

Original Article

Short stature in African pygmies is not explained by sexual selection[☆]

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Initial receipt 4 October 2011; final revision received 18 March 2012

Abstract

African pygmies' short stature has been studied for more than a century, but the evolution of this extreme phenotype remains unknown. The present study tests the hypothesis that sexual selection, through preference for short partners, may have contributed to the evolution of pygmies' stature. We gathered anthropometric and familial data from 72 Baka pygmy couples and 27 neighboring Nzimé nonpygmy couples from Cameroon. We found evidence for positive assortative mating and partial evidence for the male-taller norm in both groups. This is surprisingly close to results reported for many modern occidental populations, in which sexual selection is thought to exert a positive selective pressure on men height. Semistructured interviews of Baka pygmies concerning height and mate choice suggested that the male-taller norm matches mating preferences. Stature was also positively correlated with the number of serial marriages contracted by men of both populations, while the stature of women was not related to their mating success. Finally, we did not detect any linear or quadratic effect of height on reproductive success for either men or women. Altogether, our results demonstrate that stature influences mate choice in pygmies, and we argue that, if of any influence for sexual selection, mate choice should have favored tallness rather than shortness in our pygmy population. Consequently, this study establishes that sexual selection is a very unlikely candidate to account for the evolution of pygmies' short stature.

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Keywords: African pygmies; Short stature; Sexual selection

1. Introduction

African pygmies are the shortest human populations worldwide (Froment, 1993; Perry & Dominy, 2009). Various evolutionary hypotheses have been put forward to explain this short stature (reviewed in Perry & Dominy, 2009). To date, all proposed explanations have been based on adaptations to particular features of the rainforest environment such as hot and humid climate (Cavalli-Sforza,

1986), food scarcity (Shea & Bailey, 1996), high density of the forest cover (Diamond, 1991), or high mortality (Migliano, Vinicius, & Lahr, 2007). However, these hypotheses remain controversial (Becker, Verdu, Hewlett, & Pavard, 2010; Perry & Dominy, 2009) and are difficult to test rigorously due to the lack of data and current changes in the pygmies' life conditions (Bahuchet, 1991).

Surprisingly, pygmies' stature has never been considered as a potential adaptation to mate choice. Stature is known to be a strong determinant of physical attractiveness (Fink, Neave, Brewer, & Pawlowski, 2007; Pierce, 1996) and to ultimately influence both mating and reproductive success in several human populations (Mueller & Mazur, 2001; Nettle, 2002b; Pawlowski, Dunbar, & Lipowicz, 2000; Sear, 2010, Stulp, Pollet, Verhulst, & Buunk, 2011). Because height is a highly heritable trait (Silventoinen et al., 2003; Visscher et al., 2006), selective pressures exerted by mate choice can influence the evolution of human stature. Mate choice could

[☆] This work was supported by Institut de Recherche pour le Développement, the Bonus Qualité Recherche of the Département Homme, Natures, Société of the MNHN, ATM-MNHN: «Les relations Sociétés-Natures dans le long terme» 2009–2012, the Kone Foundation (Finland), the Wissenschaftskolleg zu Berlin (Germany), and the Fondation pour la Recherche Médicale (France).

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therefore have contributed to the pygmies' phenotype if mating preferences for short stature have evolved. Theoretically, population differences in mating preferences for any trait can evolve either because of stochastic events such as genetic drift and mutation (Kirkpatrick, 1982; Lande, 1981) or because of a differential relationship between the trait and potential benefits (direct or indirect) that are provided for the partner (Endler, 1992; Reynolds & Gross, 1990). Because several studies suggest that both costs and benefits associated with height vary between environments (Sear, 2010), it is possible that particular mate preferences favoring short height have emerged in certain populations.

