

Protein Limitation Explains Variation in Primate Colour Vision Phenotypes: A Unified Model for the Evolution of Primate Trichromatic Vision

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1. Introduction

Primate colour vision has intrigued scientists for many decades and will likely continue to do so for the foreseeable future. Primates are the most visually adapted order of mammals and a considerable proportion of their large brain size is devoted to processing visual information (e.g. Barton, 2006). Most eutherian mammals have dichromatic (two-colour) vision, and chromatic distinctions are based on discriminating relatively shorter from relatively longer wavelengths within the visual spectrum (~400-700nm). These distinctions are made by neural comparison of cone cells possessing short (S) wavelength-sensitive photopigments, which are maximally sensitive to bluish light, and long (L) wavelength-sensitive pigments, which are maximally sensitive to greenish light. These photopigments are encoded by an autosomal S opsin gene and an X-chromosomal L opsin gene respectively. Primates have an additional colour channel enabling trichromatic vision via a duplication and divergence of the L opsin gene, resulting in long and middle (L-M) wavelength-sensitive photopigments (reviewed in Hunt et al., 2009; Regan et al., 2001). This arrangement permits enhanced discrimination of light and perception of different shades of green, yellow, orange and red.

Old World monkeys, apes and humans are routinely trichromatic, having two loci for L-M opsin genes on each X-chromosome due to a gene duplication event (Jacobs, 2008), in addition to the autosomal S opsin locus. Alternatively, New World monkeys and some lemurs exhibit polymorphic trichromacy (Jacobs, 2007; Tan & Li, 1999; Tan et al., 2005; Veilleux & Bolnick, 2009). This alternate path to trichromacy results from a genetic polymorphism at a single locus of the X-chromosomal L-M opsin gene. Females with two different L-M opsin genes, combined with the common autosomal S opsin gene, possess trichromacy (Mollon et al., 1984). However, males, being hemizygotes, can inherit only one L-M opsin gene and are always dichromatic; homozygous females are also dichromatic. Variation in primate trichromacy and the selective pressures that led to trichromacy are under considerable debate (Caine et al., 2010).

In order to evaluate routine and polymorphic trichromacy in primates within an evolutionary framework, it is necessary to review the behavioural, experimental, genetic, biogeographical and ecological evidence pertaining to primate trichromacy. We focus this review on the evidence for and against foraging hypotheses because the vast majority of research to date evaluates and supports the utility of trichromacy for finding and selecting food. We begin with an overview of the fruit foraging and the young leaf hypotheses. We additionally introduce a new hypothesis - that both routine and polymorphic trichromacy confer a selective advantage to primates in the detection and selection of proteinaceous foods (either leaves or fruit), and present evidence for *Ficus* (Moraceae) as a protein source for neotropical primates. To explain the foundation for this new hypothesis, we review primate foraging patterns on *Ficus*, and discuss the abundance and density of *Ficus* in African and neotropical forests.

2. The frugivory hypothesis

The oldest hypothesis for the evolution of primate colour vision is that trichromacy is an adaptation to frugivory (Allen, 1879; Polyak, 1957). This hypothesis builds on the observation that most primates rely heavily on dietary fruit (Chapman & Onderdonk, 1998; Fleagle, 1999). Given that many tropical plants produce red, orange or yellowish ("colourful") fruits and that trichromatic colour vision enhances primates' abilities to detect these colours amidst green foliage and unripe fruits, trichromatic colour vision should facilitate the detection and selection of edible fruits (Regan et al., 2001). Primates in turn may provide high-quality seed dispersal services to these fruiting plants (Garber & Lambert, 1998). The ability to distinguish between ripe and unripe fruits, fruits from leaves, and edible from inedible species is a complex task that could be facilitated by trichromacy (Smith et al., 2003), and there is compelling experimental and behavioural evidence for trichromatic advantages in these tasks.

The frugivory hypothesis was originally proposed and tested for catarrhine primates (Sumner & Mollon, 2000b) because until relatively recently platyrrhines (Mollon et al., 1984) and strepsirrhines (Tan & Li, 1999) were not known to possess trichromacy. The frugivory hypothesis has since been extended to platyrrhines and tested behaviourally (Caine et al., 2003). Theoretical studies have also assessed the conspicuity of dietary fruits to trichromatic versus dichromatic platyrrhines (Riba-Hernández et al., 2005; Stoner et al., 2005). Research evaluating the frugivory hypothesis is reviewed briefly below.

