Schistosoma mansoni infection in a natural population of olive baboons (*Papio cynocephalus anubis*) in Gombe Stream National Park, Tanzania

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SUMMARY

Infection with *Schistosoma mansoni* was studied in 5 troops of olive baboons (*Papio cynocephalus anubis*) in Gombe Stream National Park, Tanzania. Three troops were infected with *S. mansoni*. An aggregated distribution of parasites was observed among hosts. Troop membership was found to be the most significant factor influencing parasite prevalence. Age and reproductive status had no significant effect, but there was a trend for males to acquire higher levels of infection. However, age–prevalence curves showed a high infection in young baboons declining in the older baboons. Behavioural components of exposure – as measured in water-contact pattern – may be related to parasite burden. A 'peak shift' between infection in different age-classes in the different troops was observed: troops with higher schistosome prevalences displayed an earlier peak in prevalence of infection. The baboon troop with the most contact with people showed highest prevalence of infection possibly due to longer exposure to the parasite than the other troops and/or higher host density.

Key words: epidemiology, *Schistosoma mansoni*, baboons, water contact, spatial heterogeneity.

INTRODUCTION

Baboons have been used as models for human schistosomiasis in numerous studies (Greene *et al*. 1976; Sturrock *et al*. 1988; Damian *et al*. 1992; Yole *et al*. 1996). In contrast, little is known about the host–parasite interactions of *Schistosoma mansoni* in natural baboon populations. Only in the 1960s was it pointed out by Miller (1960) and Nelson (1960) that baboons can be infected with *S. mansoni* in the field. The information about schistosome infection in the wild has largely been limited to overall prevalence and intensity of infection (Kuntz & Myers, 1966; Goldsmid, 1974; McConnell *et al*. 1974; McGrew *et al*. 1988). To make the best use of baboons as animal models for the study of schistosomiasis we need to know more about baboon schistosome infections under natural conditions and the factors that shape their host–parasite interactions. Furthermore, the potential role of baboons as reservoir host for human schistosome infection (Fenwick, 1969) requires more detailed studies. On the other hand, detailed laboratory studies of baboon–schistosome interactions may complement data on natural populations and help to understand the dynamics of wildlife disease, presently an area of growing interest (Grenfell & Gulland, 1995; Ashford *et al*. 1996).

Ideally, host–parasite interactions should be studied in well-known host populations which have been monitored for some time and where sufficient information is available about each individual animal. The well-studied wild population of olive baboons (*Papio cynocephalus anubis*) consisting of 5 troops in Gombe Stream National Park, has been monitored since 1967, and offers a good opportunity to observe the epidemiology of schistosomes in a natural situation (Müller-Graf, Collins & Woolhouse, 1996). Baboons are individually known and information about sex, age, troop membership (natal troop and troop of residence) and family is available for analysis with the data on schistosome infection.

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MATERIALS AND METHODS

Study area

Gombe Stream National Park is situated on the eastern shore of Lake Tanganyika, 16 km north of Kigoma at 4° 40′ S, 29° 38′ E. The park covers an area of 52 km^2 and is bounded in the east by the escarpment of the eastern wall of the Rift Valley. The park is dissected by 13 steep-sided valleys with streams running from east to west. In the park, the altitude rises quickly from 773 m above sea level at the lake shore to over 1500 m at the top of the escarpment. Because of this difference in altitude the vegetation is varied, ranging from evergreen forest, dry forest, to wooded grassland through to grassland near the ridges. The baboons live mainly in the evergreen and dry forest area but their home ranges extend to the lake shore and to wooded grassland as well (Ransom, 1981). A permanently inhabited research station is situated within the borders of Gombe Stream National Park, and fishermen camp along the beach for approximately 3 weeks every month. The beach is also used as a footpath for local people carrying food and other items from the surrounding areas (Ransom, 1981; Bygott, 1992).

