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Final Report for Project: Color Vision and Frugivory in Costa Rican Capuchin Monkeys

Overview of Project

For my dissertation research, supported by a pre-doctoral research grant from the LSB Leakey Foundation, I investigated the consequences of color vision variation on foraging by white-faced capuchins (*Cebus capucinus*) inhabiting a seasonally dry, tropical forest. Like most other Neotropical monkeys, capuchins possess a polymorphic M/L opsin gene, leading to the presence of multiple dichromatic and trichromatic color vision phenotypes within the population and among social groups. My aim was to determine how color vision variation affected foraging choices, behaviors and efficiency. Capuchins are highly omnivorous and I investigated their foraging patterns for both fruits and insects.

Overview of Methods

My methods included behavioral observations of the individuals in four groups (N=72) of free-ranging monkeys and color vision genotyping of all group members from fecal DNA, as well as ecological measures of the use and availability of their natural foods, and colorimetric data collection to document their visual environment and to model the appearance of their diet. I conducted 13 months of field research in north-western Costa Rica between January 2007 and September 2008. I assisted with the genotyping of the monkeys, which was completed via DNA amplification and sequencing at the University of Tokyo from January 2006-December 2010.

Summary of Analyses and Results

Do trichromatic capuchins have an advantage over dichromats for frugivory?

I found that trichromatic individuals, especially those with the most spectrally-separated photopigments, were more accurate than dichromats during close-distance foraging for conspicuous (reddish) fruits. These fruits were an important component of the capuchin diet and were consumed most frequently during the hottest and driest months of the year when they provided a critical source of moisture, having higher water content than fruits of other colors. However, trichromat advantage was not universal. Trichromats did not have an advantage for selecting cryptically-colored fruits. Simulations of capuchin color vision phenotypes during computer trials emulating naturalistic foraging tasks (searching for fruits and insects against their native backgrounds) performed by human volunteers revealed a detection advantage to individuals experiencing trichromatic color vision types for brownish, yellowish and reddish fruits, but not for greenish, purple or black fruits.

Do dichromatic monkeys compensate behaviorally for their decreased capacity for visual chromatic discrimination?

Dichromatic monkeys exhibited different foraging behaviors than their trichromatic counterparts, indicating that they compensate behaviorally for their poorer chromatic vision. Dichromatic monkeys had a relatively increased foraging attempt rates (number of fruits investigated per minute) and heightened use of non-visual senses, for example smell during fruit foraging as compared to trichromatic monkeys.

Is dichromacy advantageous over trichromacy for any foraging situations?

Dichromatic monkeys did have a foraging advantage for certain food types. They had a higher capture efficiency of surface-dwelling invertebrates, while trichromatic monkeys increased their search times to achieve the same net prey intake. This is interpreted to reflect an increased ability of dichromats to penetrate the camouflage of dietary invertebrates against their natural backgrounds and reflects an interesting foraging advantage.

Relevance for human evolution

Like Neotropical monkeys, such as capuchins, and unlike other catarrhine primates, humans have a high incidence of color vision deficiencies. The evolutionary significance of this is unknown. While this may reflect a relaxation of selection pressure operating on the M/L opsin gene during human evolution, alternatively, the relatively high occurrence of human dichromats and anomalous trichromats may have an adaptive explanation. If, like capuchin monkeys, color deficient humans had an improved ability to detect camouflaged prey, or other important objects such as conspecifics or predators, then natural selection may have favoured their persistence. At the same time, the continued predominance of human trichromats indicates that color vision remained important throughout human evolution and suggests that if dichromat phenotypes were favoured under some conditions, they were not favoured under all conditions. Niche-divergence, frequency-dependant or mutual benefit of association mechanisms of balancing selection could potentially explain the stable persistence of multiple phenotypes among populations.

Conclusions

In sum, advantages can be identified for both dichromacy and trichromacy. My findings indicate that frugivory involving brownish, reddish and yellowish fruits may exert selection pressures favouring trichromacy. Advantages associated with insectivory may alternatively favour the persistence of dichromatic phenotypes among capuchin monkeys in this polymorphic system. Furthermore, dichromats can compensate behaviorally during fruit foraging, to achieve similar net fruit intakes as trichromats. Future studies should examine the associated energetic costs and benefits, as well as the long-term reproductive success of dichromatic versus trichromatic primates to better understand the evolutionary mechanisms maintaining polymorphic color vision.

