The Evolution of Vision in Nocturnal Primates

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The evolution of vision has been a complex process, and is one that continues today. Exactly how, when, and why vision occurred in life forms is still contested and undergoing research. The importance of the development of vision among animals has had immense ramifications. Some research shows that the development of morphological features to detect light could have even been one of the driving factors behind the Cambrian explosion (Parker, 2003). As far as behavioral activity, ancestral mammals were considered to originally be nocturnal (Walls, 1942; Heesy & Hall, 2010; Gerkema, Davies, Foster, Menaker, & Hut, 2013). Therefore, their foundational visual morphology adapted to nocturnal conditions. The evolution of vision in primates has resulted in the highest levels of acuity among mammals; even so, there is variation found in primate vision. However, not all primates are diurnal; there are a number of primates adapted specifically to nocturnal conditions. Nocturnal primates have developed their own particular features to adapt to a lifestyle with less light. There are variations among nocturnal primates when it comes to their level and use of vision. A particular divide in vision use and evolution can be seen between the Old World nocturnal primates, mainly prosimians, and New World nocturnal primates, consisting of only one genus *Aotus*, and the world’s only true nocturnal monkey.

Vision Development in Animals

When it comes to evolution and biodiversity, many scientists consider the most important period in evolutionary history to be the Cambrian period, beginning around 540 million years ago (Parker, 2003; Zhang, Shu, Han, Zhang, Liu, & Fu, 2014; Zhang & Shu, 2014); some sources extend the time period slightly, back to the late Ediacaran period, before the Cambrian period, and until the early Ordovician period, after the Cambrian period (Meert, 2014; Young, 2015; see Table 1). Widely known for what has been dubbed the “Cambrian explosion” by scientists, this is the evolutionary period during which more diversity in animal life evolved than any other time; most of the phyla present today developed during that time period (Land & Nilsson, 2002; Zimmer, 2001). Many scientists, including Darwin, have searched for a viable explanation behind the rapid and multi-tiered expansion in diversity (Zimmer, 2001). The acceleration of evolution in biodiversity may have been triggered by a number of environmental causes. One researcher, Parker (2003), believes that he has found the definitive one: vision.

Parker posits that the development of vision in primitive animals is what sparked the Cambrian explosion (2003). His argument is that with the advent of vision, predator and prey had to evolve and counter-evolve rapidly to keep up with the competition and pressure that appeared alongside with the newfound use of vision. Before animals could perceive light and other visual changes in their environment, predation occurred more as a matter of chance, but as visual morphology developed, predation became more driven, more focused, and garnered a higher success rate for predators. Prey then counter-evolved and developed their own set of adaptations to deal with issues created from predator vision. This process of evolution and counter-evolution continued over time (Parker, 2003). Other researchers have confirmed that even from the early Cambrian, fossils have been found of species with complex eyes belonging specifically to predators that operated in low-light conditions (Lee, Jago, Garcia-Bellido, Edgecombe, Gehling, & Paterson, 2011).

Parker (2003) considers light itself to be a very powerful stimulus for evolution. Once predators were able to sight prey from a distance, however dimly, they gained an advantage in hunting and feeding. Adaptations which occurred afterwards were utilized by prey in response to predatory vision, according to Parker (2003): the development of camouflage, armor, and adaptations in flight and hiding. The absence of light limits animals adapted for a world that Parker considers to be a sight-driven one. Land and Nilsson (2002) also corroborate the correlation of the development of great biodiversity and modern phyla (or modern phyla precursors) alongside with the development of eyes among many of the species of this time, and since. Zimmer (2001) acknowledges the significance and far-reaching effects of the development of sighted animals, but states that both eyes and brains were necessary: the development of a full nervous system. Without a full and functional nervous system and brain, the information gathered by visual morphology can never be processed.

When it comes to nocturnal animals, they have developed a number of adaptations to deal with the absence of light, such as larger eyes, larger ears, the use of radar, the development of sound-deafening capabilities or behaviors, and camouflage. The proof of sight as success is cited in the lower biodiversity and behavioral complexity found in nocturnal animal species (Parker, 2003). However, as it stands currently, not all of Parker’s claims can be corroborated by other researchers. There are several reasons for this. One is the fact that not all animals can easily be divided into wholly nocturnal or diurnal categories; some have great variation in their temporal behavioral activities (Refinetti, 2008). Research supporting Parker's claim that nocturnal animals were lower in diversity and in number could not be found, and he includes no information on resources that he used to reach this statement. The presence of vision in nocturnal-dominant higher-level animals, particularly mammals, will be explored in the next section.

