The influence of colostrum on early *Schistosoma mattheei* infections in calves

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SUMMARY

The study investigated whether the susceptibility of calves to an early *Schistosoma mattheei* infection may be modified by intake of colostrum from infected cows. Twelve calves born to non-infected mothers were randomly divided into 2 groups of 6. The animals from group 1 were fed colostrum originating from a pool collected from non-infected cows, the calves from group 2 received colostrum from a pool collected from cows infected with *S. mattheei*. One month after birth all calves were infected by exposure to 1000 cercariae of a local strain of *S. mattheei*, and perfused 12 weeks later to determine the worm- and tissue egg counts. IgG_{H+L}, IgG_1, IgG_2 and IgA levels against soluble adult worm antigen preparation of *S. bovis* (SWAP *bovis*) were analysed in both colostrum pools and in the serum from the calves collected during the study before and after receiving colostrum, then on days 7, 30, 73 and 122. Faecal egg counts were determined from day 73 onwards. The IgG_{H+L}, IgG_1 and IgA levels of the positive colostrum pool were higher than those of the negative pool. Calves of group 2 showed significantly higher levels of IgG_{H+L} and IgG_1 until day 73, to reach equal levels at necropsy. Calves of group 2 showed significant reductions of 42, 28 and 42% in total worm counts, female worm counts, and tissue egg counts, respectively, and a reduction of 25% in cumulative faecal egg counts. These findings indicate that there was a significant impact of colostrum on the parasitological and serological course of early *S. mattheei* infections.

Key words: *Schistosoma mattheei*, cattle, colostrum, immunity.

INTRODUCTION

At least 165 million cattle are infected with schistosomes worldwide (De Bont & Vercruysse, 1997). These infections are generally characterized by a high prevalence of low to moderate worm burdens in the cattle population (De Bont & Vercruysse, 1998).

In endemic areas, virtually all cattle form herds in contact with cercarial-infested water become infected very early in life. Faecal egg excretion has been observed as early as the second month after birth (Majid *et al.* 1980), but it is more commonly observed between 4 and 8 months of age (Majid *et al.* 1980; De Bont *et al.* 1995 *a*). Egg counts increase rapidly to reach a maximum of 70–310 eggs per gram faeces at the age of 6–15 months, then decrease markedly by the age of 18 months (Majid *et al.* 1980; Pitchford & Visser, 1982; De Bont *et al.* 1995 *a*). In contrast to egg counts, worm burdens in cattle exposed to natural challenge increase with age of the host (De Bont *et al.* 1991). Several studies have demonstrated that, at least in cattle, protection against challenge infections acts mainly through a reduction of worm fecundity (Bushara *et al.* 1980; Majid *et al.* 1980; Kassuku *et al.* 1986; De Bont *et al.* 1995 *b*), and to a lesser extent through prevention of re-infections (Bushara *et al.* 1980, 1983 *c*; De Bont *et al.* 1995 *b*). The immunological character of the acquired protection has been demonstrated through experimental infection and worm transfer studies (Bushara *et al.* 1980, 1983 *a–c*), as well as during vaccine trials (De Bont *et al.* 1997; Grzych *et al.* 1998). However, little is known on the protective mechanisms involved. Bushara *et al.* (1994) showed that multiple transfers of immune serum during the period of maturation (between 4 and 10 weeks after exposure to cercarial challenge) of a *Schistosoma bovis* infection caused reductions in worm counts and fecundity. Their experiment provided some evidence that the effect is due at least in part to serum-borne factors, though the antibody classes on which protective mechanisms depend have not yet been identified.

