

rate phylogenetic trees were compared by using a likelihood ratio test.

Estimates and confidence intervals of the SFV divergence times were determined on the maximum-likelihood tree topology with the nonparametric rate smoothing algorithm implemented in the r8s program²¹. The branch lengths of the COII tree were re-estimated by enforcing a molecular clock with the PAUP* program. Confidence intervals for the COII divergence times were estimated with the r8s program by using the penalized likelihood algorithm²⁹ and 95% confidence intervals are given by 1.96 σ . The split of the Cercopithecoidea from the Hominoidea 25–30 Myr ago was used as a calibration point for the molecular dating of both SFV and COII sequences^{18,19}. The number of synonymous (d_s) and non-synonymous (d_n) substitutions per site were estimated with the program Diverge in the Genetic Computer Group Wisconsin Package (http://www.accelrys.com/products/gcg_wisconsin_package).

Reconciliation analysis and comparison of branch lengths of the SFV and COII trees were performed with the TreeMap (v1.0) program in accordance with the author's instructions (<http://taxonomy.zoology.gla.ac.uk/rod/treemap.html>)³⁰. A single optimal reconstruction was found with the heuristic search option. The significance of the observed fit between the SFV and primate trees and branch lengths was determined by comparison with the distribution of the same measure of fit for 10,000 randomly generated trees or branch lengths by using the proportional-to-distinguishable model of the randomization test incorporated in TreeMap.

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Genetic relatedness predicts South African migrant workers' remittances to their families

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Inclusive fitness models^{1,2} predict many commonly observed behaviours: among humans, studies of within-household violence³, the allocation of food^{4,5} and child care⁶ find that people favour those to whom they are more closely related. In some cases however, kin-altruism effects appear to be modest^{7–9}. Do individuals favour kin to the extent that kin-altruism models predict? Data on remittances sent by South African migrant workers to their rural households of origin allow an explicit test, to our knowledge the first of its kind for humans. Using estimates of the fitness benefits and costs associated with the remittance, the genetic relatedness of the migrant to the beneficiaries of the transfer, and their age- and sex-specific reproductive values, we estimate the level of remittance that maximizes the migrant worker's inclusive fitness. This is a much better predictor of observed remittances than is average relatedness, even when we take account (by means of a multiple regression) of covarying influences on the level of remittance. But the effect is modest: less than a third of the observed level of remittances can be explained by our kin-altruism model.

Migrants' remittances provide a rare window into the allocation of resources within a household, as intra-household transfers are typically not measured in surveys. The large and genetically heterogeneous nature of rural African households makes migrants and their households of origin an ideal database. The data for our study come from a nationally representative survey in 1993 of approximately 9,000 households¹⁰.

We have complete data on the income, remittances received, land ownership and composition of the household of origin, and on each migrant worker's age and schooling for 539 black male migrants. Virtually all migrants in the sample sent remittances in the year preceding the survey in 1993, and on average they sent almost half of their urban wage. Figure 1 shows the distribution of average relatedness of the migrant to the household of origin. (Consanguineous marriages are exceptionally rare in South Africa¹¹, so we assume that the migrant and his wife are unrelated.)

Hamilton's rule states that conferring a fitness benefit (b) by helping another at a cost of (c) to oneself will be selected for if $rb > c$, where r is the genetic relatedness of the donor to the beneficiary. Here we consider a case in which the choice is not

simply whether to help, but how much to help. The relationship between fitness and income will be increasing but concave because there are diminishing fitness returns to material resources. This is especially true at the very low levels of income prevalent among migrants and their households¹². As a result, the values of b and c above will vary with the amount of the remittance.

To express the concave relationship between material resources available to an individual and fitness in a way that yields a closed-form prediction of the fitness-maximizing remittance, we assume the relationship is logarithmic:

$$f^i = v \ln x \quad (1)$$

where f^i is the expected contribution to the gene pool in the future by individual i , v is the multiplicative baseline fitness and $x \geq 1$ is the income available to the individual in a given period. Income contributes to reproductive success by increasing the likelihood of survival to reproductive age, the expected period of reproductive life for those who attain this age, and the number of resulting offspring surviving to reproductive age. The inclusive fitness of individual m (the migrant) is:

$$F^m = \sum r^{im} f^i \quad (2)$$

where r^{im} is the relatedness of the migrant to individual i , one of the $n + 1$ persons with whom he interacts (the n members of the migrant's household of origin, plus himself, with $r^{mm} = 1$) and the summation is over $i = 1, \dots, n + 1$. The average relatedness of the migrant to his household members is $r = (\sum r^{im} - 1)/n$.