Nocturnality in Mammals

Mammals are considered by the scientific community at large to have led mostly nocturnal lives in their early evolutionary history (Heesy & Hall, 2010). Walls (1942) was the first researcher to write about the "nocturnal bottleneck" theory, wherein early mammal species were considered to be nocturnal in order to best survive during the periods of dinosaur species dominance. Walls performed visual morphological reviews to confirm his hypothesis (1942). Other researchers examined the original views of Walls and performed their own analyses of eutherian mammal systems, coming to the same conclusions (Gerkema et al., 2013). They included evidence related some of the original claims, such as endothermic systems and foraging/predation behaviors. Additionally, they looked at some more in-depth issues not covered by Walls, such as light-detection genes (Gerkema et al., 2013).

Heesy and Hall (2010) present a number of adaptations as well found in mammals that support this theory, and include visual adaptations specifically in their findings. For example, the eye morphology of most mammals supports higher visual sensitivity with lower visual acuity, usually associated with nocturnally-adapted animals. Large binocular visual fields and forward-facing eyes are associated with mammals and indicative of evolution under scotopic conditions. Additionally, adaptations to their circadian system indicate a more nocturnally-adapted lifestyle (Heesy & Hall, 2010). Further studies on visual morphological features have been conducted by other researchers as well. Hall, Kamilar, and Kirk (2012) administered a study wherein they studied the eye shapes and animal behavioral activity of 266 animal species, and their results supported the bottleneck theory further. Although some of the features of nocturnal animals overlapped with cathemeral animals, in the end they concluded that the bottleneck theory was still substantiated (Hall, Kamilar, and Kirk, 2012). The majority of mammal species are still considered to be nocturnal animals or possess features of nocturnal animals, despite the fact that many of them have managed to branch out into other temporal niches, including diurnal, cathemeral, and crepuscular (Bennie, Duffy, Inger, & Gaston, 2014). Retinal cone proportion in mammals has been shown to be highly correlated with temporal behavioral activity and lifestyle (Hunt & Collins, 2014).

Vision in Mammals

Vision among mammals consists of a number of features. First of all, eyes contain photoreceptor cells, which are actually photosensitive neurons found in the retina. Of these, there are three main types of cells: rods, cones, and photosensitive Retinal Ganglion Cells (pRGCs). For the purposes of this paper, only rods and cones will be discussed, considering that pRGCs consist of less than one percent of overall retinal cells (Wong, Dunn, & Berson, 2005). Rods are photoreceptor cells which are capable of detecting light and dark; they are far more sensitive than cones are. Cone cells, on the other hand, are capable of detecting color, and are much more structurally diverse; they are also associated with higher visual acuity (Gehring, 2014). According to phylogenetic analysis, Bowmaker (1998) found that of the two types of photoreceptors, rods and cones, rod pigments appear to have evolved after cone pigments. While most mammals are dichromatic (only capable of detecting color through the use of two cone classes), primates differ in possessing trichromatic vision, or vision based on the use of three cone classes; this is considered to be a higher level of colour vision, because they are able to detect more color wavelengths (Bowmaker, 1998; Regan, Julliot, Simmen, Vienot, Charles–Dominique, & Mollon, 2001).

Trichromatic cones consist of short-wave (S), middle-wave (M), and long-wave (L) sensitive cones, with each type capable of detecting a different set of color wavelengths (Regan, et al., 2001). The S-wave cones appear to have the most influence on the color vision of primates, and have greater diversity among species where they are present (Zhao, Rossiter, Teeling, Li, Cottons, Zhang, & Goodman, 2009). The path to achieving trichromacy differed among New World and Old World primates. In Old World primates, uniform trichromacy can be found, with peak sensitivities distributed in an even manner; in New World primates, however, trichromatic vision is polymorphic, meaning that there is variation in color vision even among individuals of the same species, due to features being found on X-linked opsins (Regan, et al., 2001; Kawamura, Hiramatsu, Melin, Schaffner, Aureli, & Fedigan, 2012). This can change depending on whether individuals are male or female, or homozygotic or heterozygotic. Not all primates have access to the same type and level of vision. New World primate species that experience more dichromatic vision, particularly the males (Kainz, Neitz, & Neitz, 1998; Regan et al., 2001). Males were found to exhibit more instances of dichromatic vision due to the fact that certain photopigment genes were found on the X chromosome (Kainz, Neitz, & Neitz, 1998; Zhou, Hewett-Emmett, Ward, & Li, 1997). One possible theory for the evolution of trichromacy in Old World primates is the co-evolution of tropical orange/yellow fruits which would be more easily detected among green foliage with trichromatic vision (Bowmaker, 1998). Another set of researchers that looked specifically at the spectral positioning of primate cones, fruit coloration, and primate selection tasks did not feel there was enough evidence to make any final definitive conclusions about fruit-plant co-evolution; they pointed out that trichromacy could have evolved for a number of reasons, such as conspecific recognition, and that not all fruits consumed by primates had necessarily evolved with primates as the intended seed dispersers (Regan et al., 2001).