In regions where schistosomiasis is endemic, most calves born to infected mothers are exposed to cercarial challenge at an age when their capacity to react

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to infection could depend on the genetic inheritance received from the mother. Studies of parasitic infections in different mammalian species, including cattle, have shown that immunoglobulins, parasite circulating antigens, immune cells, cytokines and other cell-related products, transferred from the mother to offspring can give protective effects, but can also down-regulate the latter's immune response (reviewed by Carlier & Truyens, 1995). Boes *et al.* (1999) demonstrated that colostrum from infected sows could give partial protection against *Ascaris suum* infections in piglets. Antibodies against *Eimeria bovis* have been detected in the serum from the newborn calf, after intake of colostrum from their infected mothers (Fiege *et al.* 1992). However, Faber *et al.* (2002) failed to identify a protective effect of this transfer in the offspring. In mice infected with *S. mansoni*, Taylor, Denham & Nelson (1971) failed to demonstrate neonatal transfer of immunity against infection with *S. mansoni*, while Lenzi *et al.* (1987) described a transfer of antibodies or antigens via placenta and/or via colostrum from infected mothers to their offspring causing a hyporesponsiveness to a *S. mansoni* infection in newborn mice. Finally, in man, Santoro *et al.* (1977 *a*, *b*) and Eissa *et al.* (1989) suggested that intake of colostrum from infected mothers, could transmit cellular hypersensitivity to *S. mansoni* antigen to the infant.

In bovine schistosomiasis nothing is known about the transfer of maternal/colostral immunity and its importance. The placenta of ruminants is syndesmochorial. In this type of placenta, the transplacental passage of immunoglobulin molecules is normally prevented, the passive transfer of colostral immunoglobulins is for the calf the most important way of receiving immediate immunological protection (Kruse, 1983). The level of antibodies in the colostrum of cows is high, up to 70–80% of the total protein content (Stott & Fellah, 1983; Lilius & Marnila, 2001), mainly consisting of IgG_1, but also IgG_2, IgA and IgM.

The objective of the present study was to investigate whether a transfer of specific maternal immunity via intake of colostrum from *S. mattheei*-infected cows occurs and, if so, how this transfer may influence a subsequent (early) experimental infection of calves with *S. mattheei*.

MATERIALS AND METHODS

Colostrum pools

Two colostrum pools were prepared by mixing samples (0·1–1 litre/cow) collected on several Zambian farms before the start of the trial. The first pool (negative pool) consisted of samples collected from 22 Friesian cows confirmed to be non-infected by faecal examination, and grazing on 2 dairy farms where no habitats for potential intermediate snail hosts were found. The second pool (positive pool) consisted of samples collected from 27 Simmental-Boran cows with *S. mattheei* faecal egg counts of 5–150 eggs per gram and grazing on 4 beef cattle farms with active transmission sites.

The colostrum samples were collected within 6 h after calving and kept at −20 °C until use. Samples of the pools were kept for later analysis. Each pool was sufficient to feed 6 newborn calves.

Calves

A total of 12 male Friesian calves newly born to non-infected cows were purchased, before intake of colostrum. The dams were confirmed to be non-infected on the following criteria: (1) they were living on a farm without transmission sites, (2) schistosome eggs could not be detected on faecal examination, and (3) specific *Schistosoma* antibodies could not be detected in their serum. All calves were kept on a concrete floor at the School of Veterinary Medicine, Lusaka; they were weaned at the age of 8 weeks and thereafter fed hay and calf starter pellets. The milk given to the calves until weaning originated from a non-infected commercial dairy farm.

Experimental design

The calves were divided randomly into 2 groups. Within 12 h after birth, calves from groups 1 and 2 received colostrum (3 litres per calf) from the negative and positive pool, respectively. At the age of 1 month each calf was exposed to 1000 cercariae of *S. mattheei* and subsequently slaughtered about 12 weeks later, for worm recovery and tissue egg counting (see parasitological techniques).

Each calf was blood sampled immediately before receiving colostrum (day 0), the following day (day 1), and subsequently on day 7, day 30 (time of challenge), day 73 (start of egg excretion) and day 122 (time of necropsy), for serum production and subsequent specific antibody determination. Faecal samples were collected on days 73, 80, 87, 94, 108 and 122 for determination of faecal egg counts.

Parasite strain and parasitological techniques

The parasite strain used was a Zambian strain of *S. mattheei*, maintained in laboratory-bred *Bulinus globosus* snails (De Bont *et al.* 1995 *a*, *b*). Calves were infected by cercarial exposure of the skin of their shaved tails for 30 min (Bushara *et al.* 1980). Different batches of *S. mattheei* cercariae were applied during exposure at age 1 month since the calves were not all born on the same day.

