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Primate Coloration: An Introduction to the Special Issue

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Color plays a significant role in the ecology and behavior of many animal species, including in food detection and foraging, intraspecific signaling, predator detection, and camouflage. However, understanding the role of color in the lives of animals offers many challenges, as animal coloration sits at the boundary between chemistry (the chemical basis and properties of colors exhibited and encountered), physics (the composition and structure of light, and physical patterns of reflection and absorption), and numerous aspects of animal biology. As such, color and its perception are at the interface between an animal's behavioral and sensory ecology and the wider physical environment.

Primates are the most colorful group of mammals, and many species display striking sexual dimorphism in pelage, facial, and anogenital skin coloration. The range of colors exhibited by primates of diverse taxa suggests the importance of color in primate behavior and social signaling, but empirical studies of primate color were rare until relatively recently. Primate coloration research has lagged behind work conducted on other taxa such as fish, birds, insects, and reptiles in the number of studies of adaptive function, as well as in the sophistication of the methods used to overcome the inherent problems of color quantification, and in the appreciation of differences in the sensory systems with which animals detect and interpret color. The limited ability to conduct controlled experiments on primates, and the obstacles of studying colorful primates that often live in wet, dark forests (making the use of photographic equipment difficult), have provided further challenges to color research in this group.

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On August 5, 2008, a symposium entitled "Primate Coloration: Measurement, Mechanisms and Function" took place as part of the 22nd Congress of the International Primatological Society in Edinburgh. This symposium brought together researchers who have studied various aspects of coloration in diverse species, including nonprimates, and sought to highlight the growing range of research on primate coloration, to shed light on the underlying mechanisms determining color expression, and to elucidate the functions of color signals in the lives of primates. This issue is a result of that symposium, and features papers by the majority of the speakers who participated on the day. I would like to take this opportunity to thank Russell Tuttle for first inviting this special issue, and Jo Setchell for being so enthusiastic and supportive of it after she became Editor-In-Chief. Jo's own contribution to this issue was invited, and was in preparation, before she was asked by Springer to take up her current role as EIC. Special thanks are due to the British Ecological Society, who provided generous sponsorship, and to Melissa Gerald, who originally co-proposed the symposium with me. Springer very kindly offered to produce color figures for free throughout the issue. Janet Slobodien, Myrene Grande, Theresa Kornak, and various editorial assistants, all helped enormously at various stages of the process, ensuring that the issue was produced quickly and to a high standard. I would also like to thank all of the referees who reviewed papers; the quality of the final manuscripts is testament to their hard work.

The issue begins with a study by Melin *et al*., who show that there is variation in foraging strategies among white-faced capuchins (*Cebus capuchinus*) according to visual system type, with dichromatic individuals apparently using other senses such as olfaction to compensate for reduced visual discriminability when selecting ripeness of figs by color. A number of studies then focus on the importance of skin color variation in various Old World primate species. Dubuc *et al*. show that variation in rhesus macaque (*Macaca mulatta*) female facial color correlates with the timing of ovulation, such that facial color has the potential to signal this to others. Bergman *et al*. present data on gelada (*Theropithecus gelada*), showing that male chest patch color acts as a badge of status, with harem leader males being more colorful than others, and males with larger harems being more colorful than those with smaller harems. Marty *et al.* present data on one of the most colorful but least studied of catarrhines, the drill (*Mandrillus leucophaeus*). They show that color of male drills is positively related to rank, but that rank appears to be a more important factor than color in determining male-female association patterns and rates of sexual behaviors. Setchell *et al.* combine data from their long-term studies on mandrills (*Mandrillus sphinx*) with new data, to ask whether mandrill coloration acts as a signal of overall individual quality. They find no evidence from their study population that this is the case, despite the many previous exciting results from this population showing that color is linked to status. Finally, Stephen *et al.* show that facial color can be important in signaling health and condition in our own species (*Homo sapiens*), with observers changing the color of human faces to make them appear healthier. This study reminds us that investigating how color may signal underlying physiological condition is relevant for understanding ourselves as well as the nonhuman primates we study.

Though the aforementioned manuscripts reveal the large recent increase in the number of studies addressing the function of primate skin color signals, this has

unfortunately yet to be matched in the number investigating pelage color. As such, it is especially pleasing to be able to include studies on the underlying mechanisms and adaptive significance of fur coloration. Clough et al. provide one of the first studies to measure pelage color objectively in the wild. They show that, although variation in color of the rufous crown of male red-fronted lemurs (*Eulemur fulvus rufus*) does not correlate with variation in male reproductive success or rank, it is nonetheless related to interseason differences in androgen levels, and hence may provide some information about male condition. In a second study of pelage color, Kamilar presents interesting new comparative analyses testing the function of countershading in primate groups, and finds support for hypotheses linking the evolution of countershading to antipredation strategies. Overall, the research manuscripts assembled collectively highlight the importance of color in the lives of many primate species, including our own, in both social and sexual signaling, camouflage, and in detecting and obtaining food.

Numerous studies in this issue measure color objectively via digital photography. However, it is important to remember that the detection and interpretation of color signals is not objective; it is entirely subjective, according to receiver perception. In this regard, Stevens *et al.* present a detailed methods paper that includes techniques for the analysis of color with respect to specific visual systems, linking the study of primate color signals to the visual sciences. Given information about visual system properties, discrimination threshold modeling can be used to determine how different colors appear within the visual system(s) of the relevant receiver(s). Primatologists are well placed to use such methods given that the visual systems of a broad range of primate species have been studied in detail.

The approach outlined in the contribution of Stevens *et al.* would seem particularly well suited to investigating the significance of color in species with polymorphic color vision, such as many New World monkeys and lemurs. Linking genetic approaches for the determination of visual system type, detailed field studies of behavior, and visual system modeling, should allow investigation of the colors exhibited by cryptic and conspicuous fruits, camouflaged predators, and the displays of conspecifics, to occur within the context of how different group members are likely to perceive the same color signals. This is likely to be key in understanding the selective pressures that maintain such polymorphisms in natural populations. The utility of such methods for the analysis of signals in species with visual systems similar to our own, i.e., red, green, blue trichromats, remains to be seen, though early indications are that even here this approach can be enlightening (Higham *et al. unpubl data*). The importance of all color signals encountered by animals, from a ripe fig in a tree, to the bright face or fur of a conspecific, is in the eye of the beholder.