Tropical fruits exhibiting a "primate dispersal syndrome" (medium-sized red, orange or yellow fruits with succulent pulp, large seeds, tough exocarps; (Gautier-Hion et al., 1985)) have been found to occupy a narrow region of colour space that is detectable to trichromatic platyrrhines (Regan et al., 2001). Furthermore, the reflectance spectra of most primate-consumed fruits in Uganda were found to show chromatic changes as they ripen, and trichromatic catarrhines should be well adapted to discriminate fruit ripeness (Sumner and Mollon, 2000b). In the New World, the peak spectral sensitivities of trichromatic platyrrhine cone pigments were found to be well suited to the detection of fruits against a background of leaves under photopic conditions (Regan et al., 2001). The spectral tuning of the L-M cone pigments in the trichromatic platyrrhine *Alouatta seniculus* (Linnaeus, 1766) was found to be optimal for detecting ripe fruits against a background of leaf "noise" (Regan et al., 1998). Among six phenotypes in one white-faced capuchin

(*Cebus capucinus*, Linnaeus, 1758) population, monkeys possessing the phenotype with the most spectrally separated L-M opsin alleles showed the highest acceptance index for red fruits (Melin et al., 2009). For this same population of capuchin monkeys, colourful fruits comprise 60% of the diet and are preferred to cryptically coloured fruits (Melin, 2011).

Trichromatic vision may also afford a selective advantage by allowing trichromats to forage on fruit under a greater range of light conditions than dichromats (Yamashita et al., 2005). In two species of *Saguinus* (Hoffmannsegg, 1807), captive trichromatic individuals were more efficient than dichromats at selecting ripe fruits, both in isolation and against a background of leaves (Smith et al., 2003). In a study linking nutritional value to fruit colouration, Riba-Hernandez et al. (2005) have provided additional support for this hypothesis. Arguing that the principle reward of ripe fruits is sugar, these authors demonstrated a positive correlation between fruit glucose content and the red-green colour channel of spider monkeys (*Ateles geoffroyi*, Kuhl, 1820).

In summary, the evidence for a ripe fruit foraging advantage for trichromats is compelling. Behavioural evidence for ripe fruit foraging advantages in wild and captive trichromats, the trichromat-accessible colour space of tropical fruits, the dietary importance of colourful fruits, and a positive correlation between nutritional value and fruit colouration all indicate that a ripe fruit foraging advantage may indeed result in the evolution and persistence of trichromacy. However, the frugivory hypothesis is problematic on several accounts. In the sections below, we review problems with the frugivory hypothesis and alternate hypotheses regarding the evolution of trichromacy.

2.1 Problems with the frugivory hypothesis

There is compelling empirical evidence that trichromacy is not necessary for detection of ripe fruits. Dominy and Lucas (2001) found that four routinely trichromatic catarrhine species in Uganda did not choose fruit on the basis of chromaticity, and that consumed fruits did not differ in chromaticity from unconsumed fruits. Comparing routinely trichromatic *Alouatta palliata* (Gray, 1849) fruit choices with polymorphically trichromatic *Ateles geoffroyi* in Costa Rica, Stoner et al. (2005) found that, contrary to expectations of a fruit foraging advantage for trichromats, the polymorphic *Ateles* consumed reddish fruits more often while routinely trichromatic *Alouatta* concentrated primarily on green fruits. Further studies of wild primates have also demonstrated that trichromats do not feed on brightly coloured fruits at faster rates than dichromats (Hiramatsu et al., 2008; Vogel et al., 2007). Additionally many fruits that are consumed and dispersed by primates are dull, and green or brown (Janson, 1983; Link & Stevenson, 2004), colours that can be detected through the blue-yellow colour channel of the dichromat (Dominy & Lucas, 2001). Intriguingly, the only genus of routinely trichromatic platyrrhine, *Alouatta*, is not a frugivore, but a folivore (Araújo et al., 2008; Jacobs et al., 1996).

