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Primate Fruit Color: Useful Concept or Alluring Myth?

Kim Valenta[1] · Omer Nevo[2] · Colin A. Chapman[1]

Abstract While the importance of frugivorous primates as seed dispersers is well established, the question of the extent to which they exert selective pressure on fruit color phenotypes is contested. Numerous studies have identified suites of primate fruit colors, but the lack of agreement among them illustrates the difficulty of identifying the match between primate foraging behavior and the extent of primate–plant coevolution. This may indicate that primates do not shape fruit traits, at least in a consistent direction, or that the evolution of fruit color is affected by a complex array of selection pressures in which primates play only a part. Here, we review the role of primates in shaping fruit color in the context of primate color vision phenotypes, and fruit phenotypic constraints and selective pressures. To test the hypothesis that fruit color is subjected to selection pressures by primates, we offer six testable predictions aimed at disentangling the complex array of factors that can contribute to fruit color phenotypes, including animal mutualists, animal antagonists, and developmental and phylogenetic constraints of fruits. We conclude that identifying the importance of primate seed dispersers in shaping fruit visual traits is possible, but more complex than previously thought.

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Introduction

The existence of so many fruiting plant species that rely on animals as seed dispersers, and the high variation in the sensory and dispersal capabilities of seed dispersing animals, have led researchers to hypothesize that seed disperser behavior exerts selection pressures on fruit traits that results in the evolution of dispersal or fruit syndromes (van der Pijl 1969). Fruit syndromes are sets of co-occurring fruit and seed traits that are matched to different types of frugivores based on the frugivore's behavior, physiology, and sensory abilities (Janson 1983). This idea is nearly a century old (Ridley 1930), and since its inception many researchers have found evidence for putative dispersal syndromes, a central component of which is often color (Beattie and Lyons 1975; Fischer and Chapman 1993; Janson 1983; Lomáscolo and Schaefer 2010; Willson *et al.* 1989). For example, some have noted that fruits dispersed by nocturnal bats with poor color vision capabilities tend to not be brightly colored (Eby 1998; Janzen *et al.* 1976), and avian ecologists have long noted that bird-dispersed fruits are brightly colored, presumably to attract birds with highly developed color discrimination capabilities (Murray *et al.* 1993; Schaefer *et al.* 2014; Wheelwright and Janson 1985; Willson *et al.* 1989).

In the nearly century-long history of fruit syndrome studies, the idea of a primate fruit syndrome was a relative latecomer. This may result from the now surprising fact that it was not until very recently that fruit-eating primates were considered to be important seed dispersers. An early, seminal work on fruit syndromes noted that "monkeys and apes are … mostly destructive, eating everything edible … *they may or may not be instrumental in dispersal*" (van der Pijl 1969, p. 53, emphasis ours). Indeed, before the 1990s, there were only a handful of published accounts of seed dispersal by primates (Cant 1979; Chapman 1989; Estrada and Coates-Estrada 1984; Leiberman *et al.* 1979; Terborgh 1983). In the 1990s, there was a surge of interest in primate frugivory and seed dispersal, culminating in the 1998 publication of a special issue in the *American Journal of Primatology* on primate seed dispersal (Lambert and Garber 1998). We now know that frugivorous primates comprise between 25% and 40% of the frugivore biomass in tropical forests (Chapman 1995), and defecate or spit large numbers of seeds (Lambert 1999). Wherever they occur, frugivorous primates have been recognized as important vectors of seed dispersal (Culot *et al.* 2010; Lambert 2011; McConkey and Chivers 2007; Wright *et al.* 2005).

Although it is only recently that frugivorous primates have been identified as playing a role in seed dispersal, the role of color and color vision in primate ecology and evolution has been of interest to researchers since the nineteenth century (Allen 1879). Indeed, one of the defining characteristics of the order Primates is their increased reliance on color vision, which has been suggested to be accompanied with decreased olfactory ability (Fobes and King 1982; Le Gros Clark 1971). The understanding of primate color vision improved substantially with the introduction of genetic methods, which—combined with behavioral studies—explored proximate mechanisms and ultimate functions behind primate color vision and the variance present within the primate order. It is perhaps unsurprising that the enduring interest in primate color vision, coupled with an emergent interest in primate seed dispersal, led to the notion that primate-dispersed fruits have converged upon a nonrandom subset of the color spectrum (Regan *et al.* 2001), i.e., a primate fruit color.

