The development of schistosomiasis mansoni in an immunologically naive immigrant population in Masongaleni, Kenya

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SUMMARY

The relocation of several thousand members of the Kamba tribe from the Kyulu Hills to the Thange valley near Masongaleni in Kenya provides an excellent opportunity to study the development of the immune response to schistosomiasis mansoni in a population with little or no previous experience of the infection. An adjacent, well-established Kamba community with similar patterns of water contact provides a suitable endemic control population. The immigrants were, uniquely, examined shortly after their arrival in the endemic area, while the prevalence of infection was still low. At this time faecal egg counts peaked atypically around 30 years of age. Over the next 12–18 months infection increased rapidly, especially among teenagers, producing a pattern of infection more typical of endemic communities. This substantially narrows estimates of the time required to develop the important determinants of the age–intensity profile, supporting the notion that changes related to age *per se*, rather than duration of infection, dominate. Age-dependent factors might include behaviour or physiology, including immune response. This paper provides the background for continuing longitudinal studies on the development of immunological responses to this parasite.

Key words: *Schistosoma mansoni*, immunity, immigrant, water contact, Markov random field, age–intensity profile.

INTRODUCTION

After several decades of study it still remains unclear how and to what extent humans acquire immunity to schistosome infection. The intensity of infection in most communities studied reaches a peak in the teenage years and then falls away to low levels in adulthood. How much this pattern is the result of the development of immunity in adults or a decline in exposure has been the subject of lively debate since Warren (1973) and McCullough & Bradley (1973) discussed the issue (Butterworth & Hagan, 1987; Hagan, 1992; Butterworth, 1994; Gryseels, 1994; Woolhouse, 1995; Fulford *et al*. 1996*a*). If adults are relatively immune to infection, 2 further possibilities arise: (i) physiological differences, in innate resistance or ability to acquire immunity, protect adults relative to children or (ii), as Kloetzel & da Silva (1967) concluded from a study of migrant watercress growers in Brazil, many years of exposure are required before immunity develops.

In the usual endemic situation, it is extremely difficult to distinguish between these last 2 possibilities, since length of exposure to infection and host age are deeply confounded. Kloetzel & da Silva's (1967) study was the first to attempt to uncouple age from experience of infection but unfortunately they did not properly control for age in their analysis and their conclusion relied heavily upon a (statistically non-significant) decline in prevalence among a rather small group of long-established workers (Gryseels, 1994). Recently, other situations, in which previously unexposed communities have suddenly become exposed to *Schistosoma mansoni*, have presented themselves. One such arose in Senegal after irrigation development around Lac de Guiers and later damming of the Senegal River in 1986 (Talla *et al*. 1990). Studies of this epidemic have shown that, after only a few years, adults became infected more slowly than children, i.e. much of the difference between them did not require decades of exposure to develop (Stelma *et al*. 1993). Invaluable though this contribution has been, these studies do

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suffer 2 drawbacks: the infection was already well established and had more or less stabilized when the studies began and there was no endemic control population.

In the study we present in this paper, we followed a community in Kenya who moved *en masse* from the schistosome-free Kyulu Hills to a tract of virgin bush near Masongaleni adjacent to a community of the same ethnic background among whom *S. mansoni* was long established. It was possible to examine the immigrant community very shortly after they arrived, presenting the additional opportunity of observing the development of a stable, endemic-like pattern of infection. A further strength of this study was the existence of a suitable control population with which the immigrants could be compared. Finally, knowledge of the previous experience of infection of the immigrant and control populations is crucial to the interpretation of this study. Fortunately, much of their recent histories are well known. Evidence for the immigrants' lack of previous experience of infection could also be obtained from examination of a second group of Kyulu immigrants who moved to an area where schistosomiasis transmission is negligible.

STUDY POPULATIONS AND SURVEYS

History of the study populations

Masongaleni lies in the Thange River valley, a few kilometres to the Northeast of the Nairobi–Mombasa highway some 30 kilometres northwest of Mtito Andei in Makueni District, Kenya. The two communities described in this paper both live in the Thange valley between the highway and Athi River to the north (see map, Fig. 1). For both communities the Thange River is the only source of surface water for drinking, bathing, laundering and other domestic purposes. The terrain and economy of the valley is rather similar to that in the neighbouring Kambu valley described in a previous paper (Fulford *et al.* 1991). It lies at about 790 m above sea level. *S. mansoni* is the only human schistosome species found in the area and is known to have occurred in the Thange river since the 1950s when the discovery of infection in a troop of baboons which frequented its banks was the first demonstration that an animal reservoir existed for this parasite (Nelson, 1960). Transmission is interrupted seasonally by rains which flush away the vector snails, and occasionally by drought when the springs which feed the river run dry.