3. The young leaf hypothesis

Many frugivorous primates, and specifically catarrhines, rely on leaves as fallback foods during periods of habitat-wide fruit scarcity (Lucas et al., 2003). Building on this observation, Dominy and Lucas (2001) argued that it is the ability to distinguish young

leaves from mature leaves, rather than the ability to distinguish ripe fruits, that provided the selective force behind routine trichromacy. Measuring the luminance of young leaves and fruit consumed by catarrhines in Kibale, Uganda they found that while fruits could be reliably distinguished by the yellow-blue colour channels alone, the detection of young, proteinaceous leaves required the red-green colour channel of the trichromat. They additionally demonstrate that red-greenness of young leaves is positively correlated with the ratio of protein content to toughness. These observations formed the basis for the hypothesis that the evolution of both the routine trichromacy of catarrhines and the polymorphic trichromacy of platyrrhines results from the ability to detect fallback foods (Dominy et al., 2003).

Dominy et al. (2003) hypothesize that the evolution of routine trichromacy in catarrhines is the result of selection for colour vision that allows for the detection of fallback foods that sustain catarrhine populations during periods of low overall fruit availability¹. In the case of catarrhines, trichromacy thus evolved as a means of detecting young, red leaves as fallback foods. Fallback foods have been operationally defined as “items assumed to be of relatively poor nutritional quality and high abundance, eaten particularly during periods when preferred foods are scarce” (Marshall & Wrangham, 2007, p. 1220). Dominy et al. (2003) posit that climatic cooling at the end of the Eocene resulted in the local extinction or decimation of figs and palms which led catarrhines to “fall back” on leaf resources in periods of low fruit availability. In the neotropics, where figs and palms remain abundant, platyrrhines have evolved mixed capabilities for the detection of these cryptic fallback resources.

Young leaves in the Old World are often red (Dominy et al., 2002). An estimated 50-62% of Old World species display red young leaf flush, compared to only 18-36% of New World species (Dominy & Lucas, 2001). The redness of young leaves results from delayed greening wherein plants postpone chloroplast function until full leaf expansion (Dominy & Lucas, 2001), coupled with the presence of anthocyanin pigment (Lee et al. 1987) which has several potential selective advantages to plants. Advantages to plants include fungicidal properties, photoprotection against UV damage of new leaves, the prevention of photoinhibition, and crypsis to protect against dichromatic herbivores (Coley & Aide, 1989; Gould et al., 1995; Stone, 1979). In a review of the evidence for and against these hypotheses, Dominy et al. (2003) conclude that crypsis is the most plausible, and that young leaf reddening is thus a plant strategy to reduce new leaf damage by herbivores. Providing evidence from the colour space occupied by young leaves, Dominy et al. (2002) conclude that to a dichromatic herbivore a young, red leaf would appear dark, dead, and not worth consuming. In Old World forests where young leaf flush coincides with low fruit availability, the ability to detect these important fallback foods would provide a clear advantage favoring trichromacy (Dominy & Lucas, 2001).

¹ Though Dominy et al. (2003) use the term “keystone resources” to refer to young leaves and figs, they define these as “resources (that) sustain frugivore populations during crucial periods” and that “consistently provide food during community-wide periods of fruit dearth” (p. 27). Keystone resources are more commonly defined as preferred resources (Terborgh, 1986). Dominy et al.’s (2003) definition is more commonly applied to foods that are considered “fallback foods” (Marshall & Wrangham, 2007) and as such we use that term here.

4. The protein limitation hypothesis

Trichromacy is useful for visually detecting long-wavelength colours of food targets against a green mature leafy background, whether the food targets are young red leaves or ripe fruits. The debate regarding whether frugivory or folivory has favored trichromacy continues. Both sides are supported and perhaps both the frugivory and the folivory hypotheses are partially correct. Here we present a new hypothesis that builds on both the frugivory and the young leaf hypotheses. We suggest that trichromacy is adaptive for finding a limiting resource critical to primates - protein. We further suggest that selective pressures may vary between catarrhine and platyrrhine primates based on food availability and body size constraints. Specifically, while protein sources for Old World primates are predominantly red leaves, among New World primates, they are red figs. Below we outline the basis for our unifying protein limitation hypothesis by reviewing the evidence that protein is a crucial limiting resource and the evidence that red figs provide a consistent and favored source of protein for New World primates and that trichromats have a foraging advantage on these fruits.