But what color is a primate-dispersed fruit? Numerous researchers have attempted to answer this question (Table I). The earliest primate fruit color study noted that fruits dispersed by primates tended to be in more subdued shades of orange, brown, yellow, and green, as opposed to more visually conspicuous blue, black, or pink bird-dispersed taxa (Janson 1983). Other studies have variously identified primate-dispersed fruits as typically yellow, orange, red, green, brown, and black (Gautier-Hion *et al.* 1985; Knight and Siegfried 1983; Leighton 1983, 1993; Lomáscolo and Schaefer 2010), and as distinguishable from background leaves primarily in the yellow-blue color channel (Dominy and Lucas 2001). Overall, colors of primate-dispersed species are numerous (Table I), and partially overlap with those of bird-dispersed species (Voigt *et al.* 2004). As well, many colors of primate-dispersed species also characterize fruits in temperate regions, in which birds are the dominant animal seed dispersal vector (Burns *et al.* 2009). Moreover, most studies have recorded fruit color based on subjective human perceptions of color, rather than quantifying fruit reflectance and modeling it according to relevant visual phenotypes and light environments (Valenta *et al.* 2017). This confounds any hopes for a straightforward answer to the questions: What colors are primate-dispersed fruits, and what role did frugivorous primates play in shaping these colors?

The difficulty in providing straightforward answers to these questions lies in the fact that fruit color is the product of a complex interaction of factors in which frugivorous primates are only one part. In addition to the variation in primate color vision, which in itself is likely to drive selection for multiple primate fruit *colors* rather than any single color, fruit color evolution is also driven by several additional factors. These factors include other mutualists and antagonists that interact with fruits, abiotic factors, and phylogenetic and developmental constraints. Only by considering these factors together can genuine patterns of coloration in primate-dispersed fruits—should they exist—emerge and the role of primate mutualists in shaping them be identified. This role may turn out to be substantial in some systems and negligible to nonexistent in others. Indeed, a null hypothesis is that frugivorous primates have not had an effect on the evolution of fruit color. For example, colors that characterize primate-dispersed fruits occur in tropical systems in which primates are absent (Dominy *et al.* 2003), showing that these colors can evolve without frugivorous primates. However, in systems where primates are important seed dispersers and rely on vision to find ripe fruits, primates may indeed exert selective pressure on fruit color, though it may be difficult to identify owing to several abiotic and biotic factors. Here, we take a step in this direction and explore three main questions in color-mediated primate–plant mutualisms: 1) What does it mean to be a primate-dispersed fruit? 2) What colors can primates detect? 3) Do factors aside from mutualists affect the color of primate-dispersed fruits? We examine each of these questions in light of extant data and theory, and suggest that despite the complexity inherent in these questions, it is possible to generate predictions regarding the color of primate-dispersed fruits.

What Is a Primate-Dispersed Fruit?

Primates comprise a large percentage of frugivorous biomass in the tropics and are known to disperse large numbers of viable seeds intact (Chapman 1995). As such, it is

Table I Examples of colors of ripe, fleshy fruits consumed by primates globally

Geographical region	Primate species	Dominant colors of primate-consumed fruits	References
Neotropics	Not specified	Yellow, orange, brown green	Janson (1983)
	Callicebus torquatus	Green, yellow, brown; some purple, black, red, orange	Snodderly (1979)
	Saguinus nigrifrons	Yellow; less: green, reddish, brown/black, purple	Ripperger *et al.* (2014)
	Alouatta seniculus	Yellow, orange, red	Julliot (1994)
	Alouatta seniculus; *Ateles paniscus*	Orange, yellow, some red	Guillotin *et al.* (1994)
	Alouatta guariba; *Brachyteles arachnoides*	Yellow/orange, violet, green, brown/black	Martins (2008)
	Alouatta seniculus	Yellow/orange, red, green	Julliot (1996)
Continental Africa	Not specified	Orange, red, yellow	Gautier-Hion *et al.* (1985)
	Not specified and lumped with nonprimate mammals	Green, yellow	Knight and Siegfried (1983)
	Papio anubis	Brown/Gy, yellow, orange, green, blue/violet, black	Kunz and Linsenmair (2010)
	Not specified	Red, violet, yellow, orange, green	Flörchinger *et al.* (2010)
Madagascar	*Cheirogaleus medius*; *Eulemur fulvus* ssp.	Yellow and orange; red; some purple	Bollen *et al.* (2005)
	Propithecus diadema edwardsi	Brown, yellow/green, red	Hemingway (1996)
	Eulemur macaco	Mainly green and brown; some red, orange, yellow	Birkinshaw (2001)
	Eulemur rubriventer; *Eulemur fulvus*; *Varecia variegate*; *Propithecus diadema*	Green, brown, purple, red	Dew and Wright (1998)
Southeast Asia	*Hylobates muelleri* × *agilis*	Yellow, orange	McConkey *et al.* (2002)
	Pongo spp.; *Hylobates* spp.; *Macaca* spp.	Red, yellow	Leighton (1993); Leighton and Leighton (1982)