The population we refer to here as the established community has been living with schistosomiasis in this area for at least 20 years. They occupy an area broadly to the east of the Thange River. Their history is similar to that of the residents of the adjacent Kambu River valley, described previously (Corbett *et al.* 1992). Until recently land to the west of the established community was privately owned and unoccupied. In 1991 an act of parliament released the land to a population who had formerly lived high (about 1500 m above sea level) in the waterless, volcanic Kyulu Hills between the Nairobi–Mombasa highway and the Tanzanian border southwest of Masongaleni. We refer to this population as the immigrant community. Ethnically, both populations are almost exclusively Kamba.

Interviews with local people have revealed that the immigrants came originally from all over Ukambani (land traditionally occupied by the Kamba people including settlements such as Kilungu, Mukaa, Mbitini, Kilome, Kikumini), attracted by the fertile and largely unoccupied slopes of the Kyulu Hills. Most, although not all, of the areas they had come from are believed to be schistosomiasis-free. The volcanic rocks of the Kyulus are very porous and, as a result, although there is sufficient rainfall for agriculture, there is no surface water. Some people collected rain water in containers and even obtained water by tapping baobab trees, but most used donkeys to carry water up from covered bore-holes near the village of Utu. Utu also served as the main market where they would sell their crops and buy domestic items. When living in the Kyulu Hills, the Kamba immigrants would also have watered their animals in a temporary stream at Kwamukonza, 7 km below Utu, as the Maasai from the Kyulus can still be observed to do today. This stream is dry for all but a few weeks in a year and there is no evidence that it transmits schistosomiasis: no infected snails have been found there and levels of infection among the resident population in Utu are very low.

Many of the immigrants had apparently lived in the Kyulus all their lives but the last major wave of immigration is reported to have occurred in the 1970s, ceasing around 1976. The immigrants had occupied the Kyulu Hills without permission and were forced to vacate the land in 1990. Initially they camped in the village of Utu where they stayed for 2 years. In 1992 each family was allotted land in either Masongaleni or Mbui Nzau, a village on the Nairobi–Mombasa highway some 30 km to the northwest of Masongaleni and where there is no evidence of transmission of schistosomiasis. Plot allocation was haphazard, ensuring a more or less randomized 'study design'. In allocating plots the land in Masongaleni was divided into a number of blocks, of which only the more accessible blocks 6, 7 and 8 (see map) were included in this study. These blocks were occupied simultaneously over a period of about a year.

The first immigrant families arrived in Masongaleni in February 1992, the rest following in waves over the next 12 months. It was usual for the young men of each household to arrive a few weeks ahead of