Most studies conducted on height attractiveness have been conducted in modern western populations (reviewed in Courtiol, Raymond, Godelle, & Ferdy, 2010; Swami et al., 2008). They have reported preferences that can be approximated, in each sex, by a positive linear relationship between the height of an individual and the stature he/she prefers in a partner (Courtiol et al., 2010). On average, the taller an individual, the higher his/her favorite height (Hensley, 1994; Kurzban & Weeden, 2005; Salska et al., 2008). Such preference functions also imply that women prefer men taller than themselves and men prefer women shorter than themselves (Beigel, 1954; Gillis & Avis, 1980; Shepperd & Strathman, 1980). Actual pairings seem to be strongly influenced by such mating preferences, and indeed, many studies report a positive correlation between spouse heights, a pattern usually referred to as assortative mating (reviewed in Roberts, 1977; Spuhler, 1968). In addition, the number of couples in which the female is taller than the male is usually lower than we would expect under random mating, a pattern referred to as the male-taller norm (Gillis & Avis, 1980). Concerning the influence of height on mating and reproductive success, while very few studies have focused on women, in most male studies, tall individuals have a higher mating success than shorter men (e.g., Mueller & Mazur, 2001; Nettle, 2002a), and several studies also found an advantage of tallness on male reproductive success (e.g., Mueller & Mazur, 2001; Pawlowski et al., 2000). Overall, mating patterns seem quite consistent across modern western populations; they show that male tallness is favored by sexual selection.

Concerning influence of height on mate choice in nonwesternized populations, several studies confirm that relationships between height and mating success, reproductive success, and mating patterns can differ between populations (reviewed in Sear, 2010). For instance, mating patterns for Gambian agriculturalists and Tanzanian Hadza hunter-gatherers do not present any evidence of assortative mating or male-taller norm (Sear, 2006; Sear, Allal, & Mace, 2004; Sear & Marlowe, 2009). Additionally, height did not appear to influence mating success in the Hadza population (Sear & Marlowe, 2009), and male reproductive success was not associated with stature in the Gambian population (Sear, 2006). To our knowledge, mating patterns and the potential effect of stature on mating and reproductive success have

never been investigated in African pygmies. Yet, there is no reason to exclude the possibility that variation in the influence of height on mate choice could have led sexual selection to favor short stature in some populations.

To assess the potential role of mate choice in the evolution of small stature of African pygmies, we gathered anthropometric and familial data from married couples in the Baka pygmies from Cameroon as well as discursive data on the role of stature in mate preference. For comparison, we carried out the same procedure in the neighboring nonpygmy Nzimé. In these two populations, we tested for the presence of assortative mating and male-taller norm and studied the influence of height on both mating and reproductive success. This is the first study about mate choice in pygmies, and our goal is to determine whether sexual selection for height can account for pygmies' shortness.

2. Methods

2.1. Study populations

This study focuses on the Baka pygmies from central Cameroon and on their nonpygmy Nzimé neighbors. The traditional ecology of various pygmy populations, including the Baka, has been described as a seminomadic, hunter-gatherer, mode of life (reviewed in Bahuchet, 1991). In the Baka village studied (Le Bosquet), as in many pygmy groups nowadays, most families combined hunting and gathering in the forest with agriculture in small fields close to the village. Le Bosquet, surrounding a catholic mission, has existed for around 20 years and consists of over 850 Baka. Nzimé individuals were sampled from two villages in the same area. These villages are inhabited by both Nzimé and Baka families, and most of the Baka are related to the inhabitants of Le Bosquet. The relationship between the Baka and the Nzimé is characterized by exchanges of meat and products of the forest (gathered by the Baka) for iron tools and products of agriculture from the Nzimé. Baka individuals also frequently work in the Nzimé fields. Almost all African pygmy groups have developed a similar interdependent relationship with nonpygmy farmers (Bahuchet, 1991; Bahuchet & Guillaume, 1982).

This relationship plays an important role in the marriage system of the Baka as iron tools and other goods obtained from the Nzimé are often part of the dowry necessary for marriage in Baka society. A young Baka man usually proposes to a woman he likes and, if she accepts, both families will be consulted, the dowry will be paid to the family of the bride, and the new couple will live and work with her family for some years (bride service) before usually moving to his family camp or village. The Baka are free to choose any mate that is outside their paternal and maternal clans. This interdiction is very strictly observed even though some exceptions exist (Bahuchet, 1992; Paulin, 2010).

To our knowledge, there is no literature about the Nzimé marriage system. Interviews conducted in one of the study

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