Host population

The baboon population has been kept under observation since 1967 and troops are visited daily by the field staff. All baboons are individually identified. For each individual age, sex, reproductive status, social rank and life-history were known. In autumn 1991, the baboon population consisted of 272 animals, forming 5 troops (A-, B-, C-, D- and L-troop) varying in size from 33 to 67 members (mean = 54) with a roughly equal sex ratio in each different troop across the total population. Among the adults there were more females than males in all troops. A-, B- and D-troop are closely related: in 1969 A-troop split off from B-troop and in 1978 D-troop split off from B-troop. Little is known about the history of C-troop and L-troop; they may have been derived from B-troop before 1969 or be descendants from other troops in the park. However, all troops are related to some extent as male adult baboons migrate from the troop in which they are born and breed in other troops nearby (Packer, 1979). Troop ranges also overlap with their neighbours to some extent, less so with those further away. All troops show a similar social structure.

Sampling

The climate in Gombe is divided into wet and dry seasons. The wet season is usually from mid-October to mid-May and the dry season lasts for the other 5 months. Baboons were sampled for *S. mansoni* in 3 consecutive seasons: in spring and autumn 1991 (1.6.1991–17.7.1991; 10.11.1991–27.11.1991) and spring 1992 (14.5.1991–2.6.1991). Schistosome infection was estimated by faecal egg counts (Wilkins, 1987; De Vlas *et al*. 1992) and is given here in eggs per g of faeces (epg). A total of 396 stool samples was collected from 206 known individuals from all 5 troops. The faecal samples were collected immediately after defaecation from known individuals and preserved in 25 ml centrifuge tubes in 10% formalin on site. These samples were later sieved with a large mesh sieve to remove large contaminants and centrifuged to obtain 1 g of faeces from the pellet and then screened for *S. mansoni* eggs by the formol–ether method (Cheesbrough, 1987; Müller-Graf, 1994). Egg counts were made from 1 g of the pellet from the faeces. Water-contact behaviour of baboons was recorded at Gombe in 1975 (3 February–21 June). Observations were made on 25 days per month (with the exception of June when observations were made on only 21 days) in each troop for 2–3 h each day. During this time the troops were observed 52 times altogether on the shore of Lake Tanganyika. Data were recorded for every animal of known identity which entered Lake Tanganyika for swimming and play. Excluded were rare events when males entered the water for food and when individuals were escaping from attacks.

Statistical analysis

Prevalence is defined as the percentage of individuals of a host species excreting *S. mansoni* eggs. Abundance describes the number of eggs in a single faecal sample. Mean abundance is calculated for both infected and uninfected host individuals. Mean intensity of infection describes the mean abundance of infection for infected hosts only (Margolis *et al*. 1982).

For the statistical analyses, when there was more than 1 sample from an individual, only the first sample was used to avoid biases due to repeated measures. Prevalence for the tables was calculated from all data. Five individual baboons were excluded from the analyses because their ages were not known.

Schistosome egg counts were log $(x+1)$ transformed. The cross-sectional analyses were done using the data from autumn 1991. To test for significant differences in *S. mansoni* prevalence between age-classes, sex and troop and for up to 3-way interactions, log-linear analysis was employed (using 'SPSS'; SPSS Inc., 1990), reporting the partial χ^2 values from a saturated model. Age was treated as a categorical variable with 2 classes: young and old (young $\leqslant$ 8 years; old > 8 years) because the effect of age can not be considered linear here and due to the sample size. Above the age of 8 years baboons are fully grown adults. However, for age–prevalence and age–intensity curves 6 age classes are shown. The relationships of intensity and abundance of infection with age-class, troop, sex and interactions were analysed using General Linear Models (GLMs). GLMs are a set of statistical techniques which combine regression and ANOVA methods (= ANCOVA) and can deal with categorical and continuous variables at the same time