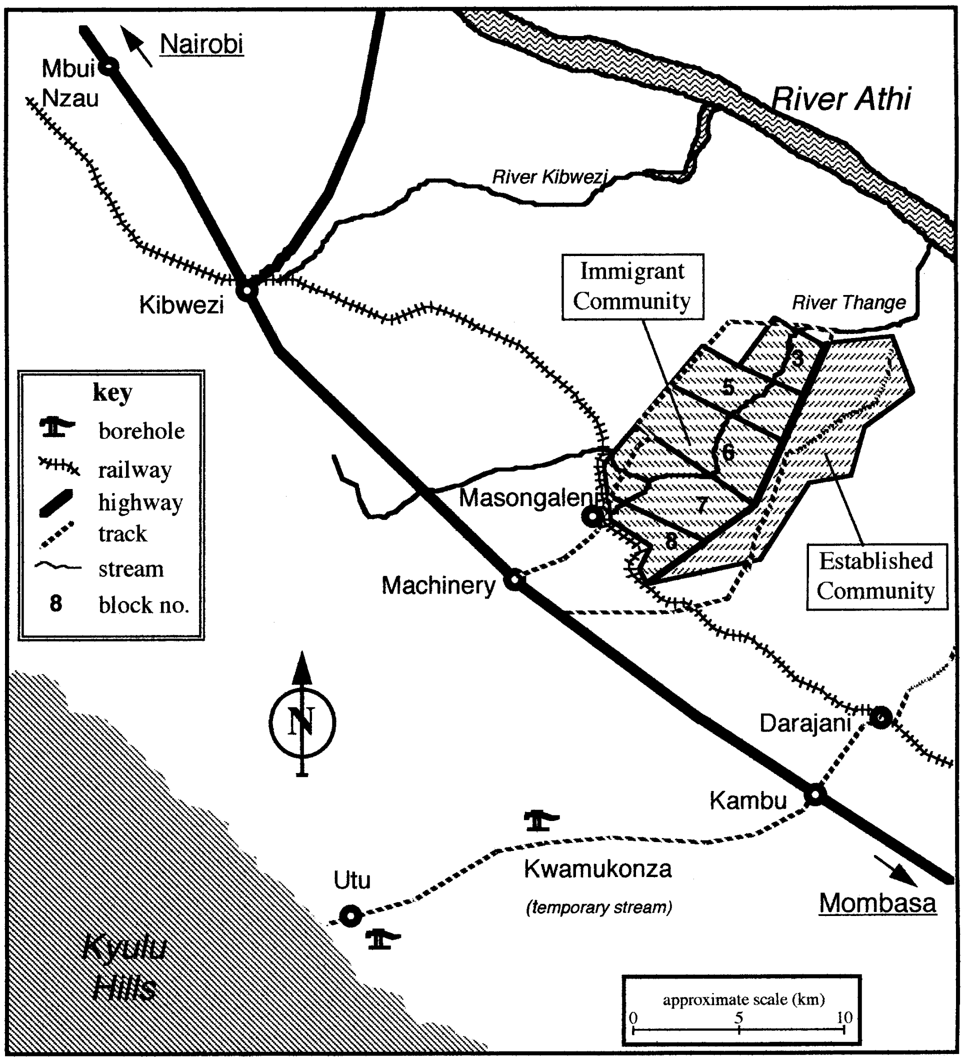

Fig. 1. Sketch map of the Masongaleni area.

their families in order to clear the land and build a home. The debate over the release of this land received extensive coverage in the local media. Consequently, we were alerted to the mass migration from the Kyulu Hills before it actually took place and were able to examine the immigrants within a few months of their arrival in Masongaleni.

The immigrant community also had little immunological experience of malaria and many succumbed to an epidemic of this disease shortly after arrival. Of 106 deaths recorded in the immigrant community between December 1992 and August 1994, at least 42 (39%) were due to malaria. A survey of schoolchildren in May 1995 revealed that 90% of 4 to 8-year-olds had blood-smears positive for malaria and among these there was considerable evidence for resistance to chloroquine (the only anti-malarial drug available locally).

Demographic and parasitological surveys

A list of the members of the immigrant community by household was drawn up in late 1992. During this registration each individual was asked where they had come from, when they had arrived in the Thange valley and how long they had stayed in their previous residence. The community was resurveyed 3 times between August 1993 and October 1994, in order to update the register. The established community was registered in early 1993 and resurveyed once more in January 1994. The question of how long they had lived in their previous residence was not appropriate to this community but they were asked how long they had been resident in Masongaleni.

Two stool surveys in each community were carried out in early 1993 and again in mid-1994. At each survey everyone present in the community at the time was asked to provide a single stool specimen (multiple stools samples are only essential when accurate intensity levels are required for each individual, such as when egg counts are used as covariables). *S. mansoni* eggs were counted in two 50 mg Kato smears prepared from each stool specimen. Slides were read by the same 2 technicians throughout and quality control maintained as in previous studies (Butterworth *et al.* 1991; Sturrock

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et al. 1997). Compliance rates, sample sizes and dates of the stool surveys are summarized in Table 1. Compliance rates were calculated as the percentage of individuals present at the demographic survey immediately preceding the stool survey who subsequently provided a stool specimen. The sample size of the second stool survey in the established community was reduced somewhat by the exclusion of several hundred randomly selected individuals who were treated as part of further, separate longitudinal studies. Although the 1993 and 1994 surveys in each community did not cover exactly the same cohort, there was considerable overlap between them and no difference in pattern or level of infection in the 1994 surveys could be detected between those who had and had not produced stool specimens for the 1993 surveys.

A single stool collection was made in the school (Nguluni Primary) in Utu in April 1997. These were all children of the original residents, the immigrants from Kyulu having already left for Masongaleni and Mbui Nzau. Three stools were collected from the immigrants in Mbui Nzau community in May 1997.

Water contact observation

Water contact was observed at 8 infective sites on the Thange River identified by snail monitoring (Ouma *et al*. 1989). Observations were made on 4 days every second week and 2 sites were observed/day.

The procedures for water contact observation and data recording closely followed those used previously (Fulford *et al*. 1996*b*). The observers employed here had all had previous experience of similar work on the Kambu River but were assisted by people recruited from the local Masongaleni population to help with identification of individuals.

