The course of thinking on the taxonomy of woolly monkeys (*Lagothrix*) and its effect on their conservation

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Abstract

Woolly monkeys provide an example of the connection between conservation and taxonomy. Whether there is one woolly monkey genus (*Lagothrix*), or two (*Lagothrix* and *Oreonax*), has been debated over the last decade. The outcome of this debate is not only that there is one genus (*Lagothrix*), but also an emphasis on the need for, and influence of, taxonomy in conservation. By splitting genera or species, population figures decrease, stressing the need for action. To group genera or species, genetic diversity and phylogenetic past must be explored, promoting further research into the species. Either classification should promote conservation. The yellow-tailed woolly monkey (*Lagothrix flavicauda*) is an example of this process, as the academic debate surrounding its classification highlighted the need for recognition in conservation.The aim of this paper is to provide a background on the taxonomic history of the yellow-tailed woolly monkey and discuss the outcomes within a conservation context. By doing so, I suggest that the debate surrounding the taxonomy of the woolly monkeys promoted the publication of new papers documenting the species and encouraged new conservation programmes. The yellow-tailed woolly monkey is still a Critically Endangered species; now that there is a relative consensus on its genus, focus should be put on continuing conservation efforts.

Keywords

yellow-tailed, woolly monkey, *Oreonax*, *Lagothrix,* conservation, taxonomy

The yellow-tailed wooly monkey: *Oreonax* or *Lagothrix?*

The discourse of woolly monkey taxonomy provides an example of how both the process and the reason for establishing accurate taxonomy is key to understanding and conserving species. An effective process of species/genus determination is of profound importance to the efforts and effectiveness of conservation programs for endangered species. One species that has engendered debate in this area is the woolley monkey. Woolly monkeys are Platyrrhine (New World) frugivores of the family Atelidae. The genus contains few species, yet there has been much debate surrounding the taxonomy of the small group. Specimens were first presented in 1812 by von Humboldt, but the contemporary name for them did not come about until Fooden's research in 1963 which identified one distinct genus – *Lagothrix*. Groves (2001) challenged Fooden's interpretations and split the genus in two: *Oreonax* and *Lagothrix*. Yet, research conducted in the past seven years suggests that the split was unnecessary and that the woolly monkey genus should remain as only the one intial genus. Central to the debate is the yellow-tailed woolly monkey (*Lagothrix flavicauda*) which is particularly challenging to define due to its scarcity in the wild and the complication this poses for behavioural observation and access to specimens. Conservation is the main driving force behind this debate, as interested organisations need specific taxonomic conclusions so that they can be effective in their efforts to conserve species. The aims of this paper are to provide a summary of the taxonomic debate surrounding the yellow-tailed woolly monkey, and to connect this back to the species' conservation status in the wild.

The challenge of defining the genus and species of woolly monkeys speaks to the overall difficulties of defining taxonomic categories. The hierarchy of taxonomic categories is as follows (highest to lowest): Kingdom, Phylum, Class, Order, Family, Genus, and Species. Within these there are subcategories:

suborder, subspecies etc. The lower the taxonomic classification the harder it is to distinguish/define, as differences may be subtle. Furthermore, there is no one universal method used to differentiate these classifications, and the different methods are used depending on circumstances such as technology, funding, and subject availability/quality. When species are difficult to define, contention is also put on their genus, as genera are a group of species that are monophyletic and are phylogenetically similar (Groves 2002; Russell et al. 2013). It was not until the 1940s that a clear definition of species arose in the field of biology, even though before then the word was commonly used (Groves 2002). The problem of taxonomic categorisation lies in the fact that evolution, speciation, and genetic divergence are all continuously changing processes, whereas taxonomic categories are meant to be fixed. Thus, we are, in effect, attempting to attach a static concept to a moving target. Despite this, accurate taxonomy is essential to our ability to communicate our observation, investigation, research, analysis, and understanding of our natural world. It should also be expected that taxonomy will change with expanding knowledge, making categorisation of living things even more difficult.