reasonable to expect that the colors of the fruits whose seeds they disperse will be under selection. However, in addition to primates, most plants are visited by other frugivores (Bueno *et al.* 2013) with different visual phenotypes, which provide different dispersal services, either in the amount of seeds or their treatment (Loiselle *et al.* 2007). Theoretically, highly diffuse mutualisms, i.e., plants that rely on multiple taxa for seed dispersal services (Herrera 1982), should not result in selective pressure on plant traits that serve to attract specific dispersers. Indeed, some have argued that diffuse coevolution should be inferred whenever selection on a plant trait by one disperser species is altered by the presence of a second disperser (Strauss *et al.* 2005). However, even if a given plant interacts with multiple frugivores, their importance to its seed dispersal and regeneration is not necessarily similar, and plants are likely to be selected to acquire traits that allow efficient dispersal by frugivores that provide most of the dispersal

services. For example, one frugivorous species may deposit seeds in locations unsuitable for germination (e.g., at middens where they defecate every day), while another frugivorous species may disperse seeds to sites suitable for germination and growth. Thus, the strength of the selection pressures frugivorous primates exert on fruit color is mediated by their relative importance to the successful seed dispersal of any particular plant, which can be exceedingly difficult to establish.

The importance of a given seed disperser to a plant results from the interaction of the quantity of seeds dispersed and the quality of the seed dispersal service (Schupp 1993). Seed disperser effectiveness has been defined as "… the number of new adults produced by the dispersal activities of a disperser" (Schupp 1993, p. 16). Unfortunately, quantifying the number of reproductive adult trees produced by primate seed dispersal activities is extremely challenging and requires robust, thorough, and longitudinal data that are almost always unavailable, particularly given that it may take more than a hundred years for a seedling of a tropical canopy tree to become an adult. Theoretical attempts to address these empirical difficulties have led some to suggest that seed dispersal effectiveness (SDE) be measured as the number of seeds dispersed and the probability that a dispersed seed produces a new adult—ultimately, the product of seed dispersal quantity and seed dispersal quality (Schupp et al. 2010). However, measuring seed dispersal quantity and quality can still be quite challenging, and can vary greatly based on the question of interest (Valenta and Fedigan 2008).

The quantity of seeds dispersed can be estimated for diurnal frugivorous species whose feeding behavior can be closely observed. Yet comparing this amount and calculating the relative importance of a given taxon is much harder, in part because it is likely that many fruit–frugivore interactions such as those with nocturnal, rare, or cryptic visitors will go unnoticed by interested observers, regardless of observation effort. This is made all the more difficult by the fact that a single tree can produce tens of thousands of fruits every year during an adult life that can span centuries. While quantifying SDE is thus challenging, estimating the quality component of SDE is even harder. Seed dispersal quality includes seed handling (Kaplin et al. 1998), the effects of gut passage on seed germination (Samuels and Levey 2005) and time to germination (Valenta and Fedigan 2009), seed-emergence responses to ingestion (Rodriguez-Perez et al. 2005), plant fitness consequences of seed emergence (Verdú and Traveset 2005), and a host of postdispersal factors such as the overall seed shadow and secondary dispersal (Schupp 1988).