Let the pre-remittance income available to each household member be y and that available to the migrant (his wage) be w , so that after a remittance of size t , the migrant has $w - t$ and each household member $y + t/n$. We assume that the income and (for the moment) the remittance are shared equally among the household members. (In our empirical calculations of the income available to household members, we count children aged less than 6 years as half of an adult equivalent, but to avoid notational clutter in the explication of the model we ignore the presence of less than adult-equivalent children.)

Differentiating equation (2) with respect to t and setting the result equal to zero, we find that the F -maximizing transfer (t^*) equalizes the marginal fitness cost to the migrant (that is, $1/(w - t)$) and the marginal fitness benefit to the recipients, weighted by their average relatedness to the migrant (that is, $r/(y + t/n)$) or equivalently:

$$r = \frac{(y + t/n)}{(w - t)} \quad (3)$$

Condition (3) requires the optimal transfer (if one exists) to

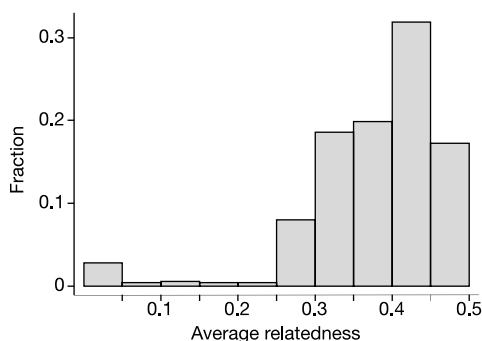


Figure 1 Average relatedness of migrants to their households of origin. More than three in ten of the migrants' households of origin include three generations, and one in five includes the migrant's aunt, uncle, niece, nephew or grandchild. The average degree of relatedness between the migrant and the members of the household is 0.37.

implement a ratio of the average post-transfer income of the household to that of the migrant (the right hand side of equation (3)) that is equal to the average relatedness of the household members to the migrant. This is accomplished (rearranging equation (3)) when:

$$t^* = \frac{(wr - y)}{(r + 1/n)} \text{ if } wr > y \text{ and otherwise } t^* = 0 \quad (4)$$

The numerator of the right-hand side of equation (4) is a version of Hamilton's rule: some positive transfer is F -maximizing if $r/y > 1/w$. Here $b (= 1/y)$ and $c (= 1/w)$ are the marginal fitness benefits and costs of an arbitrarily small transfer. The remittance that satisfies equation (4) is unique owing to the concavity of equation (1) and the resulting monotonicity of the marginal fitness costs and benefits functions. As can be seen from equation (4), the F -maximizing transfer (if one exists) increases with n ; in larger households the remittance is spread among more members, so diminishing marginal fitness returns are less pronounced. Figure 2 illustrates the optimal transfer.

The effect on inclusive fitness of assistance to a genetically related individual depends not only on the degree of relatedness but on the age, sex and other characteristics relevant to the reproductive value of the beneficiary^{13,14}. For example, owing to the very high levels of mortality among rural black children in South Africa^{12,15}, a non-negligible fraction of the children benefiting from remittances will not reach reproductive age, irrespective of the level of the remittance. Also, some closely related beneficiaries (parents, for example) have few or no years of reproductive activity remaining. Finally, fitness depends on the relative (not absolute) contribution to future gene pools¹⁶, so in a rapidly growing population such as South Africa's in the early 1990s earlier fecundity should be favoured over later, thus enhancing the reproductive value of those who have reached reproductive age compared to those who have not. An inclusive-fitness-maximizing migrant would thus give more if the members of his household of origin were his adolescent children rather than his infant children or his aged parents (despite the fact that they are equally related to the migrant). And he would also give more if he were near the end of his reproductively active years rather than at the beginning.

