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DNA fingerprinting in Speke's gazelle: a test for genetic distinctness, and the correlation between relatedness and similarity

M. A. BUTLER, A. R. TEMPLETON and B. READ*

Department of Biology, Washington University, St. Louis, MO 63130 and
**St. Louis Zoological Park, St. Louis, MO 63110, USA*

Abstract

In the absence of pedigree information, the determination of genetic distinctness of populations can only be made by genetic methods. Using DNA fingerprinting on the North American captive herd of Speke's gazelle *Gazella spekei*, we were able to address two hypotheses. First, two new individuals were found to have come from a genetically distinct population ($P = 0.008$, permutation test), and represent potential new founders to be added to the population. Secondly, genetic similarity was not significantly correlated with relatedness under extreme inbreeding and very close relationship (coefficient of relationship range 0.304–0.717).

Keywords: conservation, DNA fingerprinting, inbreeding, relatedness, Speke's gazelle

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Introduction

In the conservation or captive management of small populations, an important issue is whether a new candidate individual can be incorporated into the population as a founder. If the new individual possesses genetic variation that is not found in the current population, incorporation of its genes to maximize genetic diversity can aid in the long-term survival of the population (Templeton & Read 1983, 1984). On the other extreme, if the new individual is genetically very similar to other members of the population, the cost associated with obtaining the animal (both in funds and space available) may outweigh any benefit obtained.

To address the issue of whether candidate individuals are from a genetically distinct population in the absence of pedigree information, a measure and test of genetic variation between the candidate individuals and the managed population is necessary. DNA fingerprinting (Jeffreys *et al.* 1985a,b,c) provides many genetic markers that vary among individuals, even among closely related or inbred individuals (Brock & White 1992; Gilbert *et al.* 1991; Moritz *et al.* 1991). While it is possible to estimate standard genetic distances from DNA fingerprint data (Lynch 1991), the estimation of any population-level parameters from only a few individuals would be fraught with large errors. More germane to the problem, however, is whether the specific candidate individuals would add to the genetic resources of the managed population. We will propose a test for this purpose and illustrate its use through an evaluation of two individuals of Speke's gazelle *Gazella spekei* obtained from a private collection in Qatar as candidates for integration into the ongoing North American captive management program for this endangered gazelle (Templeton & Read 1983, 1984).

The most widely used application of DNA fingerprinting is in the determination of relationship among individuals. The relationship between fingerprint similarity and relatedness has been very actively pursued both theoretically (Lynch 1988, 1990) and empirically (Gilbert *et al.* 1991; Piper & Rabenold 1992). In studies of natural populations, it has been successfully applied to discriminating closely related from unrelated individuals and determination of parentage (Jeffreys *et al.* 1985c; Burke & Bruford 1987; Wetton *et al.* 1987; Burke *et al.* 1989; Packer *et al.* 1991). Its use to determine more distant relationships, however, has been less successful (Gilbert *et al.* 1991).

Correspondence: Marguerite A. Butler, Department of Biology, Washington University, St. Louis, MO 63130, USA. Fax 1 314 935 4432.

Testing the relationships between fingerprinting similarity and relatedness has generally been limited to categorical analysis (Gilbert *et al.* 1991), with no statistical tests of the results (but see Piper & Rabenold 1992). A quantitative testing of relatedness vs. similarity would give insight into the degree of reliability with which fingerprinting can reflect relatedness, information that is potentially useful for studies where information on relatedness is necessary.

Inbreeding is also expected to have a large effect on fingerprint similarity, but has so far only been investigated empirically through the construction of calibration curves for inbred lines (Kuhnlein *et al.* 1990). Theory predicts (Lynch 1991) that with prolonged inbreeding at small effective size, a stochastic loss of bands will occur until a new equilibrium is reached between mutation and drift. Therefore, it is possible that DNA fingerprinting may not be informative in distinguishing individuals under extreme inbreeding. Empirical study of inbred populations is necessary to further explore the utility of similarity under extreme inbreeding. We have used a captive population of Speke's gazelles to perform such an empirical investigation.