Despite the difficulties inherent in assessing the SDE of frugivorous primates, some progress has been made. Where it has been compared to that of other seed dispersers, the effect of primate gut-passage treatment on germination probability is positive, but lower than that of birds and bats (Traveset 1998; Traveset and Verdu 2002). However, the removal of pulp, even without seed ingestion, can significantly improve the survival and germination rates in some plant species (Lambert 2001). Further, seed dispersing primates, with body masses that range between a few hundred grams and several kilograms (apart from a few outliers) (Smith and Jungers 1997), are larger than other seed dispersers such as passerines (Martin et al. 2011) or bats (Thomas 1984). Thus, primates can disperse larger seeds than most other seed dispersers (Kaplin and Lambert 2002), and also tend to move seeds to greater distances (Clark et al. 2005; Nathan et al. 2008). Conversely, the large body mass of primates can also result in the ingestion of many seeds in single feeding bouts, and the deposition of conspecific seeds in clusters—

a process that might counter the positive effects of dispersal as a means of escaping density-dependent seed mortality (Howe 1986). Finally, the deposition of seeds along with fecal material can promote secondary dispersal and thereby increase the probability of establishment (Culot *et al.* 2010; Vander Wall and Longland 2004), though this has been found to be strongly dependent on habitat and landscape variables (Böhning-Gaese *et al.* 1999). Alternatively, it can attract seed predators, thereby decreasing the probability of establishment, and this will vary as a function of the insect and mammal community.

Another point to consider is that while primates show substantial variation in traits directly related to their SDE, such as foraging group size, body mass, feeding behavior, and movement patterns (Campbell *et al.* 2010), they also tend to overlap significantly with regard to the fruit species they consume (Stevenson *et al.* 2000; Yamagiwa and Basabose 2009). Thus, plants that rely on primates for seed dispersal are usually consumed by several primate species (Janson 1983; Link and Stevenson 2004). As a result, the dispersal services that primates provide can be heterogeneous and potentially complementary. For example, seed dispersal by primates may provide an individual tree with removal of large quantities of seeds and their dispersal to great distances by larger-bodied primates, and also dispersal of a smaller number of seeds in smaller clumps by small-bodied primates that may be more likely to reach forest patches in early regeneration stages (Culot *et al.* 2010b; Oliveira and Ferrari 2000).

Given the diversity of frugivores in most systems, most primate-dispersed fruits cannot be considered "primate fruits" only, and evolved to maximize a primate's ability to detect them. Although wherever they occur frugivorous primates are conspicuous members of frugivorous guilds, any selective pressures driven by primates may be altered or countered by those exerted by other frugivores. Thus, predictions regarding the evolution of fruit color as an adaptation to the attraction of primate mutualists must include the potential importance of fruit choice and SDE of nonprimate frugivores.

Given that relative SDE values should ideally be calculated for all frugivores in a system, it follows that it should be easier to establish the role of primate mutualists in systems with fewer frugivores. For example, Madagascar is a uniquely frugivore-depauperate island (Federman *et al.* 2017) in which frugivorous birds and bats are rare relative to systems in mainland Africa, South America, or Asia, and lemurs are viewed as the main vectors of seed dispersal for most plant species (Wright *et al.* 2005). Most frugivorous lemurs are dichromats (red-green color blind) (Peichl *et al.* 2017), and thus we can predict that they would select fruits that are visually conspicuous using the yellow-blue discrimination channel. However, even this simple prediction in a uniquely simple disperser setting has received only mixed empirical support (Valenta *et al.* 2013, 2015b).

In sum, the many factors involved in the SDE of a primate species affect the degree to which primate sensory ecology generates selection pressures on fruit traits. Quantifying the importance of primates to a given plant's regeneration process—especially relative to that of nonprimate dispersers—is a daunting task, and as a result, it is extremely difficult to assess how relevant the selection pressures exerted by primates are to fruit trait evolution. Even in frugivore-depauperate systems where primates comprise most of the seed dispersing fauna in a system, the lack of strong evidence for primate-specific fruit colors highlights the potential importance of nonmutualists in shaping fruit phenotypes.

