green Woodhoopoes. The divergence was, as expected, very small (0.15%), supporting the idea that interbreeding between the two species occurs – a major conservation concern in Namibia.

Revisiting the phylogenetic tree, Cooper *et al.*'s conclusion rests almost entirely on the root node for *Phoeniculus* because it is the nesting of *P. damarensis* within *P. purpureus* that provides the main evidence for subsuming the species. If *P. damarensis* was resolved as monophyletic and sister to the remaining *Phoeniculus* taxa, we assume that the data would not have been interpreted as providing evidence for sinking the species. However, the analyses presented by Cooper *et al.* are problematic as the long branch defining the outgroup potentially renders the root node ambiguous. To test the decisiveness of the data in this respect, we constrained the outgroup placement to the branch between *P. damarensis* and the remainder of the *Phoeniculus* accessions. The shortest tree found under this constraint is three steps longer than the most parsimonious tree (MPT) (length = 19, with uninformative characters excluded; 118 with these included), and this difference is not significant under a Winning Sites (sign) test ( $P = 0.37$ ).

Similarly, neither the HKY85 model used by Cooper *et al.* (2001) nor a General Time Reversible (GTR) model accommodating rate heterogeneity among sites (Yang 1994) permitted rejection of the alternative topology as tested by the Shimodaira and Hasegawa (1999) statistic (Table 1). We conclude that the data are ambiguous with respect to the placement of the root node, largely because of the outgroup chosen, and evidence based on the nesting of *P. damarensis* within *P. purpureus* is illusory. The problem could have been rectified by inclusion of less distant outgroups, for example representatives of other *Phoeniculus* species. Ignoring the dubious *P. p. angolensis* sampled by Cooper *et al.* (above), the tree as presented by them could just as readily be interpreted as indicating the existence of three species.

**Table 1.** Summary of likelihood tests on alternative topologies for the *Phoeniculus* group. Given are the differences in ln likelihood, where *P* is the probability of obtaining a more extreme *t*-value under the null hypothesis of no difference in likelihood between the two trees under the Shimodaira–Hasegawa test.

Model	–ln Likelihood		Difference	<i>P</i>
	Cooper <i>et al.</i>	<i>P. damarensis</i> basal		
HKY 85	2201.19	2201.87	0.68	0.75
GTR + $\lambda\Gamma$	1374.52	1375.59	1.07	0.40

We further question the arbitrary decision to subsume this near-endemic into a commoner species on the basis of a small divergence (average 1.06%) between Namibian Violet Woodhoopoes and South African Green Woodhoopoes *P. p. marwitzi*. Cooper *et al.*'s justification for this was based on a single comparison with a distantly related Scimitar-billed Woodhoopoe from another genus *Rhinopomastus cyanomelas* (differing by 16%) that suggested to the authors a relatively high evolutionary rate and the improbability that slow evolutionary rates in this group can explain the close similarity of the two woodhoopoes.

Certainly the divergence between *P. p. marwitzi* and *P. damarensis* (2.3%) falls within the range of interspecific comparisons shown by Cooper *et al.* and it is to this subspecies that *P. damarensis* is sister.

We note that there is no one-to-one relationship between species status and the degree of sequence divergence expected. The methodology and subsequent interpretation behind this expectation requires the assumption that most recent common ancestors (MRCAs), and the critical coalescence events for the genes analysed, post-date speciation events. No basis exists for this assumption, and 'good' species are often expected to resolve as non-monophyletic. Indeed, if the speciation events are relatively recent, polyphyly of a very high proportion of DNA loci is essentially guaranteed.

In the case of sister species, lineages of a particular locus are expected to be reciprocally monophyletic only after *c.* 1.7*N* generations (where *N* is population size) and 99% of loci are expected to be reciprocally monophyletic only after *c.* 5.3*N* generations (Hudson & Coyne 2002, Funk & Omland 2003, Rosenberg 2003). Therefore, there is no reason to expect haplotype relationships to be informative of species status.