Nocturnal Primates

The presence of trichromacy in primates has led to some debate about the temporal behavioral activity of ancestral primates. Trichromacy is indicative of higher visual acuity, which is generally more necessary in daylight vision that nighttime vision (Regan et al., 2001). Some researchers insist that ancestral primates were nocturnal, as was the case for early mammals, utilizing the nighttime niche as a way for avoiding predator detection; they say that rod cell markers in current primates confirm this (Perry & Pickrell, 2010). Other researchers disagree, maintaining that ancestral primates were absolutely not nocturnal, but in fact diurnal; for example, Zhao et al. (2009) insist that the presence of ancestral opsin genes, which may now be defunct due to mutations, are the proof required that ancestral primates were not in fact nocturnal. Opsin genes are those which control opsin, which is a type of light-sensitive protein located in photoreceptor cells; different opsins are involved in the conversion of light signals into nerve signals or impulses, vision mediation, circadian rhythms, pupillary reflexes, and other vision-related functions (Land & Nilsson, 2002). The presence or absence of opsin may be indicative of the level of vision present in an animal. Considerable variations provide the necessary evidence that nocturnality among primates in fact went through several different evolutions (Tan, Yoder, Yamashita, & Li, 2005). Ross and Kirk (2007) do not make any final statements, but do note that evolution towards “nocturnal visual predation had a major selective influence on the early evolution of the primate visual system” (p. 294).

Primates as a whole among all mammals have evolved to possess extremely developed and complex vision. According to Zimmer (2001), only very few terrestrial vertebrates developed extremely powerful vision; he singles out birds and primates specifically. Differences in evolution among primate species have shaped the type of vision present from species to species (Bowmaker, 1998; Regan, Julliot, Simmen, Vienot, Charles–Dominique, & Mollon, 2001). Nocturnal vision exhibits heightened light sensitivity over color or clarity; this means that it is more important for nocturnal primates to be able to sense variations in low-light conditions than to possess high color discrimination abilities. Nocturnal animals have developed a number of features to accommodate this condition, including larger eyes, front-facing eyes, and a tapetum lucidum (a reflective tissue layer present in many nocturnal mammals), as well as an abundance of rod cells to maximize light capture (Dyer, Martinsa, da Silva Filhod, Munize, Silveirad, Cepkof, & Finla, 2009; Heesy & Hall, 2010). Some primates historically evolved many of the same adaptations as diurnal mammals, but due to genetic mutations, these features were rendered nonfunctional, which therefore led to the utilization of a nocturnal lifestyle. For example, it has been found that in both the New World *Aotus* (owl monkey) and *Galago* (bushbaby) genera, opsin genes were present in cones, but mutations and defects in the genes had rendered them completely nonfunctional (Jacobs, 2013). Another study examined two bushbaby genera, *Otolemur* and *Galago*, comparing them to human, squirrel monkey, and marmoset X-linked pigment genes; while they were biochemically similar, in bushbabies there were substitutions present that indicated selective pressure towards dim-light sensitivity (Zhou, Hewett-Emmett, Ward, & Li, 1997).

Bearder, Nekaris, and Curtis (2006) looked at the differences among diurnal, cathemeral, and nocturnal primates, and found that vision in nocturnal primates “is more acute and variable than has previously been recognized” (p. 50). They found that even among nocturnal primates with vision specifically adapted to nocturnal landscapes, the behavior of species such as lorises and bushbabies was still affected by the level of light present. For instance, hunting and travel practices of the animals altered with the availability of light, with lorises choosing more mobile prey on nights with more moonlight, and bushbabies traveling more extensively in their territory on nights with more moonlight. They also conducted studies on eyeshine present and reactive behavior to lights in nocturnal primates, and concluded that there was quite a bit of variability among species (Bearder, Nekaris, & Curtis, 2006).