How Important Are Frugivores? Other Factors Affecting Fruit Color Evolution

Attempts to discern the selective pressure of mutualists are often at the level of the community: matching fruit traits to the sensory phenotypes of important dispersers (Lomascolo *et al.* 2010; Valenta *et al.* 2015a). However, inferring selection based on matching fruit traits with frugivore sensory capabilities can be problematic, if not uncritically adaptationist. This is because in addition to the role of animal mutualists in driving plant trait selection, there are other potential drivers involved in the selection of fruit color, including phylogeny (Ackerly 2009; Regan *et al.* 2001), constraints resulting from phenotypic integration (Valido *et al.* 2011), interactions with plant antagonists (Strauss and Whittall 2006), and abiotic factors (e.g., solar radiation) that vary as a function of latitude, altitude, and forest structure (Zoratti *et al.* 2015). Thus, even if selection by primates is inferred based on quantitative and qualitative assessments of seed disperser effectiveness, the role of other biotic and abiotic variables in shaping fruit phenotypes should not be overlooked.

The potential importance of phylogeny in constraining extant phenotypes stems from the observation that closely related species tend to share many properties owing primarily to shared evolutionary history and not to shared ecological dynamics (Harvey and Pagel 1991). Large trees especially might be expected to be phylogenetically conservative relative to animals because they tend to be much slower in reaching reproductive age. Interestingly, extant studies of the role of phylogeny in predicting variation in fruit color have found only weak phylogenetic constraints on fruit colors (Cazetta *et al.* 2012; Renoult *et al.* 2014; Stournaras *et al.* 2013; Valenta *et al.* 2017). This may result from the fact that fruit color shows lower degrees of phenotypic integration, i.e., covariation among sets of functionally related morphological traits (Valido *et al.* 2011).

The potential role of antagonists—particularly seed predators—in driving fruit color variation (Schaefer *et al.* 2004) must also be considered when evaluating the importance of frugivorous primates in the evolution of fruit color. Relative to that of mutualists, the role of antagonists in shaping fruit color has received relatively little attention in the literature, and to our knowledge no primate seed dispersal study has yet explicitly measured the role of antagonists in contributing to fruit trait evolution. However, considering the combined effects of both mutualistic and antagonistic interactions is essential to understanding plant–animal interactions (Herrera *et al.* 2002). Antagonists have been found to drive nonvisual phenotypic characteristics of fruits, and the colors of other plant parts. For example, chemical signals, particularly odorants, emitted by fruits have been found to result from selection for compounds aimed at deterring antagonists, with downstream effects on mutualist behavior (Linn *et al.* 2005). As well, although not related to fruit morphology *per se*, plant and floral characteristics have been found to drive variation in the likelihood of seed predation (Cariveau *et al.* 2004). Several studies have documented the effect of flower antagonists in shaping flower color (reviewed in (Strauss and Whittall 2006)), and young leaf redness in continental Africa has been hypothesized to be a cryptic strategy aimed at reducing herbivory by dichromats (Dominy *et al.* 2002). While the research on the evolutionary implications of fruit–antagonist interactions is limited, preliminary findings from the broader literature on the importance of antagonists in shaping plant traits is intriguing.

The effect of solar radiation is another variable that should also be considered in the context of evolutionary selective pressure on fruit color. Just as ambient light can significantly affect the detection capabilities of frugivores (Endler 1993; Veilleux and Cummings 2012), there is some evidence to suggest that the concentrations of phenolic compounds responsible for some fruit colors may respond to variation in ambient light availability. Specifically, anthocyanins, which can cause fruits to appear red, blue, or purple, have been found in higher concentrations in berries as a function of decreasing latitudes (Lätti et al. 2007) and increasing altitude, suggesting that high light levels may promote their production (Zoratti et al. 2015), with implications for berry color. A study of two bilberry species found that fruit and flower colors are not optimized for disperser and pollinator detection, but probably result from the role of anthocyanins in countering abiotic stress (Stournaras and Schaefer 2017). In addition to direct effects of environmental stress-based selection for certain fruit colors, it is reasonable to infer the possibility that some fruit colors are selected for because they reduce photoinhibition or increase photosynthetic efficiency, and that these colors may secondarily aid detection by animal mutualists. For example, reflectance in the ultraviolet part of the color spectrum (300–400 nm) may be useful in attracting avian dispersers, but it can also protect plants from the damaging effects of ultraviolet light (Hakala-Yatkin et al. 2010). Similarly, while reflectance in the green part of the color spectrum (500–600 nm) may be useful in avoiding seed predation, it may be important for photosynthesis, which may be why many large fruits that develop on the tree for a long time are green (Valenta et al. 2015a). Thus, even if fruit colors are detectable by primate mutualists, this may represent exaptation, and not coevolution.