While it is no doubt a complex process, guidelines to determine what a species is are still required. The Biological Species Concept (BSC), created by Mayr (1942:120), defined a species as '*a set of interbreeding individuals that are reproductively isolated from others*'. Put simply, reproductive incompatibility is the bases for this theory. There are issues with the BSC. For example it cannot be applied to asexual organisms or fossils. Furthermore, it also puts an emphasis on speciation caused by geographic separation, which does not account for other forms of speciation (e.g. allopatric speciation). Therefore there two main objections to the BSC—allopatric taxa do not fit the concept, and thus their categorisation becomes subjective, and sympatric taxa have been known to interbreed—undermine the concept of reproductive incompatibility (Groves 2012). An alternative method is the Phylogenetic Species Concept (PSC) (Cracraft 1983, 1997), which has many advantages over other species concepts (Groves 2002). The PSC defines a species as '*the smallest cluster of individual organisms within which there is a parental pattern of ancestry and descent*' (Groves 2002:1110) and must have a unique combination of characteristics, which are distinguishable from other clusters. The PSC relies on observable, fixed characteristics with no attachment to degree of difference or speculations about function, and allows for genetic analysis to determine cryptic species. While this concept is used by researchers for a variety different taxa (e.g. Groves and Grubb 2011; O'Leary et al. 2012), others criticise the method for being less objective than it claims to be, or for splitting species up unnecessarily (Isaac et al. 2004; Zachos 2015). Regardless of which species concept is used, phylogeny and genetic analysis are consistently relevant when categorising species.

The taxonomic debate of the yellow-tailed woolly monkey and the genus *Lagothrix* is symptomatic of the discourse surrounding the definition of species. *Lagothrix* contains four species and two subspecies all with varying coat colours (brown, copper, grey, and olive), but the genus share a black face and deep pink palms with dense, woolly fur (Fooden 1963; Groves 2001). Woolly monkeys inhabit many of the northern countries in South America, including Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela. In these forests the primates forage for fruits but will supplement their diet with leaves, seeds, and invertebrates (Di Fiore and Rodman 2001; Dew 2005). Conservation of this genera is of great importance, not only for the sake of the individual species, but to support tree prosperity as wooley monkeys are significant seed dispersers (Dew 2005; Levi and Peres 2013; González and Stevenson 2014). As woolly monkeys are larger in body size than other Neotropic primates, the genera may also be one of the few that can distribute large seeds, suggesting that some tree species may be solely reliant on wooley monkeys (González and Stevenson 2014).

The yellow-tailed woolly monkey has adapted to high altitudes by having denser fur relative to other woolly monkeys, which allows them to cope with the cooler environments in northeast Peru (Mittermeier et al. 1977; Shanee 2011). Adults of the species also have a yellow pelage at the end of their tail and a yellow pubic hair tuft (Fooden 1963; Mittermeier et al 1977; DeLuycker 2007). Furthermore, they participate in geophagy (the consumption of soil), which may help them avoid iron deficiency (Ferrari et al. 2008). They are larger-bodied than other woolly monkey species and have a slower life history relative to other New World species, making them more vulnerable to extinction. Within the last 12 years, the yellow-tailed woolly monkey has been listed on the Top 25 Most Endangered Primate Species In The World a total of three times, more than any other woolly monkey

(Mittermeier et al. 2006, 2009, 2012). While these things make the species distinct, none may be enough to conclude that the primate should be considered in a different genus. This begs the question as to why the species is involved in this debate.

Early research of yellow-tailed woolly monkeys was greatly limited by sample size, accessibility, and technology, resulting in inaccurate categorisation. Woolly monkeys live in cold, high-altitude environments and have small population sizes, making them difficult to access. Therefore, the majority of early research did not include living specimens. The yellow-tailed woolly monkey was first discovered by von Humboldt and Bonpland (1812). The findings were based on flattened skins that had been trimmed as poorly preserved saddle covers. As such, the species was incorrectly placed in the genus *Alouatta* (howler monkeys).

The next description of the the yellow-tailed woolly monkey was published by Thomas (1927a, 1927b). Thomas (1927b) compared the descriptions von Humboldt produced to his own museum specimens and considered them separate species, naming his discovery *Oreonax hendeei*. The specimens each man studied were found in the same region—where no other primates fitting the descriptions live—and, according to Fooden (1963), the descriptions of both sets of specimens are very similar. Consequently, Fooden combined the two and named the species *Lagothrix flavicauda*. It was not until the 2000s that further (notable) research was done on the elusive *Lagothrix flavicauda*, which unfortunately, also relied on museum samples.