Other studies conducted on the vision of nocturnal primates confirmed greater variation in sight, although this research in particular looked at color vision in nocturnal mammals, including primates (Veilleux & Cummings, 2012). These studies found strong correlations among the diet of mammals and their color discrimination capabilities; namely, those who had diets which consisted of flowers or fruits were proven to have greater S-cone spectral acuity. Additionally, they confirmed that the luminosity of the moon affected the spectral quality of the nocturnal landscape (Veilleux & Cummings, 2012). These studies included thirteen old world primate species, including tarsiers, lemurs, bushbabies, and aye-ayes, as well as one genus of the new world monkey, *Aotus*.

Aotus monkeys are one of the most unique genera of the nocturnal primates. The majority of nocturnal primates are the more primitive prosimians found in Asia and Africa. However, *Aotus* species are actually New World monkeys found in Central and South America, the only true nocturnal monkeys, which have developed morphological and genetic features that specifically aid in using nocturnal vision, such as particularly large corneas and lenses, forward-facing eyes, and genetic features which show a higher likelihood of light sensitivity (Jacobs, Deegan, Neitz, Crognale, & Neitz, 1993). The exact extent of their vision has been debated among researchers. One early study found that *Aotus* vision was in fact trichromatic, with the caveat that their vision was not at the same level as a typical trichromatic primate, but was instead considered to be protanomalous, meaning there is a reduced sensitivity to red light (Jacobs, 1977). Later research contradicted these results and further testing confirmed monochromacy in *Aotus* monkeys (Jacobs et al., 1993). It was extrapolated from human vision tests that since rod signals had been used in color vision tests, this may have been what happened in the 1977 trials with *Aotus* monkeys; trichromacy could not be confirmed in the 1993 tests. Further research revealed exactly why *Aotus* monkeys did not have color vision, with a failure specifically found in their S-cone genes (Jacobs, Neitz, & Neitz, 1996). Another set of researchers specifically names *Aotus* vision as monochromatic in their studies among New World monkeys (Kainz, Neitz, & Neitz, 1998).

Evolutionarily speaking, the development of *Aotus* vision is quite recent, occurring around 15 million years ago; in that time, they have been found to develop a number of morphological and genetic features that maximize adaptability in a nocturnal world, including a "reduced numbers of opsins, changed photoreceptor complements, changed intraretinal connectivity, loss of the fovea, and increased eye size" (Dyer et al., 2009, p. 8967). The fovea is found in all other New World monkeys except for *Aotus*, and facilitates high visual acuity or detail (Dyet et al., 2009). The relatively recent nature of the development of monochromacy in *Aotus* monkeys suggests diurnal ancestry for this particular primate, and in fact this has been confirmed by several other researchers as well (Jacobs et al., 1993; Wikler & Rakic, 1990). The case of *Aotus* monkeys provides a clear example of recent evolution as well as repeat evolution, wherein an evolutionary path repeats itself in response to selection pressure. What exactly forced *Aotus* to return to a nocturnal lifestyle is still not completely clear; it is also unclear why *Aotus* should be the only primate genus to utilize this particular niche.

Conclusion

The evolution of vision among primate species has been an ongoing process, and as with all evolutionary paths, has not been a process with uniform results. As shown in this review paper, some of the information on primate vision, particularly nocturnal primate vision, has been contested among researchers. Even now, the exact origins of primate vision have not yet fully been mapped. Studying vision in nocturnal primates can provide some clear and vital clues to evolutionary paths among primate species of the past. Most research agrees that ancestral mammals were nocturnal. At the foundational level, mammals developed features to survive in an environment dominated by the night. Many primates now live diurnal and cathemeral lifestyles, with only a particular subset maintaining the nocturnal ecological niche. Clues can be found in nocturnal primates demonstrating that for some nocturnal primates, such as the *Aotus* genus, there are morphological and genetic clues pointing to possible diurnality at some point in their evolutionary past. As more research is completed on nocturnal primates, more variation in vision can be found than was previously assumed, and more adaptability to temporal behavioral activity. This sheds light not only on the evolution of nocturnal vision genetically and morphologically, but also in the field of primate culture and animal behavior. In the most recent IUCN conference in Singapore, over half of the world's primates were found to be endangered, and some still do not have enough information to make an accurate determination (IUCN, 2015; More, 2015). Further studies on adaptability of primates, both in vision and behavior, could prove useful in a world where habitat destruction in the wild is on the rise.

Table 1.

Paleozoic Time Periods with Highest Species Diversity*

Period name	**Range of years**
Ediacaran period	635-541 (±1 mil) million years ago (mya)
Cambrian period	541 (±1 mil)-485.4 (±1.9 mil) million years ago (mya)
Ordovician period	485.4 (±1.9 mil)-443.8 (±1.5 mil) million years ago (mya)

*Source: ICS, 2015

Table 2.

