It is hypothesized that human faces judged to be attractive by people possess two features—averageness and symmetry—that promoted adaptive mate selection in human evolutionary history by way of production of offspring with parasite resistance. Facial composites made by combining individual faces are judged to be attractive, and more attractive than the majority of individual faces. The composites possess both symmetry and averageness of features. Facial averageness may reflect high individual protein heterozygosity and thus an array of proteins to which parasites must adapt. Heterozygosity may be an important defense of long-lived hosts against parasites when it occurs in portions of the genome that do not code for the essential features of complex adaptations. In this case heterozygosity can create a hostile microenvironment for parasites without disrupting adaptation. Facial bilateral symmetry is hypothesized to affect positive beauty judgments because symmetry is a certification of overall phenotypic quality and developmental health, which may be importantly influenced by parasites. Certain secondary sexual traits are influenced by testosterone, a hormone that reduces immunocompetence. Symmetry and size of the secondary sexual traits of the face (e.g., cheek bones) are expected to correlate positively and advertise immunocompetence honestly and therefore to affect positive beauty judgments. Facial attractiveness is predicted to correlate with attractive, nonfacial secondary sexual traits; other predictions from the view that parasite-driven selection led to the evolution of psychological adaptations of human
beauty perception are discussed. The view that human physical attractiveness and judgments about human physical attractiveness evolved in the context of parasite-driven selection leads to the hypothesis that both adults and children have a species-typical adaptation to the problem of identifying and favoring healthy individuals and avoiding parasite-susceptible individuals. It is proposed that this adaptation guides human decisions about nepotism and reciprocity in relation to physical attractiveness.

**KEY WORDS:** Aesthetics; Fluctuating asymmetry; Heterozygosity; Mate choice; Nepotism; Parasites; Reciprocity; Sexual reproduction.

**INTRODUCTION**

The evolution of mate choice and the traits that evolve by mate choice are topics of considerable interest to biologists. In many species, individuals clearly choose mates partly for their ability to deliver material benefits, such as protection, food, and care to the choosing sex and its offspring (e.g., Thornhill and Alcock 1983; Trivers 1985). *Homo sapiens* is among these species (Kaplan and Hill 1985; Borgerhoff Mulder 1990; see also Buss 1989; Symons 1979). In many other species, however, individuals of one sex (generally males) do not provide material benefits. Yet even in many of these species, certain potential mates are consistently preferred over others. Biologists have sometimes explained these preferences by arguing that preferred mates possess superior viability that is passed on to their offspring. That is, the choosing sex has been claimed to prefer individuals who evidence "good genes" (e.g., Trivers 1972; Williams 1966; Zahavi 1975).

Historically, many population geneticists have doubted that preferences for "good genes" could evolve (e.g., Kirkpatrick 1987). The evolution of such preferences requires heritable variation in fitness: Parental fitness advantages must be passed on to offspring. According to classical population genetic models, however, selection removes genetic variation in fitness so that little exists at any given time. Hence, these models assert that preferences for "good genes" over "bad genes" shouldn't evolve because relatively few "bad genes" should be around. These models have assumptions, of course, one of which is that populations are subject to constant selection pressures. For decades, evolutionary geneticists have known that, theoretically, shifting selection could maintain heritable fitness differences indefinitely. Nonetheless, few had rea-