Specimens in the American Museum of Natural History (AMNH) provided further insights into the woolly monkey genus that have since been contended. In 2001, Groves published *Primate Taxonomy*, within which he reflected upon many primate taxa and overall taxonomic thinking. Possibly because it was so revolutionary, the book has been scrutinised heavily ever since. In the book, Groves revisits *Lagothrix*, specifically *Lagothrix flavicauda* (yellow-tailed woolly monkey). He performed a parsimony analysis of cranial characters using Phylogenetic Analysis Under Parsimony (PAUP) on many museum specimens. This method looks at the evolutionary relationships between groups of organisms and seeks the hypothesis that requires the fewest evolutionary changes. PAUP compliments the PSC, which seeks to find the smallest cluster of organisms sharing an ancestry pattern to group as a species. The particular species of *Lagothrix* used by Groves were *L. flavicauda* and *L. lagotricha*. Aside from the two woolly monkey species, no other species names were given and were instead picked at random from the museum's collection (Groves 2001).

The two woolly monkeys species were compared to specimens of other genera within the Atelidae family: *Alouatta, Ateles*, and *Brachyteles*. Groves (2001) found that *L. flavicauda* is more closely linked with the genus *Ateles*, not *Lagothrix,* and therefore cannot be considered monophyletic with other species in the woolly monkey genus. He concluded that because of this, *L. flavicauda* should be in its own genus, and reinstated the genus *Oreonax*, founded by Thomas (1927a). Thus Groves renamed the yellow-tailed woolly monkey *Oreonax flavicauda*, raising the rank from subspecies to separate genus. This was initially well supported (e.g. Rosenberger et al. 1996; Rylands 2000), yet within the last seven years it has been strongly contested.

From 2008 the argument for yellow-tailed woolly monkeys to be considered *Oreonax flavicauda*—instead of *Lagothrix flavicauda*—has been systematically undone using PAUP and larger, more diverse sample groups. Many taxonomists now conclude that *Lagothrix flavicauda* is the most accurate scientific name for the yellow-tailed woolly monkey (Mathews and Rosenberger 2008; Ruiz-García et al. 2014; Botero et al. 2015; Di Fiore et al. 2015). Mathews and Rosenberger (2008) recreated Groves' analysis with samples from the AMNH as well as the British Natural History Museum. Unlike Groves' analysis, which only used two *Lagothrix* species, Mathews and Rosenberger used all the species within the *Lagothrix* genus (*L. lagotricha, L. cana, L. lugens, L. poeppigii,* and, of course, *L. flavicauda*) and attempted to use a female and male for each species. Mathews and Rosenberger (2008) deviated from the method of analysis in a few more ways. For example, the weighing of some of the characteristics was lessened because not all characteristics were considered independent of each other (Mathews and Rosenberger 2008). The authors found that when certain taxa were used (*Alouatta seniculus* and *Lagothrix lagotricha*) the results of Groves' (2001) study could be supported. Yet, when all available samples of the *Lagothrix* genus were incorporated, the application of the genus *Oreonax* becomes

unsupported. The authors argue that if *Oreonax* is supported as its own genus, new genera would have to be added for species *L. cana* and *L. poeppigii*, as they were as genetically different to each other as they were to *L. flavicauda*. Thus, they concluded that a limited selection of taxa may have skewed the results of previous studies. Moreover, they conclude there is little evidence that suggests that *L. flavicauda* should be split at the genus level. Mathews and Rosenberger's (2008) stance on the *L. flavicauda* debate has since been supported by more than cranial morphology, with current researchers using molecular-based analysis.