To determine faecal egg counts (EPG) a modification of the concentration technique of Lawrence (1970) modified by De Bont *et al.* (1991, 1995 *a*) was used. To recover worms from the mesenteric and

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hepatic veins calves were perfused according to the technique described by De Bont *et al*. (1995 *a*). Total worm counts (TWC) and female worm counts (FWC) were determined. Representative samples (5%) of the intestines and liver were collected and tissue egg counts (TEC) were determined after digestion in potassium hydroxide according to De Bont *et al*. (1995 *a*).

Enzyme-linked immunosorbent assay

Both colostrum pools and the sera collected from calves were analysed for determination of *Schistosoma*-specific Ig levels (IgG_{H+L}, IgG_1, IgG_2, IgA). A standard micro-well antibody enzyme-linked immunosorbent assay (ELISA) with soluble adult worm antigens preparation of *S. bovis* (SWAP *bovis* = total *S. bovis* antigen) was used. Optimum reagent dilutions were determined by titration. ELISA plates (Maxisorp Nunc, Brand Products) were coated with 100 μl (2·5 μg/ml) of SWAP *bovis* in phosphate-saline buffer (PBS 0·01 M, pH 7·2) and stored overnight at 4 °C. After the SWAP *bovis* solution was removed, wells were blocked (30 min at room temperature) with 200 μl of a 2% horse serum solution in PBS and then washed 3 times with PBS 0·05% Tween before adding 100 μl of appropriately diluted bovine serum (1/500 for Total IgG – IgG_{H+L}, 1/400 for IgG_1, 1/100 for IgG_2, 1/25 for IgA). After incubation overnight at 4 °C, the plates were washed and incubated with 100 μl of sheep anti-bovine isotype antibodies (Serotec): IgG_{H+L} at 1/15 000, IgG_1 at 1/80 000, IgG_2 at 1/100 000 and IgA at 1/15 000 in PBS Tween 0·05% and 1% horse serum, respectively. After incubation (1·5 h at 37 °C) the plates were washed and developed for 30 min with 1,2-phenylenediamine dihydrochloride (OPD, DAKO) substrate at room temperature. The reactions were stopped using 1 M H_2SO_4. The optical densities (OD) of the colours developed in the plate were read at 492 nm (reader: Labsystems Multiskan MS). The colostrum pools were diluted in PBS Tween 0·05% to 1/1000 for the detection of IgG_1 and IgG_{H+L}, to 1/100 for IgG_2, and to 1/50 for IgA.

Delta optical densities (Δ OD) were calculated according to the formula:

$$\Delta \text{OD} = \text{ODx} - \text{ODneg},$$

where ODx is the individual OD value of the test serum, and ODneg the OD of a known negative sample. Arithmetic group means were calculated for each sampling day.

Statistical methods and calculations

Assuming a normal distribution, 2 sample *t*-tests ($P<0·005$) were used to evaluate the differences in immunoglobulin levels in the sera from the calves. To reach a family confidence coefficient of $1-\alpha$ (that all individual statements are true at a level of $1-\alpha$) the significance levels for the individual comparisons need to be reduced. The Bonferoni method ($1-\alpha/2g$ where g is the number of levels of x) was used to adjust calculated significance levels from multiple comparisons.

A Poisson model with default log link function with response variable eggs per gram (EPG) and factor day was used to compare temporal variation of EPG between both groups (= overall faecal egg counts). For each day interaction was allowed. Hypothesis testing was done using the χ^2 procedure. The significance level was set at $P=0·01$. Preference was given to the 1% cut-off level to detect only important differences.

Cumulative faecal egg counts were determined as followed: for each calf a geometric mean EPG was calculated between 2 successive sampling days (days 73–80; 80–87; 87–94; 94–108; 108–122) and this mean was multiplied by the number of days between the samplings. The total cumulative egg count over the 50-day period was then calculated for each animal. Finally, a geometric group mean was calculated, giving the mean total cumulative EPG over the whole period (50 days).

A Poisson model with default log link function was used to compare the total worm counts between both groups (arithmetic means were used). Hypothesis testing was done using the χ^2 procedure, with the significance level set at $P=0·01$.