Let v^j be an age- and sex-specific effect such that the individual fitness of the age-sex class j is $f^j = v^j \ln x$. Then, using equations (1) and (2):

$$F^m = v^m \ln(w - t) + \sum v^j r^{im} \ln(y + t/n) \quad (5)$$

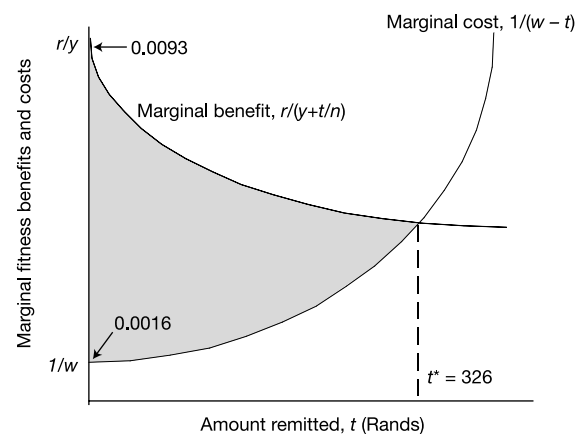


Figure 2 The optimal remittance t^* equates the marginal fitness cost to the migrant with the sum of the relatedness-weighted marginal fitness benefits to the members of the household of origin. The total inclusive fitness is the shaded area. The numerical values are for a migrant with mean values of r , y , n and w .

where v^m and v^i are the reproductive values (respectively) of the migrant and the i th household member ($i = 1 \dots n$). Now we define the reproductive-value-adjusted average relatedness of the household, $r^v = \sum v^i r^{im} / n$. Maximizing F^m as above, the resulting optimal transfer (t^v) equates the ratio of the two post-transfer incomes to r^v / v^m (the analogue of equation (3) above), or:

$$t^v = \frac{(wr^v - yv^m)}{(v^m/n + r^v)} \text{ if } wr^v > yv^m \text{ and otherwise } t^v = 0 \quad (6)$$

which is identical to equation (4) if $v^i = 1$, for all i .

We estimate the v^i in equations (5) and (6) as the present value of the sequence of years of reproductive life that an individual of age j may expect, discounted by the rate of population growth and normalized to equal one for a child aged 1 year. Estimates and methods of calculation of v^i appear in Fig. 3. The rise in reproductive value before attaining reproductive age is expected in societies with high child mortality and substantial rates of population growth, and is observed in other southern African data¹⁷.

We use the migrant's schooling and age to estimate his expected wage, which, along with data on the other variables above, allow an estimate of t^* and t^v for each migrant. The first numeric column of Table 1 gives the simple correlations ρ between observed transfers t on the one hand and our measures of relatedness and optimal transfers on the other. As can be seen, t^* and t^v are more highly correlated with t than are r and r^v , and taking account of reproductive values significantly increases the correlation of the observed and predicted remittances (from 0.25 to 0.32). Using the larger correlation, one-tenth (0.32²) of the variance of observed remittances is explained by the inclusive-fitness-maximizing transfer.

To estimate the causal importance of inclusive fitness in explaining migrants' remittances we need to control for other influences on t that do not represent inclusive-fitness effects but that are correlated with t^v . The age and years of schooling of the migrant, for example, are a measure of his economic standing that may be associated with claims on his income independently of genetic relatedness. Older, better-educated men are likely to maintain larger social networks and may be expected to give more. Conversely, the economic need of the household of origin may influence