One departure from previous procedure was necessitated by the possibility that the recent immigrants could not be identified reliably. Where the observers and their helpers were uncertain of an individual's identiy, this fact was recorded. This had repercussions for data analysis. It was necessary to rely on the estimated ages of unidentified individuals as their true ages could not be checked in the demography register. Also, water contact observation can, for most purposes, only be analysed in relation to a list of population members, since many individuals will never be observed at the water at all. In this case, however, it was not possible to tell whether or not unidentified individuals belonged to the population list. Fortunately, the age distribution of unidentified individuals seen at the water appeared very similar to that for those who were identified and the proportion of contacts by unidentified individuals was not high (immigrant community 5 %; established community 12 %). The apparently greater difficulty in identifying individuals in the established community may reflect that neither the observers nor their assistants came from this community.

In the immigrant community a total of 6209 water contacts were recorded between October 1993 and September 1995 while observation of the established community between October 1993 and July 1995 yielded 3189 recorded contacts.

Statistical analysis

Egg counts were converted to eggs per gram (epg) and analysed in the logarithm, $\log_e(\text{epg}+1)$.

In previous work (Fulford *et al*. 1996*b*), age–sex patterns of water contact were calculated by summing the observed contacts for each member of a fixed list of population members. The difficulty in identifying individuals during water contact observation invalidates this approach. Instead, all observed contacts in each age–sex group were summed and these totals divided by the number of individuals known to be present in the community at a demographic survey undertaken during the period of observation. Thus there may be some mismatch between the populations from which the denominator and numerator in the mean calculations were derived. While this may lead to some additional imprecision, it should not seriously bias the observed pattern. Water contact scores given are based on total observed contact time with no attempt to allow for the relative risk of infection that different forms of contact might carry.

Visualization of the patterns of infection and contact with age and sex requires some data smoothing. This is frequently done by stratifying the data with respect to age, calculating the mean response and age within each stratum and plotting mean response against mean age. Here, in order to allow smaller stratum sizes and hence obtain more detailed age profiles, we have used a slightly more sophisticated approach, based on a Markov random field model, details of which are given in the Appendix.

RESULTS

All but 1·1 % (18/1684) of the immigrant community stated at interview that they had come from Kyulu. The earliest member of this community arrived in February 1992. From the plot of date of arrival versus age in Fig. 2 it can be seen that the older males arrived on average a month or two earlier than the children. The correlations between age and time of arrival are statistically significant for both males and females but account only for a small percentage of the overall variation in arrival times (males $r^2 = 9{\cdot}4\,\%$, females $r^2 = 1{\cdot}7\,\%$). However, for a brief period between February and March 1992 adults outnumbered children in the immigrant community.

Table 1. Sample sizes, dates and compliance rates for stool surveys

Community	Block	1st survey Final sample size	Compliance rate (%)	Date	2nd survey Final sample size	Compliance rate (%)	Date
Immigrant	6	788	68	Feb 1993	1138	74	Jun 1994
	7	626	70	Nov 1992	612	68	May 1994
	8	270	68	Feb 1993	212	53	Apr 1994
	ALL	1684	69		1962	69	
Established	1468	73	Apr 1993	1136	73	July 1994	

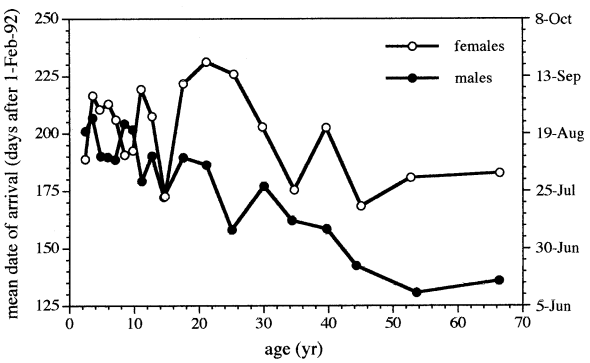

Fig. 2. Mean time of arrival of Masongaleni immigrants versus age for males and females.