Overall, disentangling the selective forces and constraints that shape fruit phenotypes is challenging; however, studies that match fruit phenotypes to frugivore behavior, preferences, and sensory capacity should account for sources of fruit phenotypic variation outside of selective pressures imposed by animal mutualists. Analyses that control for plant phylogeny, and consider the role of local environments and antagonists in shaping fruit color, will lead to a clearer picture of the potential importance of frugivorous primates as agents of selection.

What Colors Do Primates Detect?

The selection pressures primates may have exerted on fruit color originate primarily from their color vision capacities; however, many assessments of primate-dispersed fruit color have relied on subjective human color categories. Color—the selective reflectance of light in different wavelengths—is a trait that can be generated chemically through pigments, or physically (Valenta et al. 2017). Yet in an ecological context, color is in the eyes of the beholder: Perceived color is determined not only by the light reflected by an object, but by the properties of the visual system receiving it (Bennett et al. 1994). Advances in molecular techniques and extensive experimental work have resulted in the identification of the color vision phenotypes of most primates (Jacobs 2008), and the ability to subsequently model color based on an animal's ability to detect it (Osorio and Vorobyev 2008). While most mammals have been found to be dichromatic (red-green color blind), many primates are unique among eutherian mammals in possessing trichromatic color vision (Hunt et al. 1998). These trichromatic primates

possess three distinct retinal cone types, which contain pigments that are maximally sensitive to different wavelengths. The short-wavelength sensitive (S) cones are most sensitive in the range of 420–430 nm, while the middle-wavelength (M) and long-wavelength (L) sensitive cones contain pigments with peak sensitivities ranging between 530 and 565 nm.

While Old World monkeys, apes, and humans are routinely trichromatic, having all three cone pigment types (Jacobs 2008), most New World monkeys and some lemurs exhibit polymorphic trichromacy (Jacobs 2007; Tan and Li 1999; Tan *et al.* 2005; Veilleux and Bolnick 2009). Polymorphic trichromacy can result from a polymorphism at any one of three sites in the X-linked M–L opsin gene that code for middle- to long-wavelength–sensitive opsin proteins (Matsumoto *et al.* 2014). Females with two different M–L opsin alleles, combined with the common autosomal short-wavelength–sensitive opsin gene possess trichromacy (Mollon *et al.* 1984). However, males, with only one X-chromosome, can inherit only one M–L opsin allele and are always dichromatic. Because often three alleles of the middle- to long-wavelength–sensitive opsin gene are found within a species (Surridge and Mundy 2002), three dichromatic and three trichromatic phenotypes can exist within a single species and even within a single foraging group.

Strepsirrhine primates (lemurs, lorises, and galagos) are an interesting exception to the general primate trend of increased reliance on color vision because their visual systems are intermediate to those of most mammals and other primates (Rushmore *et al.* 2012), and their color vision phenotypes are highly variable. The capacity for polymorphic trichromacy has been documented in 10 species of diurnal and cathemeral lemurs: 1 species of *Eulemur*, 1 species of *Varecia*, the single species of *Indri*, and 7 species of *Propithecus* (Jacobs and Deegan 1993; Jacobs *et al.* 2017; Tan and Li 1999; Veilleux and Bolnick 2009; Veilleux *et al.* 2016). Most other lemurs have been found to retain dichromatic color vision (Peichl *et al.* 2017; Tan and Li 1999; Valenta *et al.* 2016). Further, all sampled lorisiforms are monochromats (Kawamura and Kubotera 2004), as are some species of nocturnal cheirogaleid lemurs that have lost S cones (Veilleux *et al.* 2013, 2014).

In addition to general trends in primate color vision—routine trichromacy in Old World monkeys and apes, polymorphic trichromacy in New World monkeys, and routine dichromacy in most lemurs—are some interesting exceptions. The New World owl monkeys (*Aotus* spp.) are the only nocturnal anthropoids, and in addition to a suite of visual adaptations to nocturnality, they have lost the capacity for color vision entirely and are monochromatic, having only one cone type (Jacobs *et al.* 1993). New world monkeys of the genus *Alouatta* are the only highly folivorous platyrrhines, and the only species to have developed routine trichromacy (Jacobs *et al.* 1996). The aye aye (*Daubentonia madagascariensis*) is a nocturnal strepsirrhine that has retained dichromacy, with a peak sensitivity (λ_{max}) of the short-wavelength–sensitive pigment in the violet part of the spectrum (406 nm) (Carvalho *et al.* 2012).