4.1 Protein as a limiting resource to frugivorous primates

Liebig's Law of the Minimum states that the functioning of a given organism is controlled (or limited) by an environmental factor or combination of factors present in the least favorable amount (Taylor, 1934). Since its definition, limiting resources have been shown to have profound effects on a wide array of species (Interlandi & Kilham, 2001). For primates that rely on ripe fruit as a dietary staple, that limiting factor is protein (Ganzhorn et al., 2009). Fruits are not considered to be sufficiently high in protein to meet the nutritional needs of primates (Kay, 1984; Milton, 1979; Oftedal, 1991), without supplementation from either leaves (in large bodied primates) or insects (in small bodied primates) (Fleagle, 1999). Obligate frugivores should feed on proteinaceous fruits whenever available, whereas facultative frugivores can supplement fruits with insects, seeds and leaves (Kunz & Diaz, 1995; Snow, 1981). Models of the evolution of primate diversity have identified the importance of the constraints of protein availability (Milton, 1979). The biomass of folivorous primates has been linked to nitrogen: fiber ratios of leaves in forests indicating a profound effect of protein availability on folivores (Chapman et al., 2004; Ganzhorn, 1992). Likewise in frugivores, protein as well as mineral content have been identified as factors influencing dietary selectivity (Barclay, 1995; Felton et al., 2009; Kunz & Diaz, 1995; O'Brien et al., 1998; Thomas, 1984; Wendeln et al., 2000). Further evidence for the importance of protein comes from nutritional analyses of fruits consumed by spider monkeys (*Ateles chamek*, Humboldt, 1812). Spider monkeys were found to regulate their daily protein intake much more tightly than either carbohydrates or fats, and their protein intake did not vary across seasons regardless of fluctuations in food availability (Felton et al., 2009).

Taken together, there is compelling evidence that protein is a limiting resource for primates. We suggest that acquisition of protein can provide a unified explanation of the adaptiveness of trichromacy. Protein acquisition by Old World monkeys and apes is facilitated by trichromacy via improved search efficiency for young, proteinaceous red leaves (after Dominy & Lucas, 2001). However, platyrrhines generally consume far fewer leaves than catarrhines (Dominy and Lucas, 2001). Given the general lack of leaf consumption by frugivorous platyrrhines and the abundance of proteinaceous figs in the neotropics, *Ficus*

plants are a strong candidate for helping to meet the protein requirements of platyrrhines. For the smaller bodied, less folivorous neotropical primates, we suggest that improved foraging efficiency for red, proteinaceous figs favors trichromacy. In New World tropical forests primates prefer feeding on figs over other ripe fruits (Felton et al., 2009; Melin et al., 2009; Parr et al., In Press) and polymorphic trichromacy is the rule for all but one monochromatic nocturnal genus (*Aotus*, Gray, 1870), and one routinely trichromatic folivorous genus (*Alouatta*, Gray, 1849) (Jacobs, 2008). Following previous research, we submit that this may be maintained by heterozygote advantage (Hedrick, 2007) to trichromatic females via an increased ability to detect ripe fruits (Osorio et al., 2004; Osorio & Vorobyev, 1996; Smith et al., 2003; Sumner & Mollon, 2000a; Surridge et al., 2003). However, we emphasize that the primary advantage lies in the detection of conspicuous figs, which differ from other fruits in their high protein content. Our hypothesis differs from previous ideas concerning fruit foraging, which suppose fruit sugars are the primary reward. We suggest that protein, relatively abundant in figs, is the primary element favoring trichromacy.

In a comprehensive review of paleogeographic and biogeographic evidence for the dearth of *Ficus* plants in the Old World, Dominy et al. (2003) posit that climatic cooling at the end of the Eocene resulted in the local extinction or decimation of cryptically coloured (greenish-brownish), relatively nutritionally poor fruits of figs and palms in the Old World. They suggest that where figs and palms remain abundant in the neotropics, platyrrhine polymorphism (as opposed to routine trichromacy) is adaptive because dichromacy is suitable for the detection of these cryptic fallback resources. The hypothesis is compelling, elegant and has received empirical support. Additionally, recent studies have corroborated the importance of fallback foods in the evolution of primate traits (Lambert et al., 2004). However, we suggest that two components require a closer look: 1) the role of figs in the foraging decisions of platyrrhines, and 2) the nutritional value of figs as a key source of protein. Here, we suggest that properly identifying the role of *Ficus* species allows for an ecological refinement of the young leaf hypothesis. Rather than figs as fallback resources, as they may be for Old World primates such as orangutans (Marshall et al., 2009) we propose that at least some species (i.e those producing red fruits) are preferred and limiting resources to neotropical primates.

