SPOTLIGHTS

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Understanding species-level primate diversity in Madagascar

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ABSTRACT

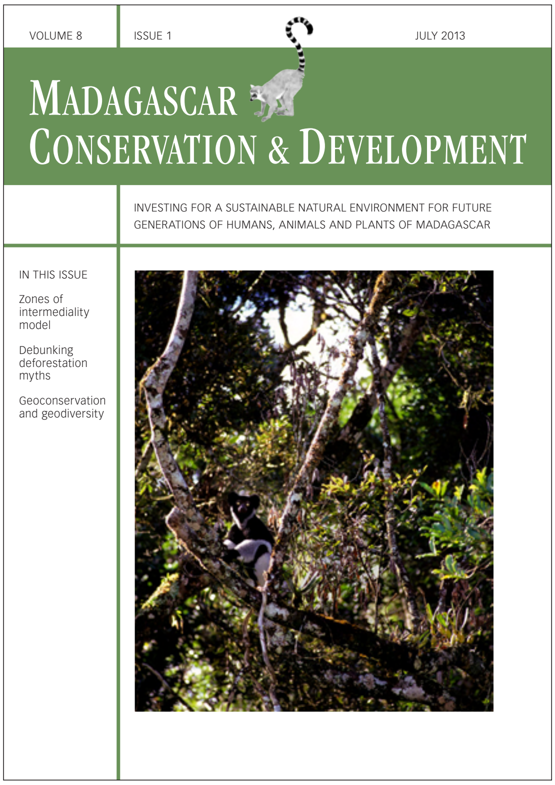
Over the past couple of decades Madagascar has witnessed an explosion in the number of primate species generally recognized. Much of this proliferation can be traced less to increasing knowledge of the lemur fauna than to the complete replacement of biological notions of the species by the Phylogenetic Species Concept (PSC), which views species as irreducible diagnosable units. The consequent focus on autapomorphy (unique possession of morphological and molecular derived features) as 'the' criterion for species recognition has led to the almost complete disappearance of lemur subspecies from Madagascar faunal lists; yet subspecies are an expected result of the evolutionary forces that gave rise to the island's current pattern of biodiversity. Thanks in part to the perspective introduced by the PSC, it has become clear both that there is much more species-level diversity among Madagascar's lemurs than was evident only a couple of decades ago, and that this diversity is much more complexly structured than we had thought. But it does not appear to be aptly reflected in the hard-line procedural adoption of the PSC across the board, a move that typically results in fifty-percent inflation in species numbers relative to those yielded by biological concepts. I argue here that the reflexive wholesale application of the PSC to Madagascar's lemurs is inappropriate from both systematic and conservation standpoints, and that a return to biological species concepts, and to the corresponding criteria for species recognition, will allow us to attain a much fuller and more nuanced appreciation of lemur diversity at low taxonomic levels.