In addition to great variation in primate color vision phenotypes is great variation in primate light environments, which can be equally critical to the detection of color (Yamashita *et al.* 2005). Primate activity patterns are diverse and include strict nocturnality, strict diurnality, cathemerality, and crepuscularity (Heesy and Ross 2001). Light availability and ambient light conditions vary greatly within activity patterns; for example, terrestrial ambient light levels decline approximately 100-fold

between midday and sunset and cathemeral animals can experience even greater variation as light levels on moonless nights can fall a further 1–10 million times (Warrant and Johnsen 2013). Variation in light availability also increases as a result of local environments; for example, ambient light will be less available and more concentrated at longer wavelengths in a closed canopy rainforest than in a forest gap or savannah, which affects the ability of animals to discern color (Endler 1993).

Given the variation in color vision phenotypes and light conditions, different primates can perceive the same color in different ways, and primate species with different color vision phenotypes have been shown to prefer different fruit colors (Stoner *et al.* 2005). This has implications for the selection pressures they may exert on fruit coloration. The main function of visual signaling is typically claimed to be increasing the detectability of fruits (Stournaras and Schaefer 2017). Enhanced detectability through visual cues and signals is achieved primarily via producing a fruit whose color contrasts against the background. This signal can be amplified by clustering of fruits or by presenting large amounts synchronously (Ordano *et al.* 2017). This means that plants that are dispersed by routine trichromatic species can create a visual contrast on both the yellow-blue and red-green channels, whereas those dispersed by dichromatic or polymorphic species are more likely to use only yellow-blue contrast. Given that blue coloration can be more expensive for a plant to produce (Valenta *et al.* 2015a), we can predict that fruits in the Neotropics and Madagascar will show higher yellow-blue contrast against leaves, whereas primate-dispersed fruits in continental Africa and Southeast Asia will have a higher red-green contrast against leaves.

In sum, different primates perceive color in different ways. As well, the same fruits can be dispersed by primate species with different visual systems or that are active under different light regimes, which further complicates the ability to make straightforward predictions since these selection pressures may conflict. Thus, even the reasonable and straightforward prediction that fruit color should be selected to increase color contrast with the background and thus facilitate detectability is hard to translate to clear predictions regarding which fruit color(s) primates may select.

Synthesis and Predictions: Do Primates Shape Fruit Color?

Modern molecular techniques allow straightforward identification of the colors primates can see and thus the selection pressures they may exert on fruit color. Yet "primate fruit color" has proved difficult to pinpoint, as fruits whose seeds primates disperse show substantial variance in their visual displays (Table I), both within and between systems, as well as an overlap with both nonprimate mammal- and bird-dispersed fruits in some systems. This is likely due to the highly complex array of selection pressures and constraints that drive fruit color (Fig. 1) and the fact that selection by primates is likely not to select a particular color, but any color which contrasts against the background and renders the fruit detectable. At least in some cases, it is possible that selection pressures by primates have been negligible. However, in systems in which primates are important seed dispersers and rely on visual signals during foraging, primates may well have played a significant role in fruit color evolution, and any resulting fruit phenotypic patterns can emerge once all confounding factors are accounted for. Here, we propose six predictions that test the hypothesis that fruit color is an adapted trait selected by

primate foraging and food selection, but that it is also affected by numerous other factors that dilute the selection pressures exerted by primates.

Prediction 1: Fruits that are heavily primate dispersed and to which primates provide important seed dispersal services should be visually salient to them, i.e., have a strong contrast against their backgrounds. In systems in which most frugivorous primates are dichromats (Madagascar), or a mix of dichromats and polymorphic trichromats (Neotropics), the contrast should be salient in the yellow-blue discrimination channel, whereas where primates are trichromatic, fruits should reflect mainly in the red part of the spectrum, thus providing a high contrast at a relatively lower cost.