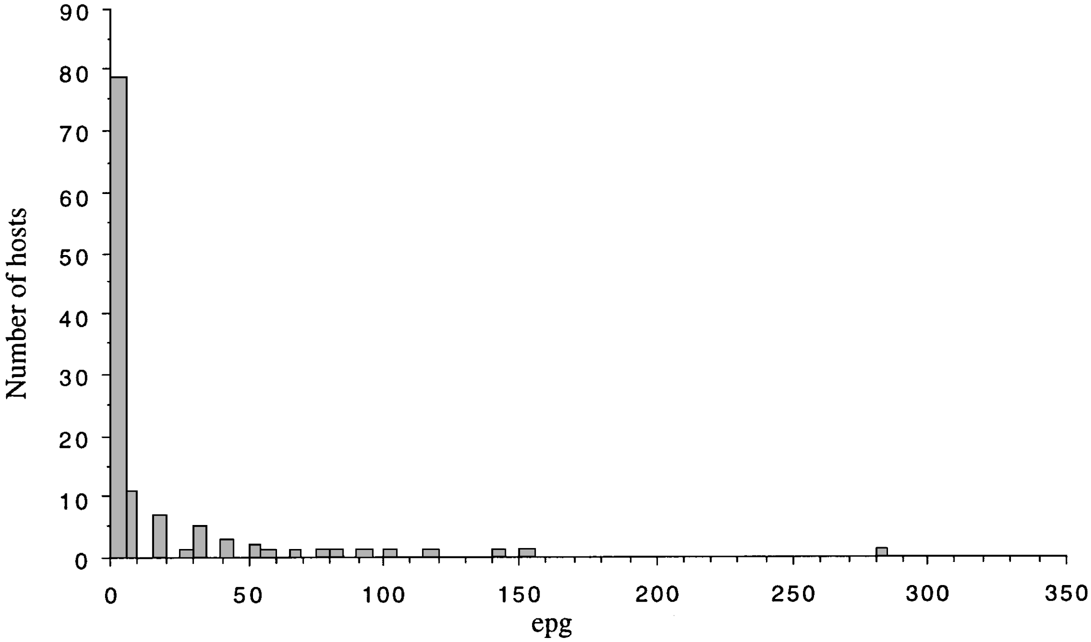

Fig. 1. Frequency distribution of abundance of infection in infected troops as measured in epg. Zero counts are included in the first bar. The bar interval is 5 epg.

(General Linear Models; MinitabInc., 1991). Confidence intervals for age–prevalence curves assumed binomial errors and were obtained from tables (Motulsky, 1995; interpolated according to Rohlf & Sokal, 1981). The effect of reproductive status (including only females which were either pregnant, lactating or cycling; omitting amenorrhoeic and subadult females) on infection was analysed using GLMs and logistic regression (using 'SPSS'; SPSSInc., 1990) with age as a covariate and controlling for troop. Seasonal effects were tested employing samples from the same 70 individuals in all 3 seasons using log-linear models and GLMs. Where repeated measures of the same individual are included in the analysis, these are controlled for sampling effort so that still 1 individual appears only as 1 data point. For the water-contact observations, Mann–Whitney *U* tests were corrected for ties. All tests were two-tailed and the level of significance was set at 0·01 due to the number of tests carried out (see Müller-Graf *et al.* 1996).

RESULTS

The distribution of egg counts was overdispersed with a variance ($\sigma^2 = 1425{\cdot}9$) much greater than the mean ($\mu = 15{\cdot}17$) (Fig. 1). Out of the 5 troops only 3 were infected with *S. mansoni*. Levels of prevalence and abundance differed significantly between the troops, whereas intensity did not show any significant difference (Table 1). Where, as was generally observed, analysis of prevalence and abundance data gave similar results, only the former are reported.

Sex had a non-significant effect (at the 1 % level) on parasite burden (prevalence: Partial $\chi^2_1 = 3{\cdot}04$, $P = 0{\cdot}081$; males = 25·8 %, females = 13·9 %; intensity; $F_{1,34} = 4{\cdot}54$, $P = 0{\cdot}041$; geom. mean males = 37·86 epg (24·35–58·55) 95 % CI, females = 16·27 (10·44–26·1). However, males tended to have higher levels of infection than females. If repeated samples from the same individual were included but controlling for sample size, the trend was stronger in intensity ($F_{1,37} = 7{\cdot}31$, $P = 0{\cdot}010$) and abundance ($F_{1,194} = 5{\cdot}90$, $P = 0{\cdot}016$). No association between reproductive status and schistosome prevalence or intensity could be observed (prevalence: Wald = 1·13, $P = 0{\cdot}77$, D.F. = 3, cycling = 11·11 %, pregnant = 0 %, lactating = 12·5 %, intensity: $F_{2,4} = 0{\cdot}2$, $P = 0{\cdot}68$ geometric mean cycling = 18·19 epg (5·97–51·80) 95 % CI, pregnant = 0, lactating = 13·28 (5·72–34·68)).