In the sections below, we present evidence for the nutritional value of fruits of the genus *Ficus*, behavioural evidence of primate feeding preference for *Ficus*, and comparative abundance data for *Ficus* in Africa and the neotropics. We additionally review behavioural and molecular evidence for the adaptive value of primate dichromacy and trichromacy, and the balancing selection that might serve to maintain polymorphic trichromacy.

4.2 *Ficus* as protein

There are approximately 750 extant species of the genus *Ficus* which together constitute one of the most distinctive and peculiar genera of tropical flora in the world (Shanahan et al., 2001). The unique complex obligatory mutualism between *Ficus* species and pollinating agaonid fig wasps results in a universal pattern of asynchronous and unpredictable mast fruiting events (Janzen, 1979). Fruits of the genus *Ficus* are not in fact strictly fruits, but syconia, or inflorescences. Syconia are clusters of multiple flowers used in pollination, and

bundled together in a single package with thousands of miniscule seeds (Janzen, 1979). These inflorescences are entered by one or more species-specific pollinating agaonid fig wasps through an ostiole in the pericarp. Wasps pollinate the florets inside the fruit as well as laying a single egg in each of the ovaries. Wasp larvae live inside the seed coat and eat developing seeds. A month or so later, wingless male wasps emerge from seed coats and mate with females through holes they have cut in the sides of ovaries. Developed female wasps are dependent upon males for this service, and where males fail to cut holes in the sides of *Ficus* ovaries, females remain trapped in their larval home. In addition to these mutualists, numerous species of parasitic Hymenoptera have been discovered. These species oviposit through the wall of the unripe fig without providing pollination services (Janzen, 1979).

The mutualism between figs and wasps, and its interruption by parasitic ovipositing Hymenoptera render the fig syconia (which we shall hereafter refer to as fruit) a bundle of protein-rich insects and larvae. Not only can grown female wasps become trapped inside of ovaries, but at some times of year parasitic larvae become so numerous that hundreds of fig fruits are eaten hollow and found completely filled with larvae (Janzen, 1979). In addition to wasp larvae, fig fruits can contain several other arthropod species, including mites, dipterans and nematodes (Frank, 1989). One analysis of a neotropical *Ficus* species found that animal matter from insects contributed 2.9% to fig dry matter, increasing protein content by 15.3% (Urquiza-Haas et al., 2008).

In addition to the presence of protein-rich insects, there is evidence of unique nutritional qualities of the actual fig fruits themselves. Many authors have referred to figs as low quality foods (Bronstein & Hoffman, 1987; Herbst, 1986; Jordano, 1983; Lambert, 1989). However, overall, nutritional analyses of tropical figs indicate that fig fruits contain moderate-to-high levels of protein relative to other fruits and relative to frugivore protein requirements (Conklin & Wrangham, 1994; Dierenfeld et al., 2002; Ganzhorn, 1988; Ganzhorn et al., 2009; Goodman et al., 1997; Kendrick et al., 2009; Molloy & Hart, 2002; O'Brien et al., 1998; Rogers et al., 1990; Wendeln et al., 2000). In one study, African fig fruits - without supplementation - were found to provide an acceptable baseline level of protein (Conklin & Wrangham, 1994). Neotropical figs may have nutritional value adequate to sustain at least some frugivores without additional food (Wendeln et al., 2000). A study of two neotropical *Ficus* species found they contained 4.5% - 6.1% (dry weight) protein, which is 2-3 times higher than that of a sympatric neotropical angiosperm, *Spondias mombin* (Anacardiaceae), and are more nutritionally balanced with higher protein:TNC and lipid ratios than sympatric species (Hladik et al., 1971). Evidence for the nutritionally balanced nature of figs is further indicated by the fact that some species of bat subsist entirely on certain *Ficus* species (Janzen, 1979; Wendeln et al., 2000) and capuchin monkeys decrease time spent foraging for insects, their primary protein source, on days they visit figs (Parr et al., In Press). Comparison of protein content (as proxied by percent nitrogen) of New World and Malagasy figs indicates that neotropical fruits contain enough protein to satisfy the needs of primates (7-11% protein, 1.1- 1.8% nitrogen), while those in Madagascar do not (Ganzhorn et al., 2009). Figs, then, might be well identified as important sources of protein for New World frugivorous primates. In order to determine the possible extent of this importance, it is necessary to review not only the nutritional value of figs, but also primate feeding patterns.