In summary, DNA fingerprinting has been used to answer two main questions concerning the Speke's gazelle captive population:

1 Can the Qatar animals be distinguished as a new genetic resource?

2 What is the effect of extreme inbreeding on DNA fingerprint similarity?

Materials and methods

Animal stocks

The Speke's gazelle is a highly endangered species that is endemic to Somalia and its border with Ethiopia (Fagotto 1979; 1985). Because of the long-lasting civil wars in the region, the status of the wild populations is unknown. Until recently, the only known Speke's gazelle in captivity were those in the North American zoo population. The population was founded by one male and three females, which were captured as calves in 1968. The current population is consequently highly inbred (Templeton & Read 1983). Despite this extreme founder event, Templeton *et al.* (1987) have demonstrated that the population has retained a level of enzyme polymorphism typical of wild mammals, as evidenced by isozyme survey (14% polymorphic loci). In 1980, Templeton & Read instituted a breeding program designed to maximize genetic diversity, while reducing the impact of a severe inbreeding depression.

In 1992, two females were donated to the St. Louis herd from the private collection of Sheik Al Thani of Qatar. (The male represented in the fingerprinting survey did not survive transport.) The Qatar population was founded by 16 animals which were caught in northern Somalia in the early to mid-1980s (Sheik Al Thani, personal communication). The donated animals are F2 descendants of the 16 founding animals. As the pedigree of the donated animals is unknown, the coefficient of relationship between the Qatar animals is assumed to be zero, although it is possible that they are related. The exact capture site of the St. Louis founders is not known. While they may be from southern Somalia or southern Ethiopia (B. Read, unpublished), it is not known how distant this capture site is from that of the Qatar gazelles, or what the genetic relationships between the two populations might be.

DNA fingerprints

Blood was collected and fractionated within 48 hours, as described in Templeton *et al.* (1987), with the exception that the white cell layer was diluted with a small amount of sera. Samples of white cells, red cells, and serum were stored at –80 °C.

Approximately 500 mL of the frozen white cell mixture was resuspended in 500 mL of STE buffer (10 mM Tris-HCl (pH 7.5), 100 mM NaCl, 1 mM EDTA). The white cells were rinsed by centrifugation at low speed, and resuspension in 500 mL of STE. The white cells were lysed and proteins degraded by adding 25 mL of 20 mg/mL proteinase K and 20% SDS. The solution was incubated at 37 °C overnight. Samples were extracted and purified with a minimum of two phenol extractions and three chloroform/isoamyl alcohol (24:1 vol./vol.) extractions, followed by ethanol precipitation. The DNA pellet was resuspended in TE buffer (10 mM Tris-HCl pH 8.0, 1 mM EDTA pH 8.0), to a concentration of approximately 0.1–0.5 mg/mL.

DNA was first quantified using the TKO 100 DNA Mini-Fluorometer (Hoefner), according to manufacturer's instructions. Five micrograms of sample DNA in 50 mL of TE was digested using 15 units of *Hae*III (NEB) at 37 °C overnight. The DNA concentrations were checked after digestion by electrophoresis of 1 mL of each digest. If necessary, more DNA and enzyme was added to the digests and incubated for 2 more hours at 37 °C. The sample volumes were reduced to approximately 20 μL using a speed-vac apparatus.

DNA fragments were separated by electrophoresis using 0.8% agarose in TBE buffer (89 mM Trizma, 89 mM boric acid and 2 mM EDTA pH 8.0) in a volume of 350 mL. Size standards (0.4 μg of λ-*Hind*III-digested DNA) were placed at each end of the gel, and a reference individual was placed twice on each gel, at approximately one-quarter and three-quarter way across the gel, to aid in aligning

the bands. The gels were run at 65 V for 22 h (until all fragments < 0.5 kb had run off the gel), or at 50 V for 47 h (until all the fragments < 2 kb had run off the gel).

