Limited dispersal in mobile hunter–gatherer Baka Pygmies

Paul Verdu\textsuperscript{1,2,\textdagger}, Raphaël Leblois\textsuperscript{3}, Alain Froment\textsuperscript{4}, Sylvain Théry\textsuperscript{2}, Serge Bahuchet\textsuperscript{2}, François Rouxset\textsuperscript{5}, Evelyne Heyer\textsuperscript{2} and Renaud Vitalis\textsuperscript{2,\textdagger}

\textsuperscript{1}Department of Human Genetics, University of Michigan, Ann Arbor, MI, USA
\textsuperscript{2}MNHN–CNRS, Université Paris 7, UMR 7206 ‘Ecoanthropology and Ethnobiology’, Paris, France
\textsuperscript{3}MNHN–CNRS, UMR 7205 ‘Origine, Structure et Evolution de la Biodiversité’, Paris, France
\textsuperscript{4}IRD–MNHN, UMR 208 ‘Patrimoines locaux’, Paris, France
\textsuperscript{5}Université Montpellier 2–CNRS, UMR 5554 ‘Institut des Sciences de l’Évolution’, Montpellier, France
\textsuperscript{\dagger}Author for correspondence (verdu@umich.edu).


Hunter–gatherer Pygmies from Central Africa are described as being extremely mobile. Using neutral genetic markers and population genetics theory, we explored the dispersal behaviour of the Baka Pygmies from Cameroon, one of the largest Pygmy populations in Central Africa. We found a strong correlation between genetic and geographical distances: a pattern of isolation by distance arising from limited parent–offspring dispersal. Our study suggests that mobile hunter–gatherers do not necessarily disperse over wide geographical areas.

Keywords: African Pygmies; dispersal; isolation by distance; microsatellites; population genetics

1. INTRODUCTION
The correlation between genetics and geography has been extensively studied at a worldwide scale to better characterize the distribution of human genetic diversity and estimate key parameters of modern humans’ expansion worldwide (e.g. Ramachandran et al. 2005; Liu et al. 2006; DeGiorgio et al. 2009). However, none of these studies have characterized parent–offspring dispersal and therefore, the dispersal mechanisms underlying the geographical distribution of human genetic diversity remain unclear.

Ethnologists have shown the great variability of mobility across human populations with different lifestyles and modes of subsistence. For example, foragers have been shown to be much more mobile than farmers (MacDonald & Hewlett 1999). However, the relationship between mobility and effective dispersal (characterized by the distances between children’s and parents’ birthplaces) often remains unknown. To explore this aspect, we studied African Pygmies, which represent the largest hunter–gatherer group of populations worldwide. African Pygmies are described as being very mobile within the rainforest for seasonal mobility and socioeconomic activities (Bahuchet 1992). Demographic data in an Aka Pygmy population further showed large mating ranges and large distances between birthplaces and places of residence (Cavalli-Sforza & Hewlett 1982). This suggests that such mobile behaviour should translate into long distances between children’s and parents’ birthplaces, but this assumption has never been explicitly tested owing to limited demographic data (Cavalli-Sforza 1986). In this context, population genetics can provide indirect estimates of effective dispersal in these hunter–gatherers. Indeed, isolation by distance theory predicts that at equilibrium between drift, migration and mutation, the regression of $F$-statistics estimates on the logarithm of geographical distances provides a robust estimate of the neighbourhood size, which is proportional to the population density and the second moment of parent–offspring distance, if individuals are sampled at a short geographical scale (Rousset 1997).

Here, we report estimates of effective dispersal based on the relationship between genetic and geographical distances in three groups of the Baka Pygmies from Cameroon. This is, to the best of our knowledge, the only genetic data for such a small geographical scale in African Pygmy populations, which provides an opportunity to infer effective dispersal using the genetics of these mobile hunter–gatherers.

2. MATERIAL AND METHODS
The Baka from Cameroon represent one of the largest Pygmy populations with 35 000 individuals occupying 75 000 km\textsuperscript{2} in the rainforest (figure 1). These values, which were compiled from ethnographic data (Vallois & Marquer 1991; Dhellemmes & Macaigne 1985; Cavalli- Sforza 1986; Sato 1992; Abégé 1998; Tsuru 2001), provide an estimate of the population density of $D = 0.47$ individuals \cdot km\textsuperscript{2}.

We consider 87 Baka adults genotyped at 28 independent tetranucleotide microsatellite loci (Verdu et al. 2009). We visited Baka settlements along three transects of approximately 50 km each (figure 1), asking volunteers to gather for DNA sampling at a single location for each transect. Frequent movements between places of temporary residence, as well as hospitality rules among Pygmies that assimilate visitors as residents during their visit, make it difficult to determine whether an individual met in a village is a resident or a visitor (Cavalli-Sforza 1986; Bahuchet 1992). Therefore, the sampling location, or the location where individuals were first met, are probably a poor predictor of Pygmies’ location after dispersal and these data were discarded. Instead, we considered that birthplaces provided more robust data to study Pygmies’ dispersal. After collecting each individual’s birthplace, we went back on the road to determine the geographical coordinates of these locations. Each donor provided appropriate informed oral consent.

Geographically limited dispersal across generations in two-dimensional habitats results in a linear relationship between pairwise genetic distances $d$, an analogue to $F_{ST}/(1 - F_{ST})$ calculated between pairs of individuals (Rousset 2000), and the logarithm of geographical distance. We used the software package GIMPoR\textsuperscript{007} (Rousset 2008) to calculate the slope of this linear regression, which, at a small geographic scale, provides a robust estimator of $1/(4D\sigma^2)$, where $D$ is the effective population density and $\sigma^2$ is the second moment of parent–offspring axial distance (Rousset 1997). We tested the significance of the correlation using a Mantel test (Mantel 1967) with 30 000 permutations. First, we considered all pairs of individuals from the three geographically distant Baka groups (figure 1). Second, we considered only pairs of individuals born within the same group and discarded pairs of individuals born in different groups. To that end, we wrote a R script (R Development Core Team 2007), available upon request, which modified the Mantel test to calculate rank correlation coefficients and to permute the pairwise distances within groups only.