RÉSUMÉ

Depuis la fin du siècle dernier, nous avons été les témoins d'une explosion du nombre d'espèces de primates à Madagascar. Cette profusion découle cependant bien moins de l'évolution de nos connaissances sur les lémuriens que de la substitution des concepts biologiques de l'espèce par le Concept Phylogénétique de l'Espèce (CPE ou Phylogenetic Species Concept – PSC), ce dernier considérant l'espèce comme le plus petit groupe irréductible d'organismes qui puisse être différencié d'un autre groupe. L'autapomorphie (c'est-à-dire la possession de caractères dérivés uniques, morphologiques et moléculaires) est ainsi devenue 'le' critère pour distinguer les espèces, de sorte que la quasi-totalité des sous-espèces de lémuriens ont disparu des listes fauniques de Madagascar ; sachant cependant que les sous-espèces sont un résultat escompté des forces de l'évolution qui ont forgé la biodiversité que nous observons aujourd'hui sur l'île. Élever toutes les sous-espèces au rang d'espèces pour la simple raison qu'elles peuvent être diagnostiquées revient à amputer la faune malgache du mécanisme que nous connaissons et qui est justement à l'origine de la fameuse diversité malgache à des niveaux taxinomiques inférieurs. C'est en partie grâce à la perspective offerte par le CPE qu'il est devenu clair que la diversité des espèces de lémuriens de Madagascar était bien plus importante qu'on ne le pensait il y a encore quelques dizaines d'années, mais aussi que cette diversité avait une structure bien plus complexe que nous ne l'avions imaginée. Il semble cependant que dans l'ensemble, le CPE n'ait pas été adopté correctement dans sa procédure pure et dure, de sorte que nous assistons à une inflation de cinquante pourcent du nombre des espèces par rapport à celles qui sont révélées par les concepts biologiques. Je soutiens ici que l'application globale et réflexive du CPE aux lémuriens de Madagascar est inappropriée aussi bien du point de vue de la systématique que de la protection de la nature, et qu'un retour vers des concepts biologiques des espèces, et leurs critères inhérents à la reconnaissance des espèces, nous permettra de mieux appréhender la diversité des lémuriens avec les nuances nécessaires pour considérer les niveaux taxinomiques inférieurs. Accepter que les espèces sont dynamiques mais aussi des entités historiquement individualisées plutôt que des unités typologiques définies par la seule présence de caractères dérivés uniques nous permettra d'y voir plus clair et de nous poser les bonnes questions afin d'appréhender la diversité et la complexité biologiques de Madagascar.

INTRODUCTION

Madagascar's biodiversity is legendary, although especially in the case of the island's endemic mammals it bears a distinctly insular aspect, with rather few major taxa represented by an undeniable profusion of species. But just how great is that profusion? The question is a deceptively simple one, for it involves not only notions of what species are in the abstract, but of how they may be operationally recognized. This is important; for, while everyone can agree that species are the basic "kinds" of organisms in the living world, opinions may legitimately differ on just how they are bounded, and even on how we can know those boundaries exist, and where they lie.



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By the mid-twentieth century most zoologists had moved beyond earlier typologies, and had come to embrace the Biological Species Concept (BSC), in which the species was regarded as the largest effective reproducing population. Individuals resembled each other because they belonged to the same species, rather than vice versa (cf. Mayr 1982). Accordingly, this was largely an age of taxonomic inclusivity. The two major systematic overviews of Madagascar's primates published in the 1970s and 1980s (Petter et al. 1977, Tattersall 1982) both hewed quite closely to Ernst Schwarz's (1931) pioneering genus- and species-level revision of several decades earlier. Based entirely on the scrutiny of museum specimens, Schwarz had reduced the total number of lemur species to 20. Nine of these were polytypic, with a total of 26 subspecies among them. By the time I completed my own synthesis more than half a century later (Tattersall 1982), students of the lemur fauna enjoyed the considerable benefit of a growing corpus of field observations in addition to the museum collections. But, even so, I was still able to recognize only 22 species. Seven of these were polytypic, to a total of 29 subspecies.

So much for minimalism. Over the last two decades, the number of species-level lemur taxa has exploded. When Mittermeier et al. (1994) published the first edition of their field guide to the lemurs, which has by now achieved canonical status, they listed 31 lemur species. By the time the second edition (Mittermeier et al. 2006) was published a dozen years later, there were 68 species, plus some cryptic allusions to species as yet unnamed. And in the third edition (Mittermeier et al. 2010), issued after an interval of only four years, the number of lemur species had soared to 97. Now the total stands at well over 100 (see Tattersall 2013). Significantly, the number of polytypic lemur species simultaneously underwent a marked decline: there were seven in 1994, but only two in 2006 and 2010.

SPECIES CONCEPTS, EVOLUTIONARY PROCESSES, AND LEMURS. Hardly coincidentally, just as lemur species were burgeoning in Madagascar, the total number of different species concepts on offer in the literature was similarly mushrooming. At last count (Coyne and Orr 2004, Hausdorf 2011) there were almost 30 such concepts. Most, however, fall into one of three classes. One large category consists of variants on the Biological Species Concept (BSC). A second contains Hugh Paterson's (1985) Recognition Concept of Species (RCS), a significant contribution that emphasizes the importance of shared common fertilization systems. But the idea of the species that is most closely identified with the recent proliferation of lemur species in Madagascar falls into the third. This most importantly includes Joel Cracraft's (1983) Phylogenetic Species Concept (PSC), a derivative of G. G. Simpson's (1961) "evolutionary" notion of the species.