Southern blotting was conducted according to the procedure of Westneat *et al.* (1988), with minor modifications. The DNA fragments were transferred to nylon (Schleicher and Shuell), and fixed to the membrane by UV cross-linking (Stratagene), then dried in an oven for 30 minutes. Hybridization was conducted at 58 °C when hybridizing with the gene III region (Vassart *et al.* 1987) of M13mp8 (M13), and 60 °C when hybridizing with the Jeffreys 33.15 probe (Jeffreys 1985a, 1985b; hereafter 33.15). The probes were labelled with [α-^{32}P]-dCTP by random priming. Unincorporated nucleotides were removed either by column purification or precipitating with absolute ethanol. Exposure times varied from overnight to three days with two intensifying screens at –80 °C, or up to 8 days with no screens at room temperature.

Data analysis

The bands were scored as presence-absence data, using the reference individuals in guiding the alignment of the bands. A standard measure of similarity was used to calculate pairwise similarities (Lynch 1990):

$$S = 2n_{pq}/(n_p + n_q),$$

where n_p is the number of bands for individual p, n_q is the the number of bands for individual q, and n_{pq} is the number of bands shared by individuals p and q.

A program in C was written to carry out a permutation test of the hypothesis that the Qatar animals are genetically distinct from the St. Louis animals using the 33.15 data set. The observed score was the sum of the pairwise similarities between each of the Qatar animals with each of the St. Louis animals. Next, all the animals were combined into one pool, and two animals were systematically chosen from this pool. For each permutation of the animals, the permuted score was the similarity between the two chosen animals and the remaining animals. The p-value was the quotient with the numerator as the number of times that the permuted score was greater than or equal to the observed score, and the divisor as the total number of possible permutations (120 in our case). This was an exact p-value. The M13 data were analysed similarly, with the permutation structure involving three Qatar animals, and seven St. Louis animals.

Correlation between coefficient of relationship and similarity

The coefficient of relationship (hereafter, relatedness) between two individuals was calculated from pedigree information using the following equation (Malécot 1969; Falconer 1989):

$$r = 2f_{pq} \div \sqrt{[(1 + F_p)(1 + F_q)]},$$

where f_{pq} is the coefficient of kinship between individuals p and q, F_p the inbreeding coefficient of individual p, and F_q the inbreeding coefficient of individual q.

Starting with the assumption that the founders are unrelated, the coefficient of kinship (f_{pq}) between any two individuals in a pedigree can be calculated iteratively using (Falconer 1989):

$$f_{pq} = \tfrac{1}{4} f_{ac} + \tfrac{1}{4} f_{ad} + \tfrac{1}{4} f_{bc} + \tfrac{1}{4} f_{bd}$$

where a and b are the parents of p, and c and d are the parents of q. A nonparametric method was used to test for correlation between relatedness and similarity. Spearman and Kendall rank-order correlations (Hollander & Wolfe, 1973) were calculated and the null hypothesis of no correlation was tested using Dietz's (1983) permutation test for association between two distance matrices program. Ten thousand random samples were conducted to approximate P-values to test the null hypothesis of no correlation vs. the alternative of correlation > 0.

The data were analysed separately for the following comparisons: 33.15 similarities vs. relatedness, M13 similarities vs. relatedness, and 33.15 + M13 similarities vs. relatedness. In the last comparisons, the band presence–absence data were concatenated for those individuals common to both datasets, and similarities then calculated. In each comparison, the permutation test was conducted separately for St. Louis animals only, and St. Louis + Qatar animals. Finally, for those individuals that occurred in both datasets, the similarity values obtained from 33.15 and M13 were tested for correlation.

Results

DNA fingerprinting was conducted on 15 Speke's gazelle from the St. Louis population, and 3 from the Qatar population (table 1). All samples were run on the same gel to avoid the many problems inherent in comparing individual profiles between gels. For the 33.15 probe, 14 St. Louis and two Qatar fingerprint profiles were obtained (Fig. 1b, Table 1; and for the M13 probe, seven St. Louis and three Qatar profiles were obtained (Fig. 1a, Table 1). With each probe, the average similarity among the Qatar animals and also among the St. Louis animals was relatively high, while the average similarity between the Qatar and St. Louis animals was lower (Table 1).