The number of days between start of excretion and slaughter for each calf varied between 42 and 64 due to practical constraints. This implies that in some animals worms have been producing eggs during a longer period, giving them a chance to accumulate more eggs in the tissue. Therefore corrected TEC values (TECcorr.) were calculated in the following way. The number of eggs counted in tissues of each animal was divided by the number of days between start of excretion and slaughter of that animal, and the result was multiplied by 50 (for 50 days) for all animals. A Poisson model with default log link function was used to compare the TECcorr. between the groups (arithmetic means were used). Hypothesis testing was done using a χ^2 procedure with the significance level set at $P=0·01$.

RESULTS

Isotype antibody levels in the colostrum pools

The results of the isotype antibody levels (expressed as optical densities) for both colostrum pools are shown in Table 1. The IgG_{H+L}, IgG_1 and IgA levels of the positive colostrum pool were higher than that of the negative pool. Only for IgG_2 no difference was observed, however, levels were very low.

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Table 1. Isotype antibody levels (optical densities) against soluble adult worm antigen preparation of *Schistosoma bovis* (SWAP *bovis*) in 2 pools of colostrum from cows either naturally infected with *S. mattheei* (positive pool) or not infected (negative pool)

Isotype	Dilution	Positive pool	Negative pool
IgG_{H+L}	1/1000	0·905	0·299
IgG_1	1/1000	0·646	0·176
IgG_2	1/100	0·016	0·027
IgA	1/50	0·936	0·579

Serum isotype antibody levels from the calves

At birth (day 0), no IgG_{H+L} antibodies against SWAP *bovis* were detected in both groups (Fig. 1) After intake of colostrum (day 1) an increase was observed in the calves of group 1 (ΔOD = 0·36), and group 2 (ΔOD = 0·8). For the calves of group 1 the IgG_{H+L} antibody levels slowly decreased after day 1 to reach almost zero at day 30, followed by a small continuous increase until slaughter (ΔOD = 0·28). In the calves of group 2 IgG_{H+L} antibody levels slowly decreased from day 1 to day 30 (ΔOD = 0·43, significantly higher ($P < 0·0005$) than for group 1) and further on until slaughter, to reach similar levels as for group 1 (ΔOD = 0·20) (Fig. 1). For IgG_1 a comparable pattern was observed as for IgG_{H+L}. IgG_1 mainly supported IgG_{H+L}, as IgG_2 levels were negligible during the whole period. IgA levels were also low, except for an increase in both groups on day 1 up to 0·42 and 0·18 ΔOD for calves of groups 1 and 2, respectively.

Faecal egg counts

Group 1 (mean EPG = 36) showed significantly higher overall faecal egg counts than group 2 (mean EPG = 25) ($P < 0·01$). The results of the cumulative egg counts are shown in Fig. 2. The mean total cumulative EPG was calculated to be 1720 and 1290 for groups 1 and 2, respectively. The geometric mean EPG on the day of necropsy was 47 for group 1 and 34 for group 2.

Worm counts and tissue egg counts

Animals of group 2 showed a statistically significant ($P < 0·01$) reduction in TWC, FWC and TECcorr. of 42, 28 and 42%, respectively (Table 2).

DISCUSSION

The present study was designed to monitor whether intake of colostrum from cows infected with *S. mattheei* may modify a subsequent (early) experimental infection of calves with *S. mattheei*. As all calves were born to non-infected mothers, possible prenatal transfers of immunological information – other than immunoglobulins – which could influence the immune response from the newborn could be excluded. Our results indicate that there was a significant impact of colostrum intake on the faecal egg counts, worm counts and tissue egg counts.

The results of the isotype antibody levels for both colostrum pools indicated higher (up to 3 times) IgG_{H+L}, IgG_1 and IgA levels in the positive colostrum pool compared to the negative pool and very low IgG_2 levels. The low levels in the negative pool could be suggestive of cross-reactivity of the antibody detection test with other organisms. Our results show that IgG_1 may be the potential effector of immune protection in cattle, as has been observed in other studies in cattle (Devery-Pocius & Larson, 1983; Ogunrinade, Otesile & Obasaju, 1984; Lilius & Marnila, 2001) where IgG_1 was the predominant immunoglobulin detected.