4.3 Who eats figs?

The concise answer to the question of who eats figs was offered by Daniel Janzen (1979): "Everybody." Indeed, figs are notable for the number of bird and mammal species that consume their fruits and they comprise a part of the diet for more species of animal than any other genus of wild tropical perennial fruit (Janzen, 1979). In this section, we focus on the role of figs in the diet and feeding ecology of platyrrhines.

A review of the literature on neotropical primates reveals that all diurnal frugivorous genera with a body mass exceeding Kay's 500g threshold (Fleagle, 1999) include figs in their diet to varying extents, with the exception of uakari monkeys of the genus *Cacajao* (Mivart, 1865) for which dietary information is scant (Boubli, 1999). Tamarins (*Saguinus* species) and marmosets (*Callithrix kuhlii*, Coimbra-Filho, 1985) have been found to include a variety of fig species in their diet across sites (Knogge et al., 2003; Raboy et al., 2008; Terborgh, 1983). Three of the four *Ficus* species present at a Brazilian site are included in the 55 "extremely valuable" species consumed by golden-lion tamarins (*Leontopithecus chrysomelas*, Kuhl, 1820) (Oliveira et al., 2009). The seventh most frequently consumed fruit of black titi monkeys (*Callicebus torquatus lugens*, Hoffmannsegg, 1807) in Columbia was the single species *Ficus mathewsii* (Palacios et al., 1997). At five different sites in South America (Yasuni, Caparu, Urucu, Tinigua and Pacaya) figs were one of the top seven genera consumed by woolly monkeys (*Lagothrix lagotricha*, Humboldt, 1812) at each site (di Fiore, 2004). In Cocha Cashu, Peru, brown capuchin monkeys (*Cebus apella*, Linnaeus, 1758) were found to eat figs whenever they were available, and South American squirrel monkeys (*Saimiri sciurius*, Linnaeus, 1758) and white-fronted capuchin monkeys (*Cebus albifrons*, Humboldt, 1812) concentrated feasting on figs whenever they were available (Terborgh, 1983). White-faced capuchins (*Cebus capucinus*) in Santa Rosa, Costa Rica prefer figs over all other ripe fruits, and concentrate their foraging efforts on *Ficus* whenever available, regardless of the presence and abundance of other ripe fruits in their habitat (Melin et al., 2009). Figs comprised nearly one-third of capuchin annual fruit foraging effort which represents over-selection relative to fig abundance (Melin et al., 2009). For black-faced spider monkeys (*Ateles chamek*) in the Guarayos Forest Reserve in Bolivia, the preference for figs relative to all other ripe fruits is striking, and when combined with data on habitat-wide fruit availability indicates that "spider monkeys consumed a diverse array of ripe fruits to overcome periods of fig scarcity rather than vice versa" (Felton et al., 2009). Even species that are considered to be folivorous show a preference for *Ficus* fruits. One study of Mexican howler monkeys (*Alouatta palliata mexicana*, Merriam, 1902) found that six *Ficus* species were amongst the eight most important species consumed at one site in Veracruz, Mexico (Serio-Silva et al., 2002). Diurnal frugivorous and folivorous neotropical primates thus all eat figs to a greater or lesser extent, with some species showing an unequivocal preference for them even during periods of high habitat wide fruit availability. The feeding ecology of platyrrhines, coupled with preliminary evidence for the protein content of neotropical figs indicate that rather than viewing figs as a fallback foods in times of habitat-wide fruit scarcity (Dominy et al., 2003; Shanahan et al., 2001) it may be more appropriate to view them as important, preferred and limiting resources.

4.4 The relative abundance of *Ficus* species in Africa and the Neotropics

In order for figs to be a more important source of protein for New World monkeys vis-à-vis catarrhines, it is necessary to demonstrate that figs are abundantly present in the neotropics

relative to Old World forests. Fig abundance is especially salient given its asynchronous and unpredictable fruiting phenology (Janzen, 1979). We reviewed a worldwide database of plant species abundance maintained by the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute (STRI) as well as our own data and published species abundance data to test the prediction that *Ficus* is more abundant in the neotropics than in Africa. Using the online database maintained by STRI, we counted the number of *Ficus* species and the number of individuals of each species recorded during the most recent census of each forest plot in Africa and in the neotropics for which data are currently available (N=3 African plots and 5 neotropical plots). A search of tree abundance literature uncovered three additional datasets containing information on *Ficus* abundance: one from Budongo Forest Reserve in Uganda (Tweheyo & Babweteera, 2007), one from Agaltepec Island in Mexico (Serio-Silva et al., 2002), and one from Santa Rosa National Park, Costa Rica (Parr et al., In Press).