A permutation test was used to test whether the fingerprint profiles of the Qatar gazelles are from the same population (in the statistical sense) as the St. Louis gazelles (see methods for description of permutation structure). For both the 33.15 and M13 probes, the P-value was

Table 1 DNA fingerprint results

Population	Average similarity		Average number of bands per individual (range)		Number of individuals	
	M13	33.15	M13	33.15	M13	33.15
Within						
Qatar	0.417	0.533	11.3 (9–13)	7.5 (6–9)	3	2
St. Louis	0.617	0.565	11.6 (7–14)	6.8 (4–9)	7	14
Between						
Qatar and St. Louis	0.341	0.023				

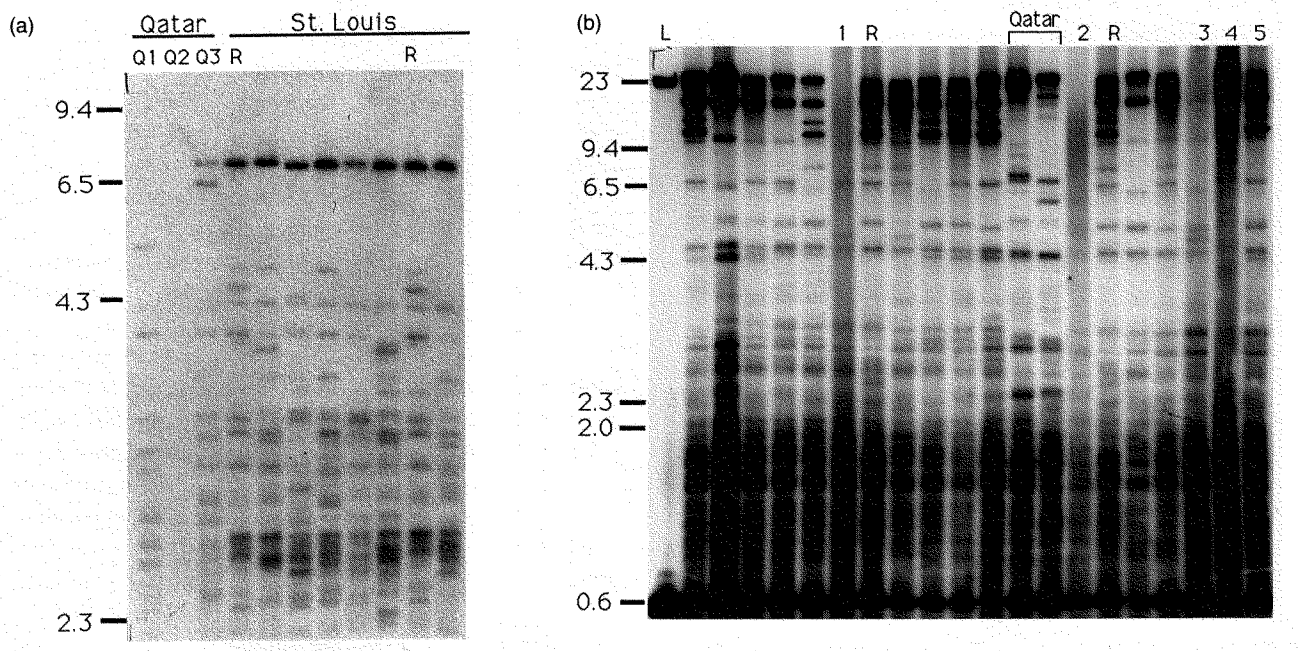

Fig. 1 (a) Fragment patterns of 7 St. Louis and 3 Qatar Speke's gazelle after digestion with *Hae*III, hybridization with the M13 probe, and overnight exposure with two screens. R indicates the reference individual (a St. Louis gazelle) that was run twice to aid in alignment of the bands. Q2 was scorable on further exposure. (b) Fragment patterns of 14 St. Louis and 2 Qatar Speke's gazelle after digestion with *Hae*III, hybridization with the 33.15 probe, and overnight exposure with two screens. L indicates the l-*Hin*dIII ladder and a small amount of probe loaded as the positive control. The Qatar samples are labelled, and the remaining profiles are those of the St. Louis animals. Lanes marked 3 and 5 are individuals from the Los Angeles zoo (all North American Speke's gazelles are descended from the same four founders). R indicates the reference individual. Lanes marked 1, 2 and 4 were not scored. A lighter exposure was also used to resolve the high molecular weight bands.