3. RESULTS AND DISCUSSION
Considering all possible pairs of Baka individuals, we found a significant positive correlation between pairwise genetic distance and the logarithm of geographical distance ($p = 0.010$): individuals born
Democratic

100

296 km, a value much larger than the distance between any two individuals’ birthplace was assuming a value of 0.0038–0.0265; p = 0.004; figure 2) providing an estimate of 4Dσ^2 = 73 individuals, which gave σ^2 = 12.4 km^2. Here, the maximum distance between two sampled individuals’ birthplaces (26 km) was shorter than d_{max} = 53 km, indicating that this estimate of σ^2 should no longer be biased by mutation. But we cannot exclude that reducing the sampling scale potentially excluded some long-distance migrants, which would lead to an underestimate of σ^2 (Rousset 2004).

Altogether, this suggests that the effective parent–offspring dispersal in the Baka Pygmies lies between 12.4 and 63.2 km^2. These indirect estimates of effective dispersal average over male and female genetic contributions, since they are based on autosomal

Figure 1. Geographical distribution of the 87 Baka Pygmies sampled in southeastern Cameroon. In each Baka group, birthplaces of sampled individuals are shown with sample sizes given in parentheses. Other Pygmy peopling areas inferred from our ethnographical fieldworks are shown. Map sources: Global Land Cover Facility.

Figure 2. Correlation between genetic differentiation and the logarithm of geographical distances among Baka Pygmies. Multilocus estimates of pairwise differentiation (d_{st}) are plotted against the logarithm of geographical distances (in kilometres). The linear regression considering all pairs of individuals is y = 0.0027x – 0.0153 (in blue). The linear regression considering only pairs of individuals born within the same group is y = 0.0137x – 0.1138 (in red).

data. Assuming that parent–offspring dispersal distances are exponentially distributed (Cavalli-Sforza & Hewlett 1982), then half of the offspring disperse at distances shorter than $\sigma \ln(2)/\sqrt{2} \approx 0.49 \sigma$. In this case, half of the Baka offspring disperse at a maximal distance between 1.7 and 3.9 km. However, using different distributions than the exponential for the dispersal distances would provide different interpretations. Therefore, dispersal distances estimated from $\sigma^2$ should be preferred here since they are independent of the (unknown) shape of the dispersal distribution.

Without quantitative demographic data on the Baka’s mobility, we used the available demographic data from the Aka Pygmies from the Central African Republic (Cavalli-Sforza & Hewlett 1982) for comparison. We calculated the second moment of the distribution of distances between birthplaces and places of residence, an estimate of $\sigma^2$ from demographic data. From table 5 in Cavalli-Sforza & Hewlett (1982), we computed $\sigma^2$ as $\sum_i i^2 p_i$, where $p_i$ is the proportion of individuals whose birthplace and place of residence are separated by $i$ kilometres. We found $\sigma^2 = 3599$ km$^2$ for men and $4061$ km$^2$ for women ($3683$ km$^2$ on average). Hence, our estimates of the Baka’s dispersal from genetic data are, respectively, 58.3 and 297 times lower than the average estimate of dispersal from demographic data in the Aka. How can this discrepancy be reconciled?

First, ethnologists show that mobility significantly differs across Pygmy populations from Central Africa (Bahuchet 1992). For instance, the mobility of the Bongo from Gabon probably decreased recently as opposed to the extended mobility of the Aka, since the Bongo nowadays live in permanent houses and widely practice agriculture (P. Verdu 2006–2007, unpublished results). In this context, the difference between our indirect estimates of dispersal in the Baka and the direct estimates in the Aka could result from differences in dispersal behaviour between these groups. Second, Cavalli-Sforza & Hewlett (1982) provide the distribution of distances between birthplaces and places of residence. This demographic data primarily reflects exploration behaviour rather than effective parent–offspring dispersal. To consistently compare demographic and genetic estimates, demographic estimates require an accurate knowledge of parents’ and offspring’s birthplaces, which is particularly challenging in Pygmies (Cavalli-Sforza 1986).

In conclusion, we found a strong signal of isolation by distance among the Baka Pygmies, a pattern owing to limited parent–offspring dispersal. Although our results do not challenge the view that hunter–gatherer Pygmies have frequent movements in their socio-economic area, we demonstrate that extended individual mobility does not necessarily reflect extended dispersal across generations. Limited effective dispersal may have reinforced genetic isolation among Pygmy populations, which could be a key mechanism explaining the strong genetic differentiation found among Western Central African Pygmies, despite their recent divergence from a single ancestral population about 2800 years ago (Verdu et al. 2009).

More generally, our findings also challenge the view that mobile hunter–gatherers disperse more than sedentary farmers. Hunter–gatherers are generally described as much more mobile than agricultural populations, based on mating distances (see fig. 3 in MacDonald & Hewlett (1999)). Here, we show that Baka hunter–gatherers’ dispersal is strongly localized, as is the effective dispersal previously estimated in the horticulturalist Gainj- and Kalam-speakers from New Guinea ($\sigma^2 = 1.41$ km$^2$; Rousset 1997), the only other human genetic data collected at the appropriate geographical scale for applying Rousset’s (1997) regression method (Long et al. 1987). This suggests that, despite their very mobile behaviour, foragers do not necessarily disperse more than farmers.

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