Molecular analysis of all species considered *Lagothrix* have been included in three independent studies within the last four years, and have concluded that *L. flavicauda* should not be separated into the genus *Oreonax*. Ruiz-García et al. (2014) sequenced COI and COII mitochondrial genes of 141 woolly monkeys. Through genetic distance and phylogenetic analyses, evidence of genetic introgression and recent hybridisation was found. It was concluded that molecular results verified *L. flavicauda* instead of *O. flavicauda*. Furthermore, Di Fiore et al. (2015) found, after relative evaluation of the cyto-chrome oxidase subunit 2 (COX2) gene displays, that any genetic distance between *L. flavicauda* and the other *Lagothrix* taxa—regardless of geographic distribution—is completely within the normal range of species-species divergences. It was also found that *L. flavicauda* separated from other *Lagothrix* during the Pleistocene, 6.5 million years after the separation of *Lagothrix* and its closest genus, *Brachyteles*. From the point of taxa, Di Fiore et al. (2015) suggest that *Oreonax* may be seen as synonymous with *Lagothrix*. Regarding the difficulties associated with research pertaining to species of vastly reduced numbers living in remote habitats, Di Fiore et al. (2015) recognised the difficulty in collecting samples of yellow-tailed woolly monkeys and noted that with the opportunity for a larger research sample further evidence could arise to contradict their conclusion that there is only one woolly monkey genus: *Lagothrix*. Regardless, the most recent molecular research appears to end the ongoing woolly monkey genus debate (Table 7.1), confirming that there is only one genus of woolly monkey in family Atelidae.

Table 7.1: Summarising the chronology of taxonomy of the yellow-tailed woolly monkey

Year	Author(s)	Summary
1812	von Humboldt	Method: Analysed trimmed skins that had been used as saddle covers Conclusions: Skins are from a new species of howler monkey, and named the species *Simia flavicauda*
1927	Thomas (a,b)	Method: Analysed skins in better condition Conclusions: Considered them a different species to von Humboldt's specimens and renamed the species *Oreonax hendeei*
1963	Fooden	Method: Analysed many museum specimens and compared previous papers Conclusions: *Simia flavicauda* and *Oreanax hendeei* are a single species, and re-renamed the species as *Lagothrix flavicauda*
2001	Groves	Method: Analysed many museum specimens, specifically cranial characters Conclusions: *L. flavicauda* is more closely linked with *Ateles* than other species in the genus are, therefore *L. flavicauda* is not monophyletic with the genus and needs to be in a genus of their own: *Oreonax flavicauda*
2008	Mathews and Rosenberger	Method: Replicated Groves' results with bigger sample size Conclusions: *Oreonax* is not different from *Lagothrix*. The yellow-tailed woolly monkey is reinstated with the name *Lagothrix flavicauda*
2014	Ruiz-García et al.	Method: Molecular analysis of *L. flavicauda* and other woolly monkey species Conclusions: Confirms *Lagothrix flavicauda* most accurate
2015	Di Fiore et al.	Method: Molecular analysis of *L. flavicauda* and other woolly monkey species Conclusion: Genetic distance between *L. flavicauda* and other woolly monkeys falls within the normal range for species

Defining what makes a species is becoming even more important and urgent as the rate of habitat loss is increasing and the majority of primate species are in decline (Estrada et al. 2017). As conservation resources are limited it is crucial that the correct categorisation are in place on which to take action. Organisations such as the International Union for Conservation of Nature (IUCN) and the Worldwide Fund for Nature require accurate nomenclature criteria to determine species at risk (Zachos et al. 2013). Therefore, the defining of species and genera has become an issue of fundamental importance at the

heart of our attempts to preserve our biodiversity. This is a particularly key for the yellow-tailed woolly monkey.

Since 1981, there has been an approximate 46–93% decrease in population size of yellow-tailed woolly monkey (Shanee and Shanee 2014). In the previously mentioned analysis done by Ruiz-García et al. (2014), it was found that of all the species in the genus *Lagothrix*, *L. poeppigii* and *L. lugens* have the highest levels of genetic diversity, *L. lagotricha* and *L. cana* have moderate levels, and *L. flavicauda* has the lowest level (at zero). Considering this, it is unsurprising that *L. flavicauda* has been classified as Critically Endangered by the IUCN since 1996 (Cornejo et al. 2008). Yellow-tailed woolly monkeys are primarily threatened by deforestation, however, commercial and subsistence hunting, the pet trade, human development, and resource extraction all contribute to the species Critically Endangered status (DeLuycker 2007; Cornejo et al. 2008; Shanee 2011, 2012; Shanee and Shanee 2014). The most effective method of conserving the species would be protecting the remaining habitat and connecting fragments to allow for interbreeding between groups, as well as community conservation programmes and management of illegal hunting (Di Fiore et al. 2015; Shanee and Shanee 2015).