One day after intake of colostrum a mean ΔOD of 0·80 (IgG_{H+L}) was detected in the calves receiving colostrum from infected cows. Colostral immunoglobulin binds to a specialized Fc receptor on the intestinal epithelial cells of newborns and eventually, at least in calves, all immunoglobulins are absorbed and reach the systemic circulation. Newborn calves thus obtain a massive transfusion of maternal immunoglobulin (Aldridge, Garry & Adams, 1992). Because of the nature of the absorptive process, peak serum immunoglobulin levels are normally observed between 12 and 24 h after birth. The slight increase noticed in the serum from the calves receiving colostrum from uninfected cows (ΔOD of 0·36) could also be indicative for some cross-reactivity in the detection test.

The steady decrease detected in specific antibody levels after day 1 corresponds with the findings of Husband & Lascelles (1975) who determined a half-life of passively acquired IgG_1 of 16–32 days, and suggested that this may be due to normal catabolic processes. The low levels of IgA in the sera from the calves – except on day 1 – were expected because IgA is actively absorbed and then passed back into the intestinal lumen through external excretions (Thatcher & Gershwin, 1988).

At the time of parasite challenge, average IgG_{H+L} and IgG_1 were still significantly higher in group 2, compared to group 1, which might explain the parasitological results. After the challenge no increase in immunoglobulins was observed in either group. A low response in the calf could have been masked or prevented by the existence of specific or cross-reacting antibodies as described by Carlier & Truyens (1995), indicating that intake of colostrum from infected cows induces partial protection, but could also, however, prevent the priming of specific immune cells when challenged.

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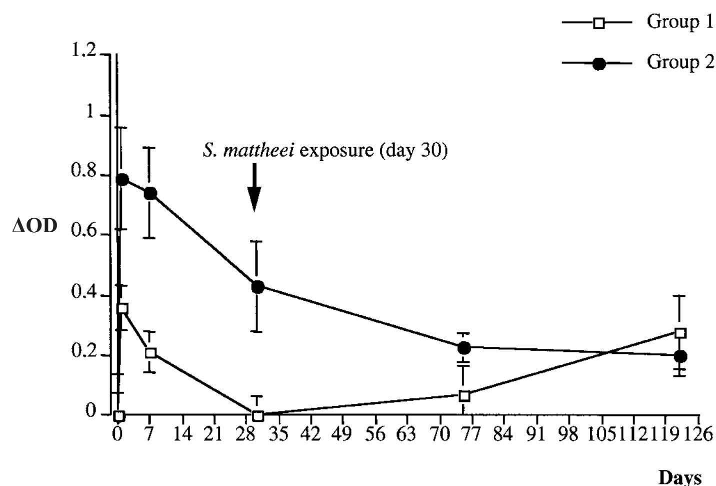

Fig. 1. Mean IgG_{H+L} levels (delta optical densities) against soluble adult worm antigen preparation of *Schistosoma bovis* (SWAP *bovis*) in the sera from calves infected with *S. mattheei* 1 month after receiving colostrum from non-infected cows (negative colostrum: group 1) or from infected cows (positive colostrum: group 2). Error bars indicate ±2 S.E.

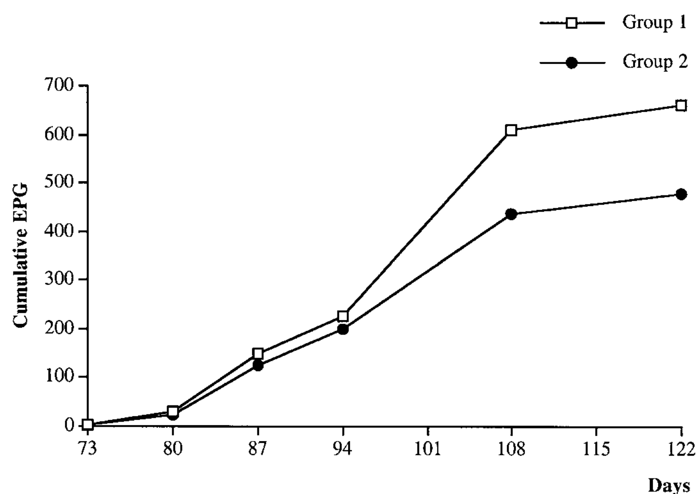

Fig. 2. The cumulative faecal egg counts of calves infected with *Schistosoma mattheei* 1 month after receiving colostrum from non-infected cows (negative colostrum: group 1) or from infected cows (positive colostrum: group 2).