No significant effect of age-class on parasite infection was observed (prevalence: Partial $\chi^2_1 = 3{\cdot}79$, $P = 0{\cdot}051$; young = 24·2 %, old = 77 %; intensity: $F_{1,34} = 1{\cdot}30$, $P = 0{\cdot}262$; geom.mean young = 33·77 epg (23·73–47·89) 95 % CI, old = 13·59 (5·79–30·34)). However, the age–prevalence (Fig. 2) curve showed age-related changes. The prevalence rises from a very young age, peaks in the age-classes 2 and 3 (which are the juveniles and subadults) and then declines. The age–intensity curve does not show such a clear pattern. However, there is a trend for lower intensity in the older baboons (Fig. 3).

Season had no significant influence on parasite infection (prevalence: Partial $\chi^2_2 = 0{\cdot}97$, $P = 0{\cdot}62$; intensity $F_{2,36} = 1{\cdot}22$, $P = 0{\cdot}31$).

There was not only a direct effect of troop membership on parasite infection, *S. mansoni* infection also interacted with the age-classes in the respective troop. A troop-age-class interaction was

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Table 1. Variations of *Schistosoma mansoni* prevalence and intensity among troops

(The 95% confidence intervals are reported after the geometric mean (Kirkwood, 1988). Troops are ordered according to home ranges. The adjusted mean is not the simple mean but adjusted for the other variables (Minitab, 1991).

			Prevalence	Intensity	
Troop	Size of troop	*n*		Geometric mean	Adj. geom. mean
L	64	41	0	—	—
A	66	46	0	—	—
D	67	50	42·0%	32·3 (22·0–47·1)	23·7 (13·4–41·5)
C	42	37	24·3%	10·5 (7·5–14·5)	13·5 (5·6–26·5)
B	33	31	32·2%	40·4 (17·8–90·2)	28·6 (14·8–53·3)
Test statistic			Partial $\chi^2_4 = 54{\cdot}1$		$F_{2,34} = 1{\cdot}05$
P-value			$< 0{\cdot}0001$		$< 0{\cdot}36$

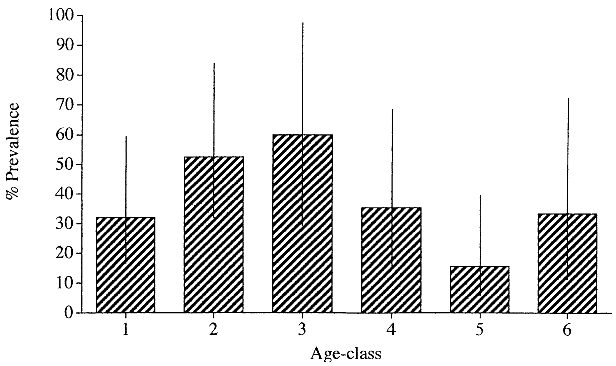

Fig. 2. Age–prevalence profile. The age–prevalence profile was calculated for the schistosome-infected troops only. Age-classes are classified as follows: (1) up to 2 years (infants), $n = 25$; (2) 3–4 years (juveniles), $n = 19$; (3) 5–6 years (subadults), $n = 10$; (4) 7–8 years (young adults), $n = 17$; (5) 9–15 years (adults), $n = 32$; (6) > 15 (old individuals) $n = 12$. Vertical bars indicate 95% confidence intervals.