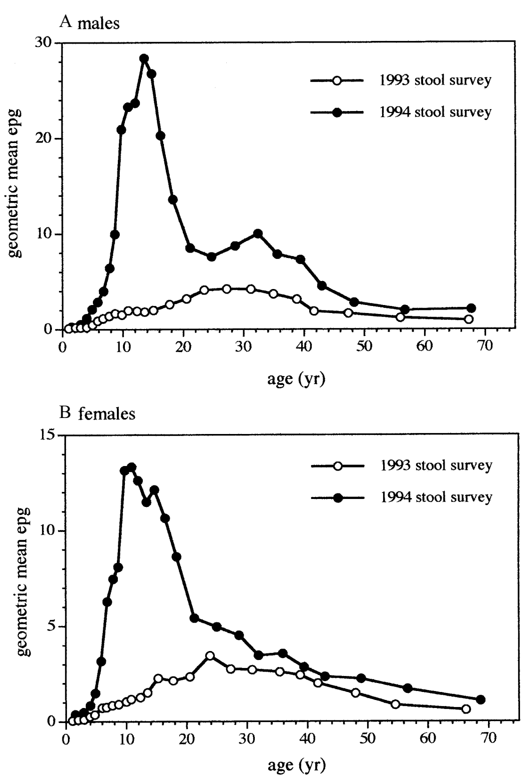

Fig. 3. Immigrant community faecal egg counts and water contact versus age. (A) Males; (B) females. The Markov random field smoother was applied to the logarithm of the faecal egg counts (see Appendix).

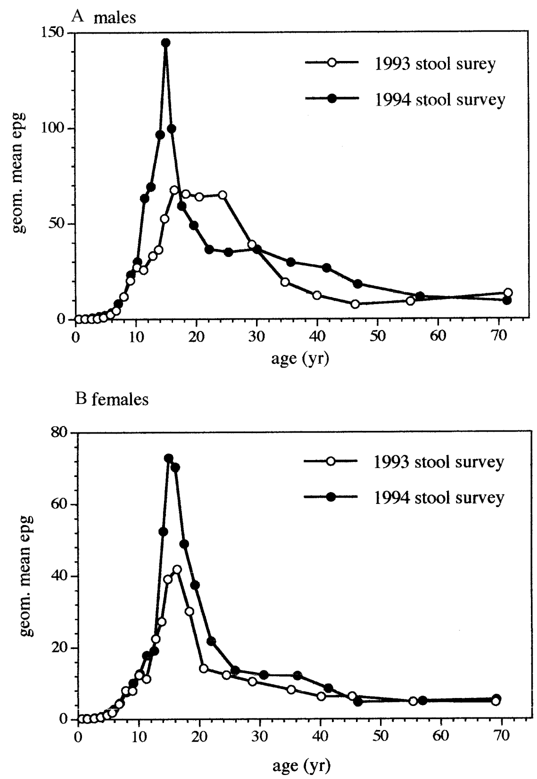

Fig. 4. Established community faecal egg counts versus age. (A) Males; (B) females. The Markov random field smoother was applied to the logarithm of the faecal egg counts (see Appendix).

Figs 3 and 4 show the patterns of infection (as measured by faecal eggs) for the immigrant and established communities respectively and Fig. 5 the patterns of water contact with age and sex in the 2 communities. People from Block 8 were rarely exposed (see below) and hence were uninformative with respect to the pattern of development of infection. They were therefore omitted from Figs 3 and 5.

Levels of infection were very low among the immigrant community at the first survey. At that time the pattern of infection was unusual in that the most heavily infected age was around 30 years. The

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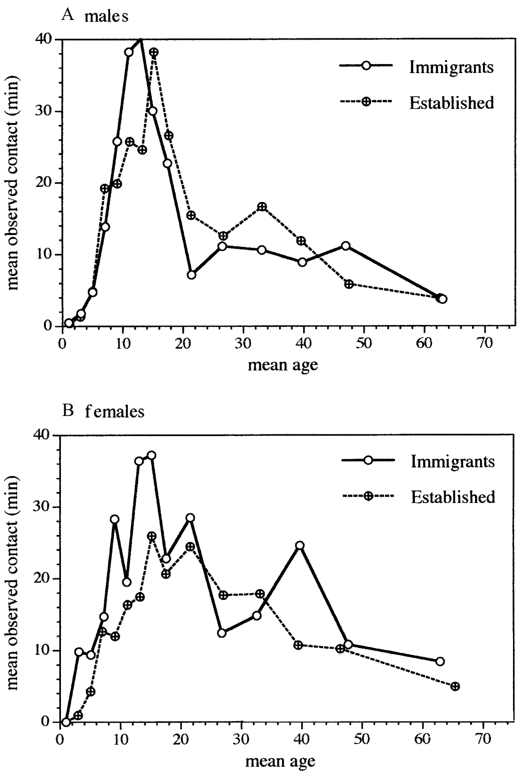

Fig. 5. Established and Immigrant community water contact versus age. (A) Males; (B) females. The Markov random field smoother was applied to the logarithm of the observed contact time (see Appendix).