In what was probably his most influential single articulation of the PSC, Cracraft (1983: 170) defined the species as "an irreducible cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." For operational as well as theoretical reasons, most subsequent practical applications of the PSC have tended to overlook the last part of this definition, and to focus instead solely upon the criterion of diagnosability (Tattersall 2007). Where it has been applied in vertebrate systematics, the PSC has by one estimate led to a multiplication of species compared to the BSC of around 50 percent (Agapow et al. 2004).

The simplified focus on diagnosability is quite understandable, appealing as it does to the innately reductionist proclivities of the human mind. What's more, on the operational level, narrowing the emphasis to this single criterion hugely simplifies the complex task of identifying species. Whether you are in the field, or in a museum, or in your laboratory, if you can recognize it, it's a species. All it takes is one nice distinguishing feature to do the trick. Both in the forest and in the storage cabinet, favored species-group features of this kind have traditionally consisted of what we used to call 'external' characters, visible to the naked eye: pelage coloration, ear size, and so forth. Particularly in the case of cryptically-colored and mostly small-bodied nocturnal primates, field workers have long also leaned upon vocal characteristics as species recognition criteria. And most recently, of course, the ultimate reductive weapon of DNA distance has been extensively deployed, albeit often via crude base-substitution counts at various marker positions, principally in the mitochondrial genome.

Hence the massive loss of lemur subspecies between 1982 and 2010, as the PSC began to bite in strepsirhine systematics. Via the stringent application of the diagnosability criterion, virtually every subspecies out there was promoted to the species level. And while the investigators involved in this wholesale splitting may not always have been aware of it, this stratagem involved abandoning some very basic notions of evolutionary process. Under the BSC, successful and widely-distributed species had been actively expected to spawn subspecies: readily recognizable local variants that were nonetheless reproductively compatible with their conspecifics living elsewhere. Indeed the BSC, and the corpus of evolutionary theory from which it was derived (basically, the New Synthesis of the 1930s and 1940s: see Mayr 1982), saw subspecies as the engines of biodiversity, giving new species a place to start. Without subspecies, or at least differentiated populations, there could be no new species. And my contention here is that this simple proposition remains as valid now as it was twenty years ago, irrespective of whether (or not) you accept the well-substantiated proposition that speciation and morphological divergence are not simply different sides of the same coin (Tattersall 1994).

Saying this is not to deny the utility of the PSC perspective. Indeed, sophisticated applications of the approach in the systematics of a wide range of major taxa have permitted biologists (using both phenotypic and DNA criteria) to identify many cases in which unrelated but phenotypically similar populations had been incorrectly lumped under the same bio-species. As a result, most investigators nowadays would demand data of several different kinds to confirm claims of population status, whether specific or infraspecific. What is more, to acknowledge that subspecies exist as real entities, albeit elusive ones, also involves accepting that the living world is a messy place. Nature is not neatly packaged. At the lowest levels of the taxonomic hierarchy, where divergence is minimal, and where even taxa destined ultimately to be highly distinctive may be hard to differentiate from their sisters, demarcations are often blurry. Subspecies are, of course, diagnosable by definition. But even if future systematists will be able to look back and determine that diagnosably differentiated populations had in fact embarked on separate historical trajectories, prior to the critical (and probably usually fairly short-term) event of speciation the only barriers to genetic interchange among conspecific populations will be geographical ones. What is more, speciation itself is neither a simple process, nor even a unitary one. Indeed, there is a good argument to be made that it is not usefully referred to as a process at all. After all, to do so would be to imply the action of a specific mechanism (Tattersall 1986), whereas many different mechanisms may in fact be involved, acting at anywhere from the molecular to the population levels (Tattersall 1994).