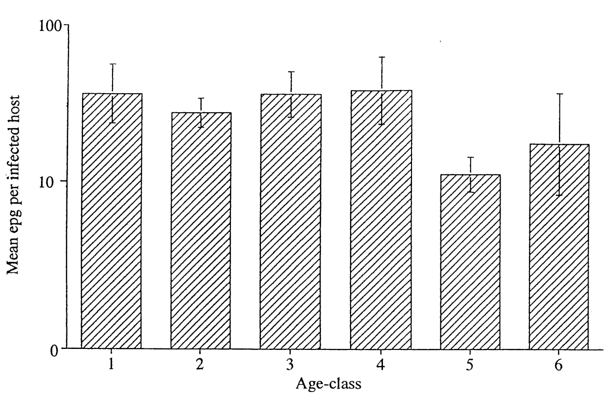

Fig. 3. Age–intensity profile. The age–intensity profile was calculated for the schistosome infected troops only using log (epg+1) transformed data. *X*-axis indicates the age-classes and *y*-axis the intensity of infection (the infected hosts only). Anti-log values are reported on the *y*-axis. Age-classes are classified as for Fig. 2. Vertical bars indicate S.E.

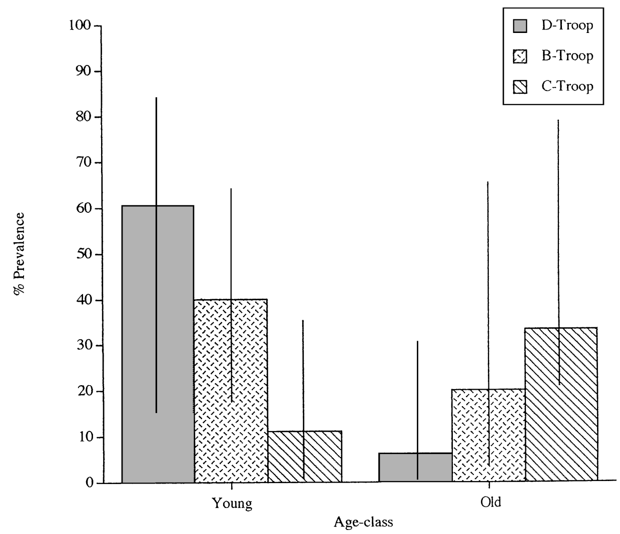

Fig. 4. Troop-age-class interaction in prevalence of *Schistosoma mansoni* infection. The following prevalences were observed: B-Troop young (8 infected of 20), old (2/10), C-Troop (2/18), (6/18); D-Troop (20/33) (1/16). Vertical bars indicate 95% confidence intervals.

observed (Partial $\chi^2_4 = 14{\cdot}6$, $P = 0{\cdot}006$) with prevalence tending to decrease with age in D- and B-troop and to increase in age in C-troop (Fig. 4).

Water contact patterns are shown in Fig. 5. Younger baboons had a higher frequency of water contacts than older baboons ($U_{(25,18)} = 11{\cdot}5$; $P = 0{\cdot}0001$) and a greater tendency to go into water at all (χ^2_1 with continuity correction $= 31{\cdot}56$, $P = 0{\cdot}0001$) than older baboons. All baboons up to the age of 6 years (the first 3 age-classes) were found to have had water contact during the period of observation, half of the 4th age-class between 7 and 8 years, only 7% of the baboons between the age of 9 to 15 years and none of the older baboons. Males showed a higher frequency of water contact than females ($U_{(21,22)} = 128{\cdot}5$, $P = 0{\cdot}0096$), but there was no significant