Terminology

Term	**Definition**
Cambrian explosion	An evolutionary occurrence during which most of the major phyla present today emerged, as shown by the existing fossil record, and also during which major diversification across all organisms occurred (Land & Nilsson, 2002; Zimmer, 2001; Zhang et al., 2014)
Cathemeral	A type of animal behavior, neither fully nocturnal nor diurnal, wherein animal activity occurs throughout the day and night (Bearder, Nekaris, & Curtis, 2006; Hall, Kamilar, & Kirk, 2012; Bennie, Duffy, Inger, & Gaston, 2014)
Cone	A type of photoreceptor cell in mammalian eyes that is capable of detecting color, and require considerably more light to function; there are 3 types of cones (Gehring, 2014)

Crepuscular	A type of animal behavior that indicates activity mostly during twilight (Bennie, Duffy, Inger, & Gaston, 2014)
Dichromacy	The vision condition in which two types of cone cells are present; generally, these are the short-wave cones (S) and middle-wave cones (M); this can result in conditions like red-green colorblindness. Dichromacy may be hereditary and sex-linked (Zhou, Hewett-Emmett, Ward, & Li, 1997; Bowmaker, 1998; Kainz, Neitz, & Neitz, 1998; Regan, Julliot, Simmen, Vienot, Charles–Dominique, & Mollon, 2001)
Fovea	Also known as the fovea centralis; a small pit found in the center of the retina, composed entirely of cones, which facilitates vision with high acuity or detail ((Dyer et al., 2009)
Long-wave cones (L)	Photoreceptor cells that detect long-wavelength light, peaking at 560 nm (Regan, et al., 2001)
Luminosity	The characteristic of brightness
Middle-wave cones (M)	Photoreceptor cells that detect middle-wavelength light, peaking at 530 nm (Regan, et al., 2001)
Monochromacy	The vision condition in which only one cone cell is present, usually resulting in black-and-white vision (Jacobs et al., 1993; Kainz, Neitz, & Neitz, 1998)
Neuron	Nerve cell (MRC Centre, 2011)
"Nocturnal bottleneck" theory	Theory posited by Walls (1942) wherein early mammal species were considered to be nocturnal in order to best survive during the periods of dinosaur species dominance, later supported by further genetic and morphological research

Opsin genes	Genes that control opsin, the light-sensitive proteins located in photoreceptor cells (Land & Nilsson, 2002; Tan, Yoder, Yamashita, & Li, 2005; Dyer et al., 2009)
Photoreceptor	Photosensitive nerve cell (Wikler & Rakic, 1990; Hunt & Collin, 2014)
Photosensitive Retinal Ganglion Cells (pRGCs)	A type of photoreceptor cell in mammalian eyes, consisting of less than 1% of overall retinal neurons (Wong, Dunn, & Berson, 2005)
Polymorphic vision	A condition found in populations wherein opsins are found on X-linked chromosomes, resulting in mixed dichromacy/trichromacy based on sex (Regan et al., 2001; Kawamura et al., 2012)
Prosimian	A type of primate; living members include the strepsirrhines (lorises and lemurs) and haplorhine tarsiers. Ranges are located on the Asian and African continents (Zhou, Hewett-Emmett, Ward, & Li, 1997; Bearder, Nekaris, & Curtis, 2006)
Protanomalous	Vision condition wherein sensitivity to red light is reduced (Jacobs, 1977)
Rod	A type of photoreceptor cell in mammalian eyes that is more sensitive to light and found in greater quantities in the eye (Bowmaker, 1998; Perry & Pickrell, 2010)
Scotopic vision	Vision adapted to low light conditions (Heesy & Hall, 2010)
Short-wave cones (S)	Photoreceptor cells that detect short-wavelength light, peaking at 420 nm (Regan, et al., 2001; Zhao, Rossiter, Teeling, Li, Cottons, Zhang, & Goodman, 2009)
Tapetum lucidum	A reflective layer of tissue behind the retina of certain nocturnal

	vertebrates (and some deep-sea creatures), which allows for better night vision (Dyer et al., 2009; Heesy & Hall, 2010)
Trichromacy	The vision condition in which three types of cone cells are present, and full color vision is achieved; this is found in many primates in some marsupials (Zhou, Hewett-Emmett, Ward, & Li, 1997; Bowmaker, 1998; Kainz, Neitz, & Neitz, 1998; Regan, Julliot, Simmen, Vienot, Charles–Dominique, & Mollon, 2001)
Visual acuity	Sharpness or clarity of vision (Regan et al., 2001)

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