Table 2. Comparison of initial (first survey) infection levels and water contact rates between blocks in the immigrant population

Block	Prevalence (%)	Intensity g.m. epg ($CI_{95\%}$)	Total observed contacts	Contacts/individual/year
6	21	1·28 (1·02, 1·57)	2882	0·93
7	23	1·53 (1·19, 1·92)	2290	1·28
8	10	0·44 (0·25, 0·67)	6	0·01

overall prevalence of eggs in stool samples was 20 % rising to 35 % in the most heavily infected age group. Male and female age–intensity profiles were similar in this first survey. The profiles (not shown) of those who arrived in the first 3 months did not differ in shape or absolute intensity from those who arrived later (in analysis of variance of log (epg+1) on 15 approximately equal age groups and 2 arrival groups, early arrivers, i.e. before April 1992, were not found to be significantly more infected in February 1993 than those arriving later: $F = 0{\cdot}24$ on 1 and 1396 degrees of freedom, $P = 0{\cdot}63$).

Between early 1993 and mid-1994 mean infection intensity in the immigrant community rose considerably in teenage children but much less so in adults. Levels rose faster in boys than girls.

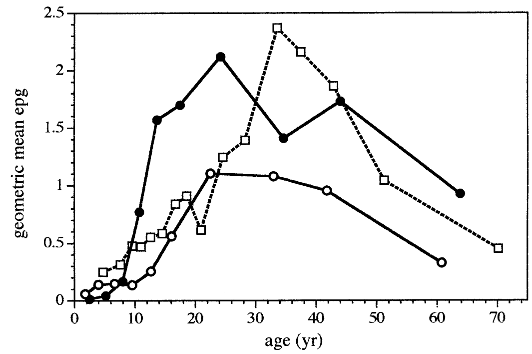

Fig. 6. Mbui Nzau and Immigrant Community, Block 8 faecal egg counts versus age. The Markov random field smoother was applied to the logarithm of the faecal egg counts (see Appendix). Note the change of scale on the *y*-axis relative to Figs 3 and 4.

Although plot allocation had been essentially random, there were differences in infection levels between blocks at the initial stool survey. Prevalence and intensity of infection in Block 8 (Table 2) was markedly, and significantly, lower ($F = 11{\cdot}05$ on 1 and 1681 degrees of freedom, $P < 0{\cdot}001$ by analysis of variance of log (epg+1)), although its pattern of infection with age was similar to the other 2 blocks (Fig. 6). People from Block 8 were recorded at the contact sites on a total of only 6 occasions over a 2-year period. Interviews revealed that people from this block obtained most of their domestic water from the nearby taps in Masongaleni village rather than the river. The increase in mean infection intensity between 1993 and 1994 in Block 8 was correspondingly slight and, unlike the other 2 blocks, was not dominated by changes in the teenagers (Fig. 6).

Initial (April 1993) levels of infection among the established community were far higher than those of the immigrants. Males showed a broad peak of infection around the age of 20 years while females gave a rather tighter peak at about 17 years of age and were generally somewhat less heavily infected. By July 1994 infection levels had increased in both sexes and across the whole age range, but especially among teenagers.

The patterns and absolute levels of crude (unweighted for risk of exposure) water contact were quite similar in the 2 communities. Contact was greatest in the second decade of life, although this peak was sharper among males than females.

Very few (4·4 %) of the 297 children attending Nguluni Primary School in Utu examined in 1997 were found to be infected, and only 1·3 % were estimated to have more than 30 epg. Of 730 Kyulu people who moved to Mbui Nzau 18 % were found to have *S. mansoni* eggs in their stools. Mean epg in Mbui Nzau were similar to those in Block 8 and were generally higher in adults than children (Fig. 6).

DISCUSSION

The immigrant community described here will inevitably attract comparison with the recently exposed population at Richard Toll in Senegal (Stelma *et al*. 1993). There are, however, a number of important differences between them. Firstly, the factors precipitating the 2 outbreaks were very different. In Richard Toll water development work involving Lac de Guiers and the Senegal River changed the local ecology allowing a build-up in the population of the water snail *Biomphalaria pfeifferi* and a subsequent increase in transmission of *S. mansoni*. The source of the initial infection is not known, but it is known that a large influx of people into the town of Richard Toll (although less so in the nearby village of Ndombo, where recent studies have been centred) occurred simultaneously with the ecological changes (Stelma *et al*. 1993). Nor are the dynamics of the increase in transmission clear since the intensity of infection was already high and the pattern of infection with age was already similar to endemic populations when the first observations were made. In contrast, the immigrants in Masongaleni were examined very shortly after they arrived when infection levels were very low and before the typical endemic pattern of infection with age had become established. Transmission was known to be on-going in the established community at the time of the immigrants' arrival (although it may have been boosted by their arrival). Thus more is known about the beginnings of this outbreak, and the established community provides a corresponding endemic control population.