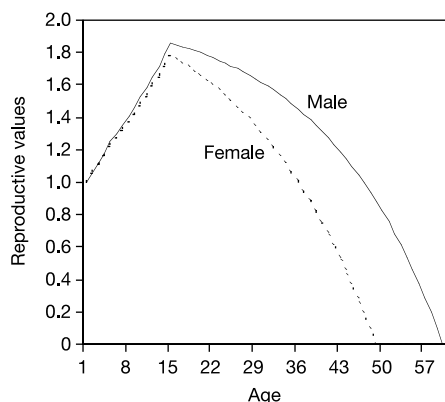


Figure 3 Normalized reproductive values: rural black South Africans around 1993 (refs 15, 21). Let d^a be the age- and sex-specific probability of not surviving from age a to $a + 1$ and let m^q take a value of 1 if q is one of the reproductive years (15 to T where T is the age at the end of one's reproductive years: 49 years for women, 60 years for men) and zero otherwise. We define the present expected value of the q th year of life of someone who is now in their j th year, discounted at the rate of population growth g , as $V^q = m^q \Pi [(1 - d^a)/(1 + g)]$, where the product is over $a = j, \dots, q$. Then the reproductive value of a person j years old is $V^j = \sum V^q$, where the summation is over $q = j, \dots, T$. Reproductive values are normalized using sex-specific reproductive values at year 1 so $v^j = V^j / V^1$.

remittance behaviour independently of its effect on the marginal fitness benefits of additional income. We therefore predict t (by ordinary least-squares methods) using the migrant's age, schooling and land ownership of the household and presence of the migrant's wife in the household as explanatory variables in addition to t^v .

When conditioned on the above controls, the estimated normalized regression coefficient of t^v (β , shown in the second numeric column of Table 1) indicates that a standard deviation difference in t^v is associated with a difference in predicted remittances of 18 per cent of a standard deviation, controlling for the effects of these other variables. To see what this estimate means, consider a migrant whose relatedness to his household of origin makes the optimal remittance zero ($wr^v - yv^m = 0$, so $t^v = 0$) but with sample mean values for all of the other predictors. This hypothetical migrant would remit 23 per cent less than an otherwise identical migrant with the sample mean relatedness and hence also the sample mean t^v . Thus, although highly statistically significant, the difference in remittance behaviour accounted for by the inclusive-fitness model is modest in size. (The analogous estimate using t^* is 15 per cent.) The fact that (in results not shown here) remittances are slightly better predicted using reproductive values assuming zero population growth (which was approximately the case in the ancestral populations of the migrants studied here¹⁷) is consistent with the view that contemporary behaviour may be an adaptation to past conditions.

Have we underestimated the inclusive-fitness effect? In all of these estimated equations, households in which the migrant's wife is present receive more (by 45 per cent of the observed mean remittance ($p < 0.001$) in the equation using t^v). The wife's presence in the household may increase remittances both for inclusive-fitness reasons (for example, care of the migrant's children, enhanced future reproductive success with his wife) and as a result of altruistic motives towards non-kin of the type documented in recent behavioural experiments¹⁸.

To incorporate the effect of the wife's care of existing offspring in our estimate of the optimal transfer, we redefine t^v assuming that if both the migrant's wife and any of his children are resident in the household, the children and the mother receive (and share equally) all of the remittance. To take account of the wife's contribution to the migrant's prospective future offspring we add one or more fictive children of the migrant to the household in calculating r^v , each with a reproductive value of less than that of a newborn infant because of the passage of time between the present and its birth some years hence (should the mother survive until then). The number of such hypothetical additions is the expected total number of children born to a rural black woman during her reproductive years¹⁹, minus the number of the migrant's children currently resident in the household, conditional on the wife having sufficient remaining years of reproductive life for this to occur.

Taking account of the wife's contributions in these two ways, we

Table 1 The statistical relationship between observed and predicted remittances

Observed remittances, t	Simple correlation, ρ (p)	Normalized regression coefficient, β (p)
Average relatedness, r	-0.03 (0.470)	0.11 (0.004)
Reproductive-value-weighted relatedness, r^v	0.14 (0.001)	0.13 (0.001)
Predicted remittance, using r , t^*	0.25 (<0.001)	0.11 (0.064)
Predicted remittance using r^v , t^v	0.32 (<0.001)	0.18 (0.005)
Predicted remittance (wife effect), t^w	0.35 (<0.001)	0.21 (0.001)

ρ is the correlation of the indicated variable with observed remittances t (with p -values in parentheses). β is the normalized regression coefficient of the variable indicated in the ordinary least-squares equation in which, in addition to the variables indicated here, predictors included the migrant's age, schooling, the land owned by the household and whether the migrant's wife is present in the household, as well as place-of-origin controls. Thus, a standard deviation difference in t^w holding these other variables constant is associated with a fifth of a standard deviation difference (21%) in t .

estimate for each migrant a new F -maximizing remittance of t^w . Using this predictor in the multiple regression described above and in Table 1, and the same methods as above, inclusive fitness accounts for 29 per cent of the observed remittances. The 'wife present' effect remains large (38 per cent of the observed mean remittance ($p < 0.0001$)) in this equation, suggesting that although the wife's contribution to inclusive fitness (as we have modelled it) helps to explain remittances, most of the 'wife present' effect cannot be explained this way.