0.008, which was the lowest possible p-value for the comparisons of St. Louis vs. Qatar animals (7 vs. 3 individuals, and 14 vs. 2 individuals). With the data sets combined for those individuals present on both gels, the p-value was 0.036, which was again the lowest possible p-value.

Dietz's (1983) Permutation Test for Association Between Two Distance Matrices program was used to test the reliability of fingerprint similarities as estimators of relatedness. For the tests involving St. Louis + Qatar animals, highly significant correlations were found for all comparisons. The Kendall and Spearman correlation coefficient estimators were 0.455 and 0.638, respectively, for the contrast between the 33.15 similarities vs. M13 similarities (Fig. 2a). The correlation coefficient estimators for the 33.15 + M13 vs. relatedness comparison (Kendall $\tau = 0.534$, Spearman $\rho = 0.786$, Fig. 2b) were intermediate between those obtained for M13 vs. relatedness ($\tau = 0.556$, $\rho = 0.823$, Fig. 2c) and 33.15 vs. relatedness ($\tau = 0.354$, $\rho = 0.525$, Fig. 2d).

When the tests were restricted to the highly inbred St. Louis animals, only the M13 vs. relatedness comparison was found to be significantly correlated at the 0.05 level ($\tau = 0.371$, $\rho = 0.558$, Fig. 2c).