In all plots censused by STRI all *Ficus* individuals >10cm diameter at breast height (DBH) were recorded. In the Budongo Forest Reserve in Uganda all *Ficus* trees >4cm DBH were recorded, and as such abundance data are overestimated. In the Agaltepec Island plot all *Ficus* trees >30cm DBH were recorded, and as such abundance data may be an underestimate. Parr et al. (In Press) recorded all *Ficus* trees >10cm DBH encountered in a transect survey of Sector Santa Rosa, Costa Rica.

Fig species are both more diverse and abundant in the New World relative to the Old World (Table 1). In the African plots *Ficus* species diversity ranges from two to four species per plot (N=70 trees, 114 hectares, 4 plots), with a mean number of 0.73 *Ficus* trees per hectare (range = 0.06 - 2.45). In the neotropical plots *Ficus* species diversity ranges from three to 12 species per plot (N = 458 trees, 145.96 hectares, 7 plots), with a mean number of 3.89 *Ficus* trees per hectare (range = 0.5 - 11.56). While the sample size is inappropriate for a statistical analysis of *Ficus* abundance data, the pattern in the data is clear. Figs are both more speciose and abundant in the neotropical plots relative to the African plots. This pattern holds despite one of the four African plot values representing an abundance overestimate (Budongo Forest Reserve, Uganda), and one of the six neotropical plot abundance values representing an underestimate (Agaltepec Island, Mexico). Removing the overestimated abundance data from Budongo Forest Reserve, the *Ficus* abundance in the remaining three African plots never meets or exceeds the abundance of the most *Ficus*-poor neotropical plot (Sherman, Panama, 0.5 individuals per hectare). This dataset supports the prediction of relatively high abundance of neotropical figs relative to African figs that has been noted elsewhere (Gautier-Hion & Michaloud, 1989; Shanahan et al., 2001).

4.5 Fig foraging

Colour vision polymorphism has persisted in primates for up to 14 million years (SurrIDGE & Mundy, 2002). In order for polymorphic trichromacy in platyrrhines to be considered as an adaptive strategy it must be demonstrated that there is some advantage to the maintenance of different colour vision phenotypes within a population (Melin et al., 2008). There exists ample evidence for a trichromat advantage during ripe fruit foraging (Melin et al., 2009; Regan et al., 1998; Riba-Hernández et al., 2005; Smith et al., 2003; Sumner & Mollon, 2000b; Yamashita et al., 2005). To our knowledge, the only published study on fig foraging by wild platyrrhines (Melin et al., 2009) found that trichromatic white-faced

capuchin monkeys (*Cebus capucinus*) demonstrate a foraging advantage when feeding on ripe figs. Conspicuous figs were more common than cryptic figs at the research site, and were fed on much more frequently. Trichromatic monkeys had a higher acceptance index of conspicuous figs than did dichromats, suggesting an ability to select riper figs based on visual cues. Dichromats, on the other hand, used longer and more diverse foraging sequences (e.g. frequent sniffing) when assessing figs. While the variation in foraging behaviour did not result in a net variation of fig intake rate, the authors suggest that it is possible that the improved discrimination ability of trichromats may lead to higher feeding rates under conditions where ripe fruit is less available and quickly depleted. Additionally, trichromatic monkeys seemed better able to select the ripest figs, while dichromats consumed mid-ripe (yellowish) figs more often (A.D Melin, pers. obs).

Site	Plot Size (hectares)	Census Date	N species	N Individuals	N Individuals per hectare	Source
Korup, Cameroon	50	1998	N/A	3	0.06	STRI
Edoro, Democratic Republic of Congo	20	2000	2	2	0.10	STRI
Lenda, Democratic Republic of Congo	20	2000	4	6	0.30	STRI
Budongo Forest Reserve, Uganda	24.13	2006	4*	59	2.45	Tweheyo and Babweteera 2007
La Planada, Columbia	25	2003	7	289	11.56	STRI
Yasuni, Ecuador	50	2003	12	30	0.60	STRI
BCI, Panama	50	2005	8	42	0.84	STRI
Cocoli, Panama	4	1998	4	9	2.25	STRI
Sherman, Panama	6	1999	3	3	0.50	STRI
Sector Santa Rosa, Costa Rica	2.66	2010	8*	4	1.5**	Parr et al, In Press
Agaltepec Island, Mexico	8.3	1996	6	81	9.76	Serio-Silva et al. 2002

* 8 species of *Ficus* are known in Sector Santa Rosa (Melin et al., 2009) however only 2 species have been encountered to date in transects (Parr et al., In Press).