The measurement of y , w and r^{im} are all subject to error, and this imparts a downward bias to our estimates of β . Moreover, other functional forms would yield different predictions. Finally, in many cases migrants have formed households and fathered children in the locality of their work²⁰, thus raising the marginal fitness costs of remitting in ways that our model does not capture. We experimented by re-estimating t^v assuming plausible (but hypothetical) values for the composition of the typical migrant's secondary family. This reduces the mean predicted transfer, as expected, but it does not increase the fraction of the remittance accounted for by inclusive fitness. We doubt that addressing these limitations would alter the conclusion that inclusive fitness explains part of remittance behaviour, but not all of it. □

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Genetic effects on sperm design in the zebra finch

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Sperm design and function are important determinants of male reproductive success and are expected to be under strong selection^{1,2}. The way that spermatozoa phenotypes evolve is poorly understood, because there have been few studies of the quantitative genetics of sperm^{3–5}. Here we show, in the zebra finch *Taeniopygia guttata*, an extraordinary degree of inter-male variation in sperm design that is independent of sperm swimming velocity. A quantitative genetics study using data from over 900 zebra finches in a complex breeding experiment showed that sperm head, mid-piece and flagellum length are heritable, that negative genetic correlations exist between sperm traits, and that significant indirect (maternal) genetic effects exist. Selection on the zebra finch sperm phenotype may be low because sperm competition is infrequent in this species⁶, and this, in combination with negative genetic correlations and maternal genetic effects, may account for the variation in sperm phenotype between males. These results have important implications for the evolution of sperm in other taxa.

The primary function of the male gamete, the spermatozoon, is to fertilize ova. Sperm are expected to be under strong selection to be efficient fertilizers for two reasons. First, within the female reproductive tract sperm face numerous physical, chemical and immunological barriers that result in only a tiny subset of inseminated sperm reaching the ovum^{7,8}. Second, widespread promiscuity among females results in sperm competition between males, which favours males whose sperm are effective competitors¹. Interspecific differences in these evolutionary forces combined with phylogenetic effects⁹ probably account for the fact that despite their common purpose, sperm vary more dramatically in size and design across species than any other cell type¹⁰. As well as the marked interspecific differences in sperm design, considerable inter-male variation in sperm phenotype exists within species¹¹.

Here, we aimed to investigate the underlying causes of inter-male variation in sperm design in the zebra finch *Taeniopygia guttata* by examining the relationship between sperm phenotype, sperm swimming velocity and the quantitative genetics of sperm traits. Heritabilities and other genetic parameters were estimated using the animal model¹² from a combined full-sibling and half-sibling animal breeding design involving 81 sires producing two sons from each of six dams (972 male offspring; entire pedigree comprising 1,526 individuals) and analysed using the multiple-trait, derivative-free, restricted maximum-likelihood program (MTDFREML)¹³.

Within males the repeatability of sperm traits was substantial, particularly for mid-piece (0.75) and flagellum (0.84) length (repeatability for head length was 0.52, all degrees of freedom (d.f.) = 913, 3,656; $P < 0.001$), and we have shown elsewhere that within-male variation in sperm design is highly consistent across ejaculates and time¹⁴. In contrast, between-male phenotypic variation in sperm design was considerable (Fig. 1 and Table 1). The inter-male coefficients of variation in sperm flagellum length and mid-piece length were two and four times greater, respectively, than for the linear morphological trait of male tarsus length (coefficient of variation = 3.38, $n = 972$ males).

Sperm motility is determined largely by the flagellum and the