As useful as it may be to think of speciation as an event that 'happens' at a point in time, the reality is that this fundamental generator of biodiversity is something that we invariably infer in retrospect, and that we recognize only via its consequences. Such consequences most fundamentally involve the historical individualization of lineages (Ghiselin 1974), and the establishment of the substantially impermeable reproductive barriers that such individualization suggests. What is more, it is not easily predictable just how those consequences will be expressed, nor even evident that they will be expressed in ways visible to the systematist. Closely related species may show considerable morphological divergence from one another, or they may show hardly any at all. This failure of newly-separated species to conform to an easily quantifiable pattern of morphological divergence not only argues strongly for the notion that speciation is 'not' an 'event' of an inherently specifiable kind, but also for the parallel fact of life that a comprehensive definition of species – like the identification of a unitary 'mechanism' of speciation itself – will always remain out of reach.

Still, nobody would dispute that species-level taxa do exist in some meaningful way. Nature really is packaged, however untidily; and those boundaries actually are there, no matter how blurry or elusive they may be. It is, of course, because they accept this unavoidable reality that the advocates of the PSC so fervently desire some simple and effective operational way of recognizing species. Yet the simple fact is that nature does not always organize itself for the taxonomist's convenience.

It is at this point that Paterson's RCS enters the picture, with its focus upon how conspecifics mutually recognize that they belong to the same exclusive breeding pool. From Paterson's perspective, the significant thing is that the subjects of our studies know perfectly well who they are, irrespective of how difficult it may be for us to 'read their minds' on the matter. Accordingly, he emphasized the importance in species recognition of inter-individual signaling systems, whether vocal, or chemical, or behavioral, or visual (Paterson 1985). Sometimes candidate signaling systems may mislead human observers, as in Madagascar they evidently have done in the case of the several easily recognizable varieties assigned to the *Eulemur fulvus* group. By Mittermeier et al.'s (2010) last count, there are seven species in this group. All are differentiated by marked chromatic differences in the pelage, and some of them are additionally sexually dichromatic. They are certainly diagnosable, at least in terms of mean chromatic tendencies. But since almost all of these purported species readily and successfully interbreed when given the opportunity, and almost anyone who has wandered extensively in the forests of Madagascar has observed *fulvus*-group variants that defied ready classification, the distinguishing features that are so evident to us clearly have little to do with these lemurs' own senses of identity. Similar observations also apply, if less dramatically, to certain other largish-bodied diurnal lemurs, such as some variants of the *Propithecus verreauxi*-group (e.g., King et al. 2012).

Different problems apply to the categorization of the typically smaller-bodied and more cryptically colored nocturnal forms. Between them, the two genera *Microcebus* and *Lepilemur* account for a large proportion of the recent increase in the number of lemur species: in 1982 there were two species of *Microcebus* and only one of *Lepilemur* (albeit with six subspecies); while in 2010 the respective counts were 18 and 26, respectively. Most of these purported species have been diagnosed principally or purely on the basis of mtDNA distances, a procedure recently criticized on multiple grounds by Frankham et al. (2012). Even leaving aside these authors' cogent technical objections, whether the mtDNA distances reported for *Microcebus* and *Lepilemur* samples actually correlate with other valid criteria for species recognition is in many cases unknown. This having been said, however, there is no doubt that there are many more species of both *Microcebus* and *Lepilemur* out there than I was able to recognize in 1982; and indeed, the existence and identities of some of those additional *Microcebus* species have already been quite convincingly demonstrated via the deployment of multiple criteria (e.g., Zimmermann et al. 1998, Rasoloarison et al. 2000, Yoder et al. 2002).