The early stool survey of the immigrant population confirmed that their levels of infection on arrival were, at most, very low. What infection there was, was concentrated among the adults around the age of 30 years, quite unlike the usual endemic pattern typified by the established community. Those immigrants carrying an infection at the start of the study may have acquired it between the time of their arrival and the first stool survey. Alternatively, they may have acquired their infections whilst living in Kyulu, perhaps when watering their animals at the temporary stream at Kwamukonza (children and older people would have been less likely to make this long journey). Finally, it is also possible that these initial infections were of longer standing, acquired elsewhere in Ukambani before they migrated to the Kyulus. The last wave of immigration to the Kyulus was reported to have taken place about 15–20 years before they arrived in Masongaleni. Thus the late-peaking age profile of intensity seen when they first arrived in Masongaleni may have been the shadow of the more usual profile, peaking in the second decade of life, which the population had when they originally arrived in Kyulu.

Data from Block 8 and Mbui Nzau indicate that at the time of the initial stool survey those immigrants who had been little exposed since they left Kyulu were less heavily infected than the rest, suggesting that at least some of the infection seen in the first survey was acquired since arrival in the Thange valley. In this regard we note that the immigrants in Mbui Nzau may have had some exposure to infection during occasional visits to their former neighbours in Masongaleni. However, why early infection rates, between arrival and the first stool survey, should have been greater among adults than children can only be guessed. The adult males certainly did tend to arrive earlier than their families but this does not explain why females also initially showed the same atypical pattern of infection with age. Alternatively, perhaps men and women are usually more heavily exposed but, unlike children, rapidly become immune. Observed water contact appears to conflict with this hypothesis; while crude contact times do not necessarily measure true risk of exposure, in this area it is usual for children's activity to be relatively more risky than adults' (Fulford *et al*. 1996*b*). If, on the other hand, the immigrants had acquired these initial infections in or around Utu before arriving in Masongaleni, some evidence for transmission among the residents of Utu might have been expected, yet levels of infection in Nguluni Primary School were very low. Whether the low levels of infections seen in the initial survey were acquired recently or longer ago, the majority of immigrants arrived uninfected and during the course of the study we witnessed a profound change both in the absolute level of infection and its pattern with age. Furthermore, immunological studies, to be presented in later papers, show that the immigrant and established communities had markedly different cellular and humoral responses, supporting the notion that they had very different experiences of infection.

Comparison of the 1994 stool survey results and the water contact data confirms the adequacy of the established community as a control for the immigrants. The age and sex patterns of water contact appear to be quite similar in the 2 communities. Both communities also showed lower rates of infection among females than males and a peak rate of infection in the second decade of life. The age–intensity profiles of the immigrant and established communities can only be compared indirectly since the first represents the recent rate at which infection has been acquired while the second is the net result of all acquisition and loss of worms over the life-span of the host.

The difference between the 1993 and 1994 profiles in the established community is statistically significant. The reason for the observed changes is not known but we note that snail data from the Kambu and Thange rivers indicate that transmission was raised in the period between the surveys

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(Kariuki, personal communication). Transmission on the Thange may also have been boosted on the arrival of the immigrants by bush clearance. It is unlikely that infection among the immigrants themselves contributed much towards this transmission since the average number of eggs they excreted did not reach more than a fraction of that of the established community. While transmission may not have been stable, it is known to have occurred for many decades.

Data from the recently exposed populations in Senegal and Kenya broadly concur that the endemic pattern of infection is established rapidly (withing 14 months in the case of the Masongaleni immigrants) but contradict the findings of Kloetzel & da Silva (1967). All 3 studies attempted to uncouple age from experience of infection in order to distinguish the slowly acquired immunity proposed by Kloetzel and da Silva from simple age-dependent changes in behaviour, innate resistance or adaptive immune response. It is generally recognized that Kloetzel and da Silva's (1967) study was too small to be reliable, whereas the current study adds weight to the conclusion of Gryseels (1994) that age-dependent changes in host physiology, possibly including the immune system (Fulford *et al*. 1998), or behaviour must underlie the differences in infection rates between adults and children. However, while these studies show that slowly acquired immunity cannot be the only factor governing the decline in infection in adulthood, they do not preclude its existence. The age-related changes in physiology and/or behaviour required to explain the rapid establishment of the endemic pattern of infection may obscure additional differences in age-specific infection rates between recently exposed and endemic populations resulting from slowly acquired immunity. Indeed the observation that, prior to intervention, the age of peak intensity tends to fall earlier in more heavily infected populations suggests a role for a gradually developing immunity (Woolhouse *et al*. 1991; Fulford *et al*. 1992), although other explanations may account for it (Fulford *et al*. 1992, 1996*a*).