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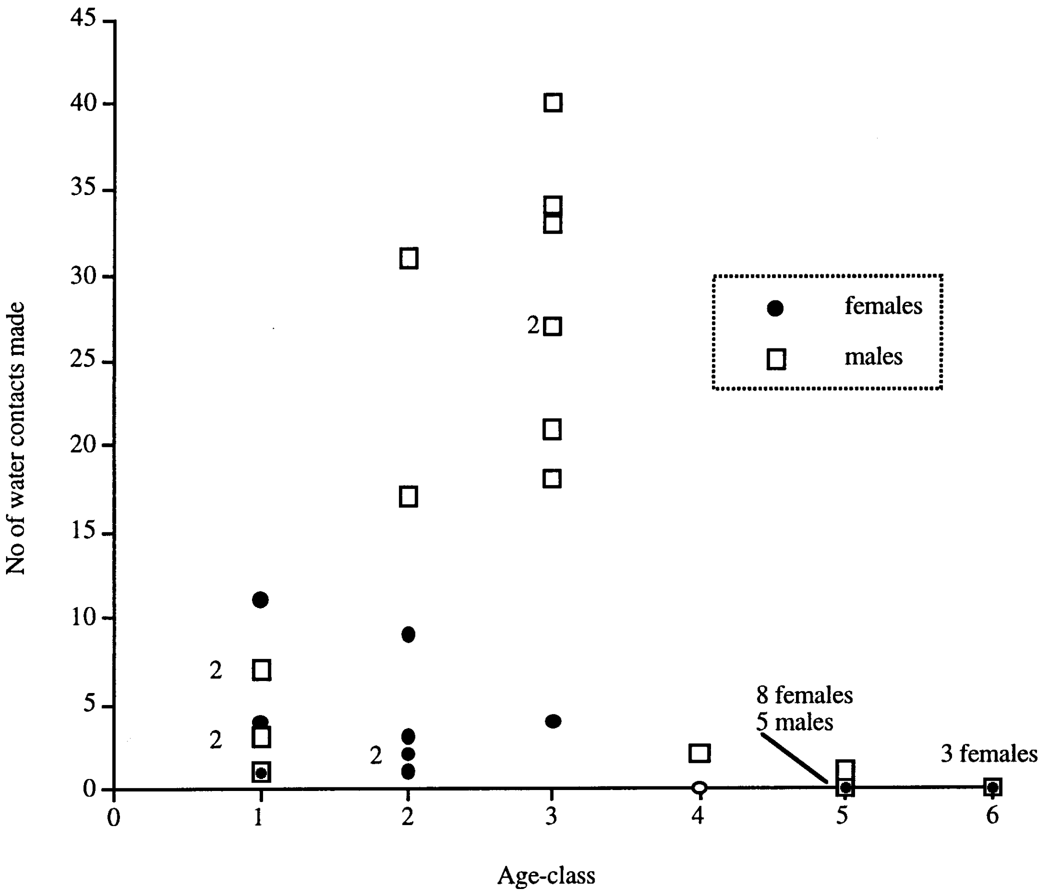

Fig. 5. Water contact patterns in relation to age. The number next to the symbol indicates if more than 1 individual showed the same number of water contacts. Observations were made on 121 days during the period from 3 February–21 June 1975 per troop for 2–3 h/day. The figure shows the total number of water contacts over the observation period. The quality of water contact is not taken into account. However, females and males showed similar kinds of water contact.

difference between the sexes as to whether they went into the water at all (χ^2_1 with continuity correction = 2·81, $P = 0{\cdot}094$).

DISCUSSION

The frequency distribution of *S. mansoni* showed an aggregated pattern as would be expected for a helminth infection in a natural population (Crofton, 1971; Shaw & Dobson, 1995). This aggregation can reflect heterogeneities in exposure, innate susceptibility and acquired immunity between the hosts (Woolhouse, 1994). Across all troops, troop membership appeared to be the most important determinant of parasite prevalence.

Although age did not have a significant impact on parasite infection, the age–prevalence curve looked similar to those observed for humans (Jordan & Webbe, 1982; Anderson & May, 1985, Wilkins, 1987). The age–abundance curve showed a congruent pattern to the age–prevalence curve. Several factors, such as behaviour or immunology, may be important for this age-related curve. We do not have any data relating to the immune status of the observed animals. However, we can compare the parasitological data with behavioural data from the survey of water-contact patterns of the Gombe baboons carried out in 1975. Baboons enter the water during play and during fights and occasionally for food. Lake Tanganyika is assumed not to harbour snails in this area and therefore not to be a transmission site. However, researchers have observed similar water contact patterns at nearby water sources such as pools and stream beds inland and it is there that transmission is assumed to take place. For instance, *Biomphalaria pfeifferi* – the intermediate host of *S. mansoni* – was found inland at one of these marshy water sites. The water contact observations showed that juvenile baboons had much higher water contact than older baboons. No baboon older than 11 years was observed in the water during this water contact study but, over a longer period, baboons of all ages have been observed to enter the lake and streams, for instance for food. Therefore, even the older baboons do contact water, only less frequently.