I have reviewed much of the evidence for taxonomic proliferation among the lemurs elsewhere (Tattersall 2007, 2013). It does not seem particularly helpful to repeat this exercise here, except to note that in both contributions I concluded that fully individuated status cannot at present be considered conclusively substantiated for many more than half of the 100-odd lemur species listed in the latest Field Guide (Mittermeier et al. 2010). Still, I would also emphasize that, in pointing to a paucity of decisive evidence for some of the more extravagant estimates of lemur species numbers, I am not in the least disputing that there is far more lemur biodiversity in the forests of Madagascar than we had thought there was only four decades ago. Clearly, there are many species and distinctive populations of lemurs in those forests, some of them with highly limited distributions. Equally evidently, the remarkable diversity of Malagasy primates is systematically, geographically, genetically, morphologically and ecologically structured in a much more complex fashion than we had ever dreamed, even as recently as at the beginning of this millennium.

However, I do urge the exercise of caution in using the criterion of diagnosability as the sole arbiter of species status, whether the diagnostic evidence at hand is molecular, or morphological, or vocal, or whatever. Diagnosability is certainly a major factor to be taken into account in any alpha-taxonomic decision; but using this criterion alone, as the PSC in its currently fashionable form advocates, simply takes us back to the phenetic cacophony of species from which Ernst Schwarz (1930) rescued us the best part of a century ago. In order to determine with any confidence whether or not our subject populations 'behave' as individuated entities – which should surely be our goal – we require evidence from multiple sources, including morphology (in its broadest sense, embracing superficial characters and olfactory signaling systems as well as internal anatomy), DNA markers, social behaviors, vocal and visual communication, geographical and ecological distributions, environmental preferences, and interactions with sympatric populations including putative gene flow.

We are obliged, in other words, to proceed in the manner of many judicial systems, also operating in a complex and murky world, in which decisions are reached on a preponderance of the evidence. Still, we have to be careful with our metaphors; and the familiar criterion of 'beyond reasonable doubt' used in criminal cases may be a little too stringent for some real-world biological data sets. We might more appropriately look to civil law, in which more general probabilities apply. Much as tidy-minded systematists might wish they were not, very closely related species are often genetically leaky vessels, which means that reasonable doubt as to individuation can in some cases be very difficult to banish. As a systematist, I would instinctively prefer in those cases to apply the presumption of innocence, and to regard sister populations as conspecific unless there are compelling reasons to conclude otherwise. But it is also apparent that from a conservation standpoint the evidence might be interpreted differently, particularly where distinctive and highly localized populations are imperfectly known; and clearly, in an arena as complex and nuanced as this, a 'one size fits all' solution is never going to apply. As in the law, a judicious case-by-case approach is indicated.

Still, the reasons for adopting a restrained general attitude toward species recognition are compelling; and they relate not simply to the multifaceted nature of species as reflected in the plethora of definitions available, but to the nature of the evolutionary process that produced the diversity we see in Madagascar today. For there is every reason to believe that, far from being some kind of passive relict that in isolation long ago established an equilibrium with its environment, the Malagasy biota is, instead, in a dynamic state of evolutionary flux (cf. contributions in Goodman and Benstead 2003). This is perhaps more than ever the case since the recent elimination of the island's megafauna.

Above the level of the genome, the fixation of heritable novelties in local populations belonging to existing species is the most fundamental process involved in generating biodiversity. This process is synonymous with the formation of those diagnosable variants we call subspecies. And it is an essential part of the evolutionary dynamic. To promote all subspecies to species simply on the grounds that they are diagnosable is to rob the Malagasy fauna of the very mechanism that we know must have operated to produce the island's famous diversity at low taxonomic levels.

CONSERVATION AND SPECIES. So, what does all this imply for conservation? People concerned with protecting the whole environment at particular places on the planet's surface – which, captive propagation of individual species aside, is all that can be effectively done in this arena – often get rather impatient at what they see as the quibbling of taxonomists, who peddle an inherently unstable product. Their attitude is often a pragmatic "let's just have a set of names that everyone can agree on, so we can get on with protecting what we know is there anyway." Even taxonomists can sympathize with such sentiments; and it is unfortunate indeed that their subjects, as the products of complex and untidy evolutionary processes, do not always compress easily within neat species boundaries. But regrettable as it may be, this messy reality is also unavoidable – even though, because of their understandable frustration, those involved in conservation seem at times to have felt impelled to import their own imperatives into taxonomy.