** If only those fig trees with a DBH of 10cm or greater are included, then the number of individuals drops to three, and density drops to 1.13 (N.Parr, pers. comm.).

Table 1. Number of species and individuals of the genus *Ficus* in African and neotropical forests.

5. Conclusion

While most hypotheses for the variation in colour vision capabilities of catarrhines and platyrrhines posit the importance of either the ability to detect ripe fruit (Regan et al., 2001) or young leaves (Dominy et al., 2003) there is evidence that this variation stems from visual

adaptive strategies aimed at the detection of proteinaceous foods. In continental Africa where frugivorous primates rely on young, reddish leaves as protein sources (Dominy et al., 2003), routine trichromacy is the rule. In New World tropical forests efficient foraging for conspicuously coloured proteinaceous figs may favor trichromats and maintain colour vision polymorphism via heterozygote advantage. It is also worthwhile to mention that the selection pressures acting on trichromacy may be less in the New World because insects represent a protein source to many neotropical monkeys and dichromacy is useful in the detection of surface-dwelling insects (Melin et al., 2007; Melin et al., 2010) via the enhanced ability of dichromats to break camouflage (Caine et al., 2010; Morgan et al., 1992).

Rather than viewing figs as fallback resources (Dominy et al., 2003; Shanahan et al., 2001) we propose that they are preferred and limiting resources. Additionally, given the timing of Old World phenophases, where young leaves are most widely available during periods of overall fruit scarcity (Dominy et al., 2003), it is not possible to clearly identify young leaves as fallback foods, since the definition of a fallback food requires spatial and temporal ubiquity (Marshall & Wrangham, 2007). The evolution and maintenance of polymorphic trichromacy is a response to variation in the detectability not of fallback foods, but of the limiting resources of frugivorous primates: proteinaceous foods.

Our analysis has been restricted to continental Africa and the neotropics due to the availability of data from these continents. However, the recent discovery of polymorphic trichromacy amongst some Malagasy strepsirrhines (Tan & Li, 1999; Veilleux & Bolnick, 2009) will provide an interesting comparative dataset against which to test hypotheses. Under the protein limitation hypotheses, we predict that balancing selection will favor polymorphic trichromacy via a heterozygote advantage in frugivorous strepsirrhines whose protein source is conspicuous. Given current evidence for the low abundance of *Ficus* in Malagasy forests and the recent discovery of a paucity of available protein in Malagasy *Ficus* fruits (Ganzhorn et al., 2009), it seems likely that Malagasy protein resources and resulting effects on strepsirrhine colour vision capabilities will be found elsewhere.

Many hypotheses regarding primate morphological adaptations hinge on the importance of fallback foods (Dominy & Lucas, 2001; Marshall & Wrangham, 2007), and foods that are dominant in primate diets (Osorio & Vorobyev, 1996; Regan et al., 2001; Smith et al., 2003). This represents an unusual departure from studies of primate behaviour which tend to focus on the centrality of limiting resources (e.g. Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980). Studies of primate foraging adaptations might benefit from the additional consideration of morphological and sensory adaptations to foraging on limiting resources.

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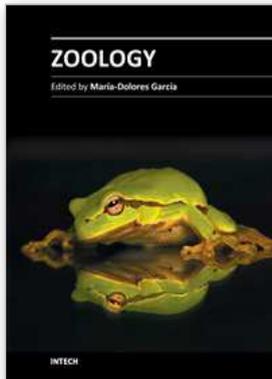
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The present book is not a classical manual on Zoology and the reader should not expect to find the usual treatment of animal groups. As a consequence, some people may feel disappointed when consulting the index, mainly if searching for something that is considered standard. But the reader, if interested in Zoology, should not be disappointed when trying to find novelties on different topics that will help to improve the knowledge on animals. This book is a compendium of contributions to some of the many different topics related to the knowledge of animals. Individual chapters represent recent contributions to Zoology illustrating the diversity of research conducted in this discipline and providing new data to be considered in future overall publications.

How to reference

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