## BEHAVIOUR AND BIOGEOGRAPHY

What the authors did not consider are behavioural or ecological differences between the two taxa, because their research was lab-based. We have recorded that the species apparently differ in ecology and behaviour, but the

manuscript in which these results are described (M.A. du Plessis & R.E. Simmons unpubl. data) was rejected by a prominent conservation journal because of the birds' unresolved genetic status. This 'Catch-22' situation needs unwrapping; all appropriate evidence and biogeographical patterns of woodhoopoe distribution are relevant here. Preliminary behavioural data suggest that Violet Woodhoopoes differ because they occur in smaller groups (2–5 birds: Jarvis & Robertson 1999) than Green Woodhoopoes (2–12 birds: du Plessis 1997), they forage more often away from the ephemeral rivers where they (and Green Woodhoopoes) roost in hollow trees, they only strongly defend the core area of their home ranges around their roost holes, and they appear to engage in more terrestrial (as opposed to arboreal) foraging than Green Woodhoopoes (M.A. du Plessis & R.E. Simmons unpubl. data). These are tentative differences given that our comparisons of Violet Woodhoopoes also took place in areas where the birds occur in mixed flocks in western Namibia.

Biogeographically, two forms of the Violet Woodhoopoe occur in Africa, one in Namibia/Angola (*damarensis*) and the other in Kenya and Tanzania (*P. d. granti*) (Fry *et al.* 1988). This pattern of distribution is common for several arid-adapted animals at either end of the southwest–northeast arid corridor in Africa (Balynski 1962, Kingdon 1990) and is mimicked by birds such as Spike-heeled Lark *Chersomanes albofasciata*, Chestnut-banded Plover *Charadrius pallidus* and Pale Chanting Goshawk *Melierax canorus* (Clancey 1986, Simmons *et al.* 1998, Barnes 2000), and mammals such as Black backed Jackal *Canis mesomelis*, Oryx *Oryx gazella* and Dik Dik *Madoqua kirkii* (Coe & Skinner 1993). This has two consequences: first, this northeast–southwest pattern makes it more likely that the lineages we are seeing are indeed independent; and secondly if global warming promotes the expansion of the arid corridor that once linked these now geographically isolated species at the expense of more mesic-adapted species (IPCC 2001, Simmons *et al.* in press), we may see a contraction of the range of the Green Woodhoopoe and the emergence of the Violet Woodhoopoe out of the shadow of their closest cousin.

## PHILOSOPHICAL CONSIDERATIONS

The main philosophical question remains: is a 1% genetic difference big enough to distinguish these particular species? For Namibian conservationists, even subspecies that differ by 1% from nearest extant neighbours will continue to be treated as a conservation priority, not only for current generations but for future ones who may see such species emerge from the range of the Green Woodhoopoe under global warming scenarios mentioned above. We therefore disagree with Cooper *et al.*'s conclusion that 'it is the status of *Phoeniculus purpureus* [Green Woodhoopoe] that should be considered in formulating avian conservation plans in Namibia, which may have been overweighted in

terms of avian endemism.' In our view an endemic relegated to subspecific level on tenuous grounds with a population estimated at fewer than 2000 birds (Jarvis & Robertson 1999) rates a higher conservation ranking than other Red-listed species whose range extends to other parts of the world. Such evolutionarily significant units as these will be given the highest status in Namibia's emerging red data book (Simmons & Brown in press) because of their uncertain futures and the responsibility that near-endemic status places on their countries of origin. Furthermore, conservation must consider future options and evolutionary eventualities such as the possible emergence of a subspecies to full species status in future generations.

We conclude that there are few grounds for subsuming Violet Woodhoopoes into the commoner Green Woodhoopoe, and further sampling of the *Phoeniculus* tribe would better forward science and conservation than rushing into print with a barely leafed tree, even in arid places such as Namibia.

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