If a species occurs uniquely at a particular site, that site might rise in the priority list for protection; and certainly in purely pragmatic terms it might be easier to raise funds for a particular locality possessing its own 'flagship' species. A conservationist might well be tempted to believe that, if this perceived advantage has to be gained by promoting what had previously been a subspecies to full species status, then so be it. But then again, if that advantage were to come at the expense of other sites depending on the same funding pool, local conservation gain of this kind might actually lead to a misallocation of resources on a wider scale. What is more, viewing species as irreducible units might in fact produce defined species populations that are simply too small to be viable in the long term: something that for many reasons is, at the very least, unfortunate from a conservation perspective. From the taxonomist's point of view, of course, this approach might also lead to pressure for a biologically unsubstantiated proliferation of names, as one suspects may to some extent have happened in Madagascar.

Fortunately, there is an alternative conservationist view of taxonomy, one strongly advocated recently by Richard Frankham and colleagues (Frankham et al. 2012). These authors argue that, for conservation purposes, the "substantial reproductive isolation" required by the Differential Fitness Species Concept (DFSC: Hausdorf 2011) is greatly preferable to the diagnosability of the Phylogenetic Species Concept. Operationally the DFSC, which is effectively an extension of the Biological Species Concept (BSC), is more demanding than pure diagnosability, since at least in the form advocated by Frankham et al. (2012) it requires quite extensive genetic sampling (looking widely for a dearth of shared alleles at one or more autosomal loci as indicators of a lack of gene flow). But it produces species groupings that are more practical to conserve because they will have larger effective population sizes, and presumably wider distributions. What is more, recognizing species according to the admittedly rather imprecise criterion of substantial genetic isolation will, the authors claim, facilitate "genetic rescue efforts … and [when populations are crossed] the risk of outbreeding depression [will be] minimized" (Frankham et al. 2012: 30). And from a systematist's point of view, this approach also has the advantage of taking into account Nature's blurry lines.

It is true that the information necessary for applying the DFSC will not always be available. But Frankham et al. (2012) also make a persuasive more general case for applying the principles of the BSC, rather than those of the PSC, for conservation purposes. And they very wisely insist that any species listing or classification be accompanied by an explicit statement of the species concept from which it was derived. Crucially, their conservation-oriented recommendations have the additional advantage that they should also be entirely acceptable to any taxonomist who is aware of the complexities of the multi-level evolutionary process(es). If there is one thing we can certainly all agree upon, it is that descent with modification is the only hypothesis we have that predicts the observed organization of biological diversity we find in Madagascar and elsewhere, both at lower and higher levels of the taxonomic hierarchy. And if we deny that species may be polytypic, we shall starve evolution of its most basic component, namely population differentiation.

The bottom line here is that we do not need to gild the lily of Madagascar's altogether remarkable biodiversity by maximizing the possible number of its species. After all, even on the most conservative estimates of species numbers, this unique diversity is already impressive enough to place the island at the forefront of conservationist awareness. To put the matter another way, more is not necessarily better. In fact, in the long run an unnecessary multiplicity of species will almost certainly complicate the conservation enterprise.

Yes, there is without doubt an enormous amount of biological diversity and ecological complexity out there in the forests of Madagascar: a diversity that requires not only to be recognized, but to be appropriately categorized. There can be no doubt that those who have applied the criterion of diagnosability to the recognition of species in the Malagasy primate fauna have performed a salutary service, in drawing attention to the amazing extent of this diversity and complexity. But the effort to understand the multi-level population dynamics involved will not be well served by simply imprisoning the actors in Madagascar's evolutionary play within an irreducible number of pigeonholes. There is clearly a lot more going on in the Malagasy biosphere than this static view would suggest. Accepting that species are dynamic but historically individuated entities, rather than typological units defined by their possession of uniquely derived characters, will free our minds to clarify this complexity. It will help us to ask the right questions.

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