Whether it is classified as a species or a separate genus, the yellow-tailed woolly monkey is still listed as Critically Endangered by the IUCN and conservation efforts are imperative. After the change in genus implemented in the early 2000s, and their subsequent placement on the Top 25 Most Endangered Primate Species List (first appearance was in 2006), there was an increase in the conservation efforts and research outputs for the yellow-tailed woolly monkey. Shanee and Shanee (2015) published a paper about an encouraging case study from a farming community in the Amazonas region. Yambrasbamba, a community conservation project, was established in 2007 (just after the species was put on the Top 25 list) to control hunting and deforestation in the area. Between 2008/9 and 2012/13 surveys of the area have shown a natural increase in the yellow-tailed woolly monkey population (Shanee and Shanee 2015). Furthermore, there has been a marked increase in research output since the genus was split and placed on the Top 25 list (Figure 7.1), which is impressive for a species that is considered hard-to-reach and underresearched in most areas (Aquino et al. 2015). Whether or not it is considered its own genus, the yellow-tailed woolly monkey requires human intervention to avoid extinction, and recognition due to taxonomy has helped the species survive.

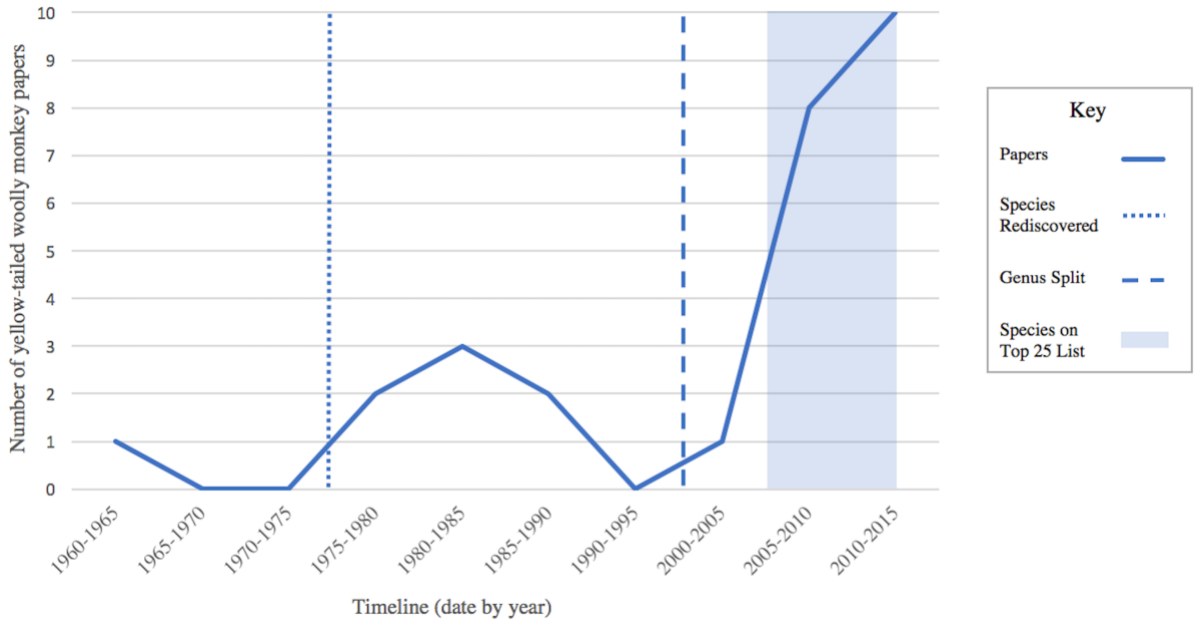

Figure 7.1: Timeline of yellow-tailed woolly monkey research publications.

Sources: Papers used are limited to those with *Oreonax flavicauda* or *Lagothrix flavicauda* in their titles (Fooden 1963; Mittermeier et al. 1977; de Macedo Ruiz and Mittermeier 1979; Leo Luna 1980, 1982, 1984, 1987, 1989; Groves 2001; DeLuycker 2007; Maldonado et al. 2007; Shanee et al. 2007; Cornejo 2008; Cornejo et al. 2008; Shanee et al. 2008; Buckingham and Shanee 2009; Clark 2009; Botero et al. 2010; Shanee 2011; Shanee and Shanee 2011: Chaves et al. 2012; Ruiz-García et al. 2014; Shanee 2014; Shanee and Shanee 2014; Di Fiore et al. 2015; Shanee and Shanee 2015).

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