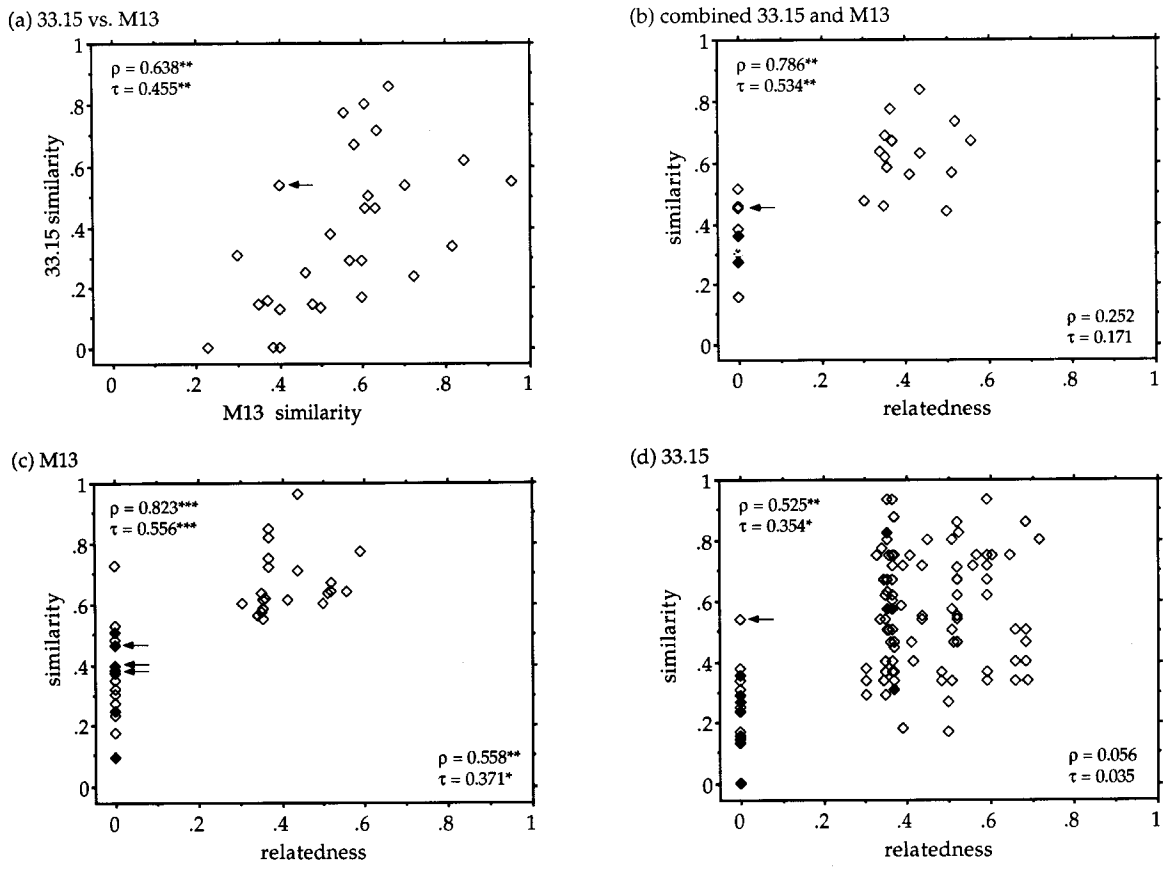

Fig. 2 The correlation between various similarity estimates and relatedness. The *P*-values and correlation coefficient estimators were generated using Dietz's (1983) program using 10,000 random resamples. Relatedness was calculated using standard algorithms (Malécot 1969; Falconer 1989). The Qatar animals are assumed to be unrelated (relatedness = 0.0). Arrows indicate points comparing the Qatar animals. Solid diamonds indicate data points that exactly (or very nearly) overlap. The upper left corners contain the Kendall's τ and Spearman's ρ correlation coefficient estimators obtained using all animals, and the lower right corners contain the estimators using St. Louis animals only. The asterisks indicate level of significance (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$). (a) The correlation between 33.15 and M13 probes. The similarities for each probe for individuals that occurred in both data sets are plotted. (b) The correlation between combined 33.15 and M13 similarities and relatedness. The similarities were calculated after concatenation of the 33.15 and M13 data sets, for individuals occurring in both datasets (six St. Louis animals and two Qatar animals). (c) The correlation between M13 similarities and relatedness. Similarities from seven St. Louis animals and three Qatar animals were obtained. (d) The correlation between the 33.15 similarities and relatedness. Similarities from 14 St. Louis animals and two Qatar animals were obtained.

Discussion

The Speke's gazelle afforded a unique opportunity to test the utility of multilocus DNA fingerprinting on an extremely inbred population. As with other zoo or inbred populations (Reeve *et al.* 1990; Morin & Ryder 1991; Brock & White 1992), we were able to find genetic variation at the individual level (Fig. 1). Using this variation, we addressed two main questions:

1 can the two recently acquired animals be distinguished as having come from a genetically distinct population;

2 how reliable is similarity as an indicator of relatedness under high levels of inbreeding and relatedness?

The permutation test on pairwise similarities was developed to test whether the Qatar animals represent a population genetically distinct from the St. Louis population. The test represents an improvement over simply graphing pairwise similarities vs. relatedness to see if the points fall into distinct distributions. The permutation test allows the extraction of useful information contained within the band sharing data, even though the distributions overlap. With a statistical test, one can obtain the exact probability of obtaining the data at random, and get a measure of whether the similarities differ significantly. In our case, the permutation test resulted in the lowest possible *p*-value of 0.008 for both the probes, showing that the band sharing profiles are as distinct as it is possible to detect with this sample size.

We had a rare opportunity to add new founders to this endangered captive population, and only anecdotal information was available on the genetic relationship between the Qatar and St. Louis populations. In the absence

of pedigree data or genetic information on the founders, testing the genetic distinctness of the new animals could only be carried out by genetic methods. DNA fingerprinting is a time intensive and expensive technique, but in our case, direct evidence on the genetic background of the Qatar and St. Louis animals is very important to the genetic management of this captive population. The Qatar animals were found to represent a new genetic resource that should be incorporated into the population to maximize genetic diversity (Templeton & Read 1983, 1984).