In the calves receiving colostrum from infected cows (group 2) a significant reduction in TWC, FWC and TECcorr. of 42, 28 and 42%, respectively, was observed. Several studies showed that experimentally infected cattle can develop an extremely effective immune response against *S. mattheei* or *S. bovis*, and that this immunity mainly acts through suppression of worm fecundity (reviewed by De Bont & Vercruysse, 1998). Our results strongly support Bushara's *et al.* (1983*b*) hypothesis that fecundity suppression following acquired resistance to *S. bovis* in cattle is due to at least serum-borne factors. In the present study the main evidence of acquired immunity was primarily a significant 42% reduction in worm counts. The observed lower cumulative egg counts and TECcorr. were probably more likely due to reduced FWC (28%) than to reduced worm fecundity, since density dependence seems to be of minor importance (De Bont, Shaw & Vercruysse, 2002).

The observed reductions in worm counts could be of long-term importance as the worm burdens observed in adult animals might reflect those acquired at the very early stage of infection and the magnitude of the immunological response to natural infection may depend on the size of this early challenge (De Bont & Vercruysse, 1997). The observations made by these authors were on tracer calves born to non-infected mothers, and aged 3–4 months when introduced on the farm, and maternal transfer of protective immunity was never taken into account. Different observations might be obtained when working with calves born to infected mothers, or when calves would have received colostrum from

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Table 2. Total worm counts (TWC), female worm counts (FWC) and corrected tissue egg counts (TECcorr.) of calves infected with *Schistosoma mattheei* 1 month after receiving colostrum

	TWC	FWC	TECcorr.
Group 1*			
1	449	94	1107 667
2	481	127	815 906
3	494	115	1465 593
4	202	62	1024 892
5	396	193	1453 183
6	279	130	863 550
Mean†	384	120	1121 799
Group 2			
7	267	113	829 867
8	255	116	865 067
9	182	74	848 191
10	125	42	290 578
11	272	102	506 178
12	225	77	552 150
Mean†	221	87	648 672
Reduction (%)	42	28	42

* Group 1: calves receiving colostrum from uninfected cows; Group 2: calves receiving colostrum from infected cows.

† Arithmetic means.

infected cows, and if they were introduced at a younger age. Our findings strongly indicate that calves, which received colostrum from infected mothers, were partially protected against early *S. mattheei* infections. Variations in the quality of the colostrum could occur depending on different factors such as lactation number (Quigley *et al*. 1994) and breed (Vann *et al*. 1995). However, Ogunrinade *et al*. (1984) determined an environmental effect rather than a breed effect on colostral immunoglobulin concentrations. Seasonal variations in the size of the first challenge could also occur (De Bont *et al*. 1995 *b*) and would therefore depend on the time of calving. In the present experiment variations in challenge size could have been caused by the different cercarial batches used when exposing the calves (Van Wyk, Heitmann & Van Rensburg, 1975).

In this study only calves born to non-infected mothers have been considered. It would be interesting, therefore, to see whether mechanisms other than the transfer of immunoglobulins through the colostrum could affect the susceptibility to an early challenge. In man, it has been confirmed that there is transfer through colostrum and/or placenta of various immunologically active substances from the mother to the foetus/newborn which might induce sensitization or tolerance (Camus *et al*. 1976; Santoro *et al*. 1977 *a*, *b*; Eissa *et al*. 1989; King *et al*. 1998), however, it is not yet clear whether this transfer actually also induces protection against an early infection. This may be important not only for generating immunological responses to natural infections, but may also be used to enhance the immunogenicity and efficacy of vaccines administered to newborns.

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