Water contact is strongly age dependent in both Masongaleni and Richard Toll (Stelma, 1997). Due to the paucity of knowledge about the relative risks of exposure associated with the different forms of behaviour adults and children engage in, it is extremely difficult to determine whether there are differences in infection rate between adults and children which cannot be entirely explained by exposure. Many studies, including the current one and that in Senegal, have reported that water-related behaviour starts to fall in the second decade of life (Dalton & Pole, 1978; Blumenthal, 1985; Chandiwana, Woolhouse & Bradley, 1991; Etard, Audiber & Dabo, 1995; Fulford *et al*. 1996*b*; Stelma, 1997). Since many aspects of host physiology also change dramatically at this age, physiological and behavioural changes may be heavily confounded. We have therefore begun studies in a fishing village on Lake Albert in Uganda, where high occupational contact with the lake water among the adults is expected to break this confounding. Initial results support the hypothesis that adults are less susceptible to infection (N. Kabatereine, unpublished).

Masongaleni presents a unique opportunity to follow the development of schistosomiasis in a population from a time before the pattern of infection has stabilized and to relate these observations to a neighbouring endemic population. Cohorts from the established and immigrant communities have been selected and bled and are being followed longitudinally. Initial results (to be presented in further papers) show marked differences between the cellular and humoral immunological profiles of the immigrant and established communities, reflecting their different experiences of infection. Continuing longitudinal study of the immigrant cohort should reveal valuable information on the course of development of the immune response to this disease.

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APPENDIX

The approach to data smoothing employed in this study is based on a Markov random field model (Mollie, 1996) used in image analysis and cancer incidence mapping. The method first stratifies (or 'bins') the *x*-variate, in this case age. It is assumed that the data within each stratum are distributed about a fixed, unknown mean. But, rather than treat each stratum independently of its neighbours, it is assumed that, prior to knowledge of the data, the mean of each stratum may take values which follow a known (Bayesian prior) distribution whose own mean is a function of the neighbouring stratum means, i.e. there is an autoregressive relationship between the strata means. The likelihood of the data and the prior autoregressive structure may then be combined mathematically, using Bayes' Law, to yield the posterior distribution for each stratum mean.

A particularly simple application of this approach arises if it is assumed that both the data and the prior distributions are Gaussian. Suppose that for the jth stratum the mean and variance of the data (Y_{ji}) are μ_j and σ_Y^2 and the mean and variance of the prior distribution of μ_j are M_j and σ_μ^2 (where M_j is some, as yet undefined, function of the adjacent stratum means). It follows that the resulting (posterior) distribution for μ_j will also be normally distributed with parameters:

$$\text{mean}_j = \frac{\sum_i Y_{ji} + \tau M_j}{n_j + \tau}; \quad \text{var}_j = \frac{\sigma_Y^2}{n_j + \tau},$$

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where n_j = size of jth stratum and $\tau = \sigma_Y^2/\sigma_\mu^2$.

An obvious function for M_j is the arithmetic mean of the adjacent stratum means: $M_j = (\mu_{j-1} + \mu_{j+1})/2$. A small problem arises for the first and last strata but is easily resolved by equating M_j with the stratum mean of its only neighbour, e.g. $M_1 = \mu_2$. If the Posterior Bayes Estimator is used to estimate μ_j, i.e. $\hat{\mu}_j = \text{mean}_j$, then a system of linear equations for μ_j can be set up and readily solved by matrix inversion for any given value of τ.

Choice of values of τ will determine the degree of smoothing employed. To aid this choice the concept of effective degrees of freedom, D.F._{eff}, is used (Hastie & Tibshiriani, 1990):

$$\text{D.F.}_{\text{eff}} = \sum_j \frac{n_j}{n_j + \tau}.$$

In this paper we have chosen τ so that D.F._{eff} lies between 7 and 8. Faecal egg count data are never normally distributed but means of samples of 20 or more of the logarithm, log (epg + 1), have been shown to follow the normal distribution to a reasonable approximation (Fulford *et al.* 1996*a*). The smoothing method described above was found to work well provided the stratum sizes did not frequently fall below 20.

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