Prediction 2: The more visually diverse a community of primates is, the less optimized fruit visual signals will be. For example, in a community in which seed dispersal is performed by nocturnal and diurnal species, fruits should be under selection to provide alternative signals such as odor. If these signals are useful to diurnal species as well, this would relax selection pressures on visual signals.

Prediction 3: The more a fruit tends to rely on nonprimate frugivores, the lower the primate-relevant color contrast will be; i.e., systems with more diverse frugivore communities should have fewer fruits that are tuned to primate visual phenotypes. This is because the higher the relative SDE of other frugivores, the more fruit displays should be selected to maximize contrast in their eyes, even at the expense of primate mutualisms.

Prediction 4: Phylogenetic constraints appear to play a minor role in fruit color and thus to not have a strong effect on the color of primate fruits. An exception could
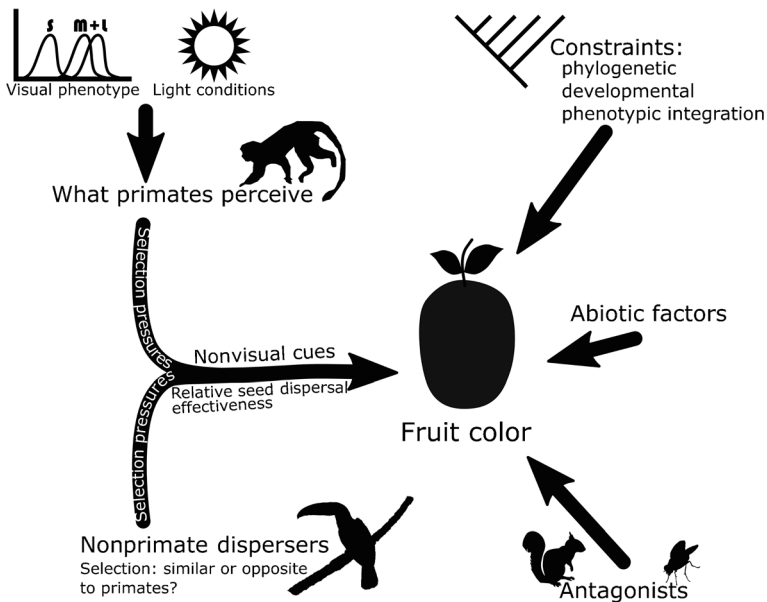

Fig. 1 Schematic showing how multidirectional selection pressures shape fruit color. An array of selection pressures from multiple mutualists and antagonists, abiotic factors, and constraints means that even though primates may affect fruit color evolution, the direction and magnitude of their effect will vary among systems and be difficult to predict

be newly introduced species that have only recently relied on primates for seed dispersal. Similarly, in disturbed systems in which nonprimate dispersers are disproportionally affected by habitat disturbance, some plants may begin relying on primates more than in the past. Their colors are likely to match the visual phenotypes of the legacy long-term disperser.

Prediction 5: Plants that are more exposed to solar radiation, either due to latitude, altitude, or microhabitat, are more likely to use protective pigments in their fruits and thus deviate from the color pattern predicted by the visual phenotypes of their primate seed dispersers.

Prediction 6: Fruits for which other deterrents (e.g., exocarp hardness) or attractants (e.g., odors) are particularly salient to primates should show reduced investment in plant coloration OR reduced reliance on vision by foraging primates.

Conclusion

In the 1998 special issue on primate seed dispersal, the editors noted that "… although it is clear that primates are likely to have an important ecological impact on seed fate and the movement of seeds away from the parent tree, a major point raised in several papers in this volume is that a co-evolutionary relationship between a given primate taxa and the fruit species it exploits is extremely unlikely" (Garber and Lambert 1998, p. 7). In the two decades since, the understanding of primate color vision has improved substantially, and the evolutionary ecology community has again become more receptive toward the idea that diffuse coevolutionary forces between large communities of frugivores and plants results in "dispersal syndromes," i.e., that fruit traits experience selective pressure from dispersers. Yet the evolution of fruit traits is complex, as it responds to numerous factors other than the sensory phenotypes of the seed disperser. Primate fruit colors may exist, but identifying them requires an integrative approach that treats primates as an important part of a complex biotic and abiotic system, rather than as sole actors.

Compliance with ethical standards

Conflict of interest   All authors declare they have no conflict of interest.

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