Furthermore, males showed higher water contact rates than females, which may explain the trend in higher abundance and intensity of infection in the male baboons. The observed swimming behaviour of the baboons may indicate that behavioural components of exposure have an impact on parasite burden. These findings agree with results of studies on humans, where there is evidence that age and sex-related changes in behaviour (contact with water) affect infection rates (Jordan & Webbe, 1982; Wilkins, 1987; Chandiwana & Woolhouse 1991).

The relationship between age-class and prevalence of infection differed between the troops. These differences may be related to variations in rates of infection experienced by the respective troops. Troops which had higher schistosome prevalences also displayed an earlier peak in infection. This is compatible with the predictions of epidemiological theory if acquired immunity has significant effects. However, it has been argued that this pattern may also be explained by other models (Fulford *et al*. 1992, 1996). Patterns showing these differences related to rates of infection agreed with observations in human communities for *S. mansoni* and *S. haematobium* (Woolhouse *et al*. 1991; Fulford *et al*. 1992; Woolhouse, 1994).

No seasonal variation in schistosome egg output could be found. However, the prevalence of *S. mansoni* has been increasing over the years. A survey by McGrew *et al*. (1988) on baboon parasites in this area in the 1970s did not find any *S. mansoni*; nor was *S. mansoni* recorded in humans in Gombe before 1975. By 1983, *S. mansoni* was present in humans in Gombe indicating that the parasite was introduced at some time during those 8 years. Therefore, when interpreting age-related levels of parasite infection, it has to be also taken into account that the rate of infection experienced by the older animals may have been different to that experienced by the younger baboons.

At present, the *S. mansoni* infection is spreading in the baboon population. Recent observations indicate that at least 1 more troop is infected (F. Nutter, personal communication). It is possible that people introduced the parasite to Gombe and it then spread to the baboon population. People may have greater opportunities to become infected than baboons as they are more mobile and travel more frequently between Gombe and other areas. Park employees for instance take yearly leaves of a month or more and usually return to their home village. It was recently noticed that several members of one family who went on home leave to Lake Victoria were diagnosed with *S. mansoni* upon their return (F. Nutter, personal communication). The range of D-troop, the troop with the highest infection rate, includes the park village. As a consequence, baboons in this troop have the highest contact rate with water also used frequently by humans. If the high prevalence of infection is the result of the fact that this baboon troop has been exposed the longest, then this may indicate that the initial source of the parasite originates from the people. The other infected troops (B and C) have less contact with humans. The remaining 2 troops (A and L), which at the time of this study were uninfected, have the least contact with humans, although some contact exists. The higher infection of D-troop could also be the result of a higher population density of baboons and people leading to a higher concentration of contamination and exposure at the common transmission site.

Therefore, infection of baboons should be considered in the control of human schistosomiasis. However, more data are required on the population biology of the schistosomes in humans and baboons to determine if the *S. mansoni* strains are the same or different strains and to evaluate the amount of parasite exchange between the 2 species.

The study shows that the epidemiology of *S. mansoni* in baboons may exhibit similar patterns to human infection. Behaviourally mediated variation in exposure may be important for the differences of infection observed in the baboons. It has been shown experimentally that schistosome infection can have a detrimental effect on baboon health: very heavy infections with *S. mansoni* can kill baboons (Sturrock, Butterworth & Houba, 1976). Therefore it is likely that less intense infections do have more subtle effects on survival and reproduction of the baboons. Infection with *S. mansoni* is likely to have some impact on the population dynamics of the baboons in Gombe.

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