The pairwise fingerprinting similarities were also compared with the pairwise relatedness measures using a permutation method. This general type of test was first introduced by Mantel (1967). Dietz (1983) suggested using the Spearman's rho (ρ) and Kendall's tau (τ) statistics, rather than the unnormalized Pearson's product-moment correlation coefficient used by Mantel because they have greater power in many circumstances and are invariant under monotonic transformations of the data. The Mantel test assumes that the matrices are identically distributed, and that the distances within the matrices are evenly spaced. Dietz (1983) demonstrated that while the Mantel test performed well when the distances were distributed in an approximately uniform manner; the test performed poorly when uniform data were analysed using a transformed statistic or when transformed data were analysed using the untransformed statistic. Thus, the Mantel test was found to be highly dependent on the distribution of the distance measures used. There is a discontinuity in the distribution of relatedness values, because the Qatar animals are assumed to be unrelated (relatedness = 0.0), while the St. Louis animals are highly related (relatedness ranged from 0.304 to 0.717). The Mantel test was not used here because the relatedness values were distributed discontinuously, while the similarity values are more continuously distributed.

Spearman's rho and Kendall's tau are both rank-order correlation coefficients. Spearman's test statistic incorporates information on the relative distance between the paired ranks, whereas Kendall's test statistic does not. Spearman's statistic can be thought of as the classical (Pearson's product-moment) correlation coefficient on ranks, and Kendall's statistic can be thought of as a sign statistic for the test of correlation (see Hollander and Wolfe [1973] for more information).

A highly significant positive correlation was found between the similarities obtained using the 33.15 probe and those obtained using the M13 probe, with estimates of the correlation coefficients: $\rho = 0.638$ and $\tau = 0.455$ (Fig. 2a). Georges *et al.* (1990) found in cattle that data sets obtained from different multilocus fingerprinting probes contain overlapping information, with saturation at approximately 4–5 probes. As we are unable to conduct a segregation analysis because of very small sibships to correct for the above possibility, the analyses were conducted both with the data sets separate and combined.

With the Qatar animals included in the analysis, highly significant positive correlations were found between relatedness and similarity, for both probes and both tests. When the St. Louis animals were analysed separately, significant correlation was found at the 0.05 level only for the M13 data. This indicates that the significance found in the Qatar + St. Louis analysis was mainly due to the population level differences between the Qatar and St. Louis animals, further supporting the conclusion that the two groups of animals represent genetically distinct populations.

This is the first time that the 0.304–0.717 range of relatedness has been investigated empirically. Moreover, this quantitative study is an improvement over categorical studies because we were able to determine the amount of correlation that existed between the ranks of the relatedness and similarity measures. Unfortunately, we were unable to find predictive power in the similarity indices for the 0.304–0.717 range of relatedness (under random mating, first degree relatives share a 0.5 level of relatedness, and one's relatedness with oneself is 1.0). Many studies have been able to distinguish unrelated (relatedness 0.0) from closely related (relatedness 0.125–0.5, under random mating), but the range of similarity for these classes of relationship are sufficiently close that classification of more distant relationship is not possible (Jeffreys *et al.* 1991; Hoagland *et al.* 1991; Keane *et al.* 1991; Piper & Rabenold 1992).

Another factor to consider is that with prolonged periods at low effective size, the mean number of bands per locus is expected to decrease with increasing levels of inbreeding (Lynch 1991). This effect is more pronounced when the level of individual heterozygosity within the population is high, which is the case with the Speke's gazelle, based on allozyme data (Templeton *et al.* 1987). We were unable to test this prediction in this population because of the small sample size available, but it may lead to less accurate estimates of genetic similarity and consequently relatedness (Lynch 1988).

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The research presented in this paper is part of an ongoing collaboration between the St. Louis Zoo and Washington University on the genetic management of the North American captive population of Speke's gazelle (*Gazella spekei*). The work was performed in the laboratory of Alan Templeton. Marguerite Butler is a graduate student in Evolution and Population Biology at Washington University at St. Louis.