List of publications resulting from research

Peer-reviewed Journal Articles

Carnegie S, Fedigan L, and **Melin AD**. Reproductive Seasonality in Female Capuchins (*Cebus capucinus*) in Santa Rosa (Área de Conservación Guanacaste), Costa Rica. International Journal of Primatology.	**In Press**
Parr N, **Melin AD** and Fedigan LM. Figs are more than fallback foods: the relationship between *Ficus* and *Cebus* in a tropical dry forest. International Journal of Zoology.	**In Press**
Kawamura S, Hiramatsu C**, Melin AD**, Schaffner CM, Aureli F, and Fedigan LM. Polymorphic color vision in primates: evolutionary considerations. In: Post Genome Biology of Primates Hirai H, Imai H, and Go Y. eds. Springer, Tokyo, Japan.	**2010**
Melin AD, Fedigan LM, Young HC, and Kawamura S. Can color vision variation explain sex differences in invertebrate foraging by capuchin monkeys? Current Zoology 56 (3): 300-312.	**2010**
Hiwatashi T, Okabe Y, Tsutsui T, Hiramatsu C, **Melin AD**, Oota H, Schaffner CM, Aureli F, Fedigan LM, Innan H and Kawamura S. An explicit signature of balancing selection for color vision variation in New World monkeys. Molecular Biology and Evolution 27: 453–464.	**2010**
Melin AD, Fedigan LM, Hiramatsu C, Hiwatashi T, Parr N and Kawamura S. Fig Foraging by dichromatic and trichromatic white-faced capuchin monkeys in a tropical dry forest. International Journal of Primatology 30 (6): 753-775. *(Invited contribution)*	**2009**

Hiramatsu C, **Melin AD**, Aureli F, Schaffner CM, Vorobyev M and Kawamura S. Interplay of olfaction and vision in fruit foraging of spider monkeys. Animal Behavior 77: 1421-1426. **2009**

Hiramatsu C, **Melin AD**, Aureli F, Schaffner CM, Vorobyev M, Matsumoto Y and Kawamura S. Importance of achromatic contrast in short-range fruit foraging of primates. PLoS One 3(10): 1-12. **2008**

Conference Presentations

Melin AD, Kline DW, and Fedigan, LM. Human Observers as Monkey Surrogates: An Evaluation of the Evolutionary Significance of Color Vision in Food Search. Oral presentation at the Annual University of Calgary and Alberta Health Services Ophthalmology and Visual Sciences Research Conference, Calgary, Alberta. **2011**

Melin AD, Fedigan L, Parr N. Preference and Seasonal Use of "Colorful" Fruit: Implications for Primate Color Vision. Oral presentation at the Annual Canadian Society for Ecology and Evolution Conference, Banff, Alberta.* **2011**

Melin AD, Parr N, Fedigan LM and Kawamura S. Dietary selectivity by white-faced capuchins: How important are colorful fruits? Oral presentation at the XXIII Congress of the International Primatological Society, Kyoto, Japan.* **2010**

Melin AD, Fedigan LM, Young H and Kawamura S. Invertebrate Foraging by Costa Rican Capuchin Monkeys: Testing Predicted Sex Differences in Relation to Color Vision Variation. Oral presentation at the 33rd Annual Meeting of the American Society of Primatologists, Louisville, Kentucky.* **2010**

Parr N, **Melin AD** and Fedigan LM. The effect of fruiting fig trees on the ranging behavior of white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. Oral presentation at the 32nd Annual Meeting of the American Society of Primatologists, San Diego, Florida.* **2009**

Melin AD, McCabe, G and Fedigan LM. Are colorful fruits more nutritious? Implications for primate color vision. Oral presentation at the 36th Annual Canadian Association of Physical Anthropologists Conference, Hamilton, Ontario. **2008**

Parr N, Campos F, **Melin A** and Fedigan LM. Seasonal ranging behavior in white-faced capuchins (*Cebus capucinus*). Oral Presentation at the 36th Annual Canadian Association of Physical Anthropologists Conference, Hamilton, Ontario. **2008**

Melin AD, Fedigan LM, Hiramatsu C and Kawamura S. Fig foraging by capuchins: considering polymorphic color vision. Oral presentation at the XXII Congress of the International Primatological Society, Edinburgh, Scotland.* **2008**

Hiramatsu C, **Melin AD**, Aureli F, Schaffner CM, Vorobyev M and Kawamura S. Effectiveness of chromatic and achromatic signals in fruit foraging of wild spider monkeys (*Ateles geoffroyi*). Oral presentation at the XXII Congress of the International Primatological Society, Edinburgh, Scotland.* **2008**

Kawamura S, Matsumoto Y, Ozawa N, Hiwatashi T, Okabe Y, Tsutsui T, Hiramatsu C, **Melin AD**, Innan H, Schaffner CM, Filippo A, and Fedigan LM. Mutations creating novel spectral types of atelid L/M opsin alleles and the natural selection acting to maintain allelic polymorphism of L/M opsin genes in wild populations of New World monkeys. Oral presentation at the XXII Congress of the International Primatological Society, Edinburgh, Scotland.* **2008**

* Denotes peer-reviewed contribution