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Heterologous transmission with *Dictyocaulus capreolus* from roe deer (*Capreolus capreolus*) to cattle (*Bos taurus*)

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Abstract

Eight Swedish Red Breed cattle, about 2 months old, were experimentally infected with a Swedish isolate of *Dictyocaulus viviparus* (Dviv-Se) from cattle and *D. capreolus* from roe deer. The aims were to determine whether the roe deer lungworm is infective to cattle or if it can induce seroconversion in cattle against *D. viviparus* as measured with an ELISA. Four calves which were given 500 Dviv-Se infective larvae (L3) each by larval dosing for two successive days developed patent infection between days 23 and 25 post-inoculation (PI). Larval output varied among the calves and during the patent period. However, maximum recovery occurred between 28 and 56 days PI with peak shedding on day 37 PI. Shedding ceased at day 58 PI and adult worms were recovered from one calf at necropsy (day 67 PI). No immature worms were recovered from the lungs at necropsy. Seroconversion was detected on days 35–42 PI. One Dviv-Se infected calf became seronegative on day 67 PI whereas the other calves still remained seropositive during this period. Prepatency and patency periods of *D. viviparus* and serological findings in this study basically conform to previous studies. Each calf that was infected with 400 L3 of *D. capreolus* for two successive days, and about 800 L3 of the same species about 8 weeks later, did not develop to patency based on faecal and post-mortem examinations. Consequently, under the conditions of this study, *D. capreolus* was not infective to cattle. Two of the four calves that were infected with L3 from roe deer were challenged with L3 cultured from faeces of the Dviv-Se-infected calves. This infection did not develop to patency. Whether this was due to cross-protection as a result of the prior priming with L3 from roe deer is not clear. However, if it is so, it opens up the possibility of using *D. capreolus* L3 for preventing bovine dictyocauliasis.

Introduction

Parasitic bronchitis or bovine dictyocauliasis, caused by the large lungworm *Dictyocaulus viviparus*, is a major health hazard to first-grazing-season cattle in temperate regions of the world and especially in northern Europe (Urquhart *et al.*, 1996). This species has also been reported in several cervid hosts in Canada (Pybus, 1990), Germany (Enigk & Hildebrandt, 1965), Sweden (Nilsson, 1971; Christenssen & Rehbinder, 1975), and New Zealand (Mason, 1985). It has thus been suggested that wild cervids may serve as a reservoir for *D. viviparus* and that they are important in the transmission of infection (Nilsson, 1971). Experimental cross infection studies have demonstrated that cattle, *Bos taurus*, were susceptible to *D. eckerti* from fallow deer, *Dama dama* (Bienioschek *et al.*, 1996), and to *Dictyocaulus* larvae derived from roe deer, *Capreolus capreolus*, in Germany (Enigk & Hildebrandt,

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1965). This was also the case for *Dictyocaulus* larvae from red deer, *Cervus elaphus*, in New Zealand (Corrigall *et al.*, 1988) and in Scotland (Mason, 1985). On the other hand, on the American continent calves could not be infected with *Dictyocaulus* larvae obtained from moose, *Alces alces americanus* (Gupta & Gibbs, 1971), and elk, *Cervus elaphus nelsoni* (Presidente *et al.*, 1972).

Prior to our studies (Höglund *et al.*, 1999; Divina *et al.*, 2000), only *D. viviparus* has been reported in Swedish ruminants (Nilsson, 1971; Christenssen & Rehbinder, 1975). Recently, it was also demonstrated that a novel cryptic species named *D. capreolus* occurs in European roe deer and moose or European elk (*Alces alces europeus*) in Sweden (Gibbons & Höglund, 2002). This species markedly differs in its second internal transcribed spacer (ITS2) region both from *D. viviparus* and a German isolate of fallow deer derived *D. eckerti* (Epe *et al.*, 1997; Höglund *et al.*, 1999). In a survey based on molecular identification with species-specific oligonucleotide probes of 275 lungworms recovered from cattle, roe deer and moose in Sweden, we found neither *D. viviparus* in wild cervids nor any other lungworm species besides *D. viviparus* in cattle (Divina *et al.*, 2000). Sweden has a population of about 1.2 to 1.6 million roe deer (Swedish Hunters' Association, personal communication). In Sweden, these animals are often found in the same areas where cattle are grazed and there are often opportunities for co-grazing with cattle. Therefore, it was interesting to determine the infectivity of *D. capreolus* to cattle. We were also interested to determine if this species could induce seroconversion as measured with an ELISA designed for the identification of patent *D. viviparus* infections in cattle.

Materials and methods

Culture and collection of lungworm larvae

Adult lungworms and faeces of a heavily infected 55-kg Swedish Red Breed calf raised on a farm outside Kungsgården in Central Sweden and brought to the National Veterinary Institute, Uppsala, Sweden for necropsy, were collected on 15 September 1999. The faeces were cultured and lungworm infective larvae were collected according to the protocol of Borgsteede and co-workers (personal communication). Well-mixed faeces were divided into four lots of about 1 kg each and evenly spread in plastic trays ($35.5 \times 30.5 \times 6$ cm). Each tray was placed in a humidified 15°C incubator and covered with a plastic plate leaving a small part open for aeration. Faeces were moistened every 2–3 days. After 7 days, the trays were removed from the incubator and filled with water and the fluid was collected immediately into a container and poured through a sieve with an aperture of 150 μm. The filtrate was re-sieved through a mesh size of 37 μm. Material that remained in the sieve was collected by turning it upside down over a container and washing it with water. The collected material was then poured into a Buchner funnel with filter paper in order to remove excess fluid. The filter was placed in a Petri dish with a small volume of water and small rods as support. Larvae were allowed to migrate from the filter for about 2 h. Fluid from the Petri dish was collected and a small amount was examined to check the activity and developmental stage of the larvae. Fluid containing third-stage larvae (L3) was placed in an Erlenmeyer flask, covered with gauze, and stored at 4–5°C. The flask was agitated at least once a day for aeration.

In addition, eggs and first-stage larvae (L1) were collected from the fluid where the adult worms were placed after overnight incubation at 8°C. Eggs and larvae were placed in Petri dishes with a small amount of 40 mM KCl, maintained in a humidified incubator and agitated daily to enhance aeration. After 9 days of incubation, in which most of the larvae reached the third stage, the fluid was pooled and processed in a Buchner system and the L3 were collected as described above. Cultured L3, designated as *D. viviparus* Swedish isolate (Dviv-Se), from adult worms and faeces were mixed together and stored at 4–5°C for 4 days before the experimental infection. Similar procedures were also followed in the culture and collection of *D. capreolus* larvae from naturally infected roe deer (*Capreolus capreolus*).

Experimental infection

Four lungworm-free Swedish Red and White Breed calves (5258, 5259, 5260 and 5261; group 1) about 2 months of age with a mean (± SD) body weight (BW) of 82 (± 7) kg were used in the inoculation with Dviv-Se infective larvae (L3). Before inoculation, the flask containing the L3 was allowed to equilibrate at room temperature. The number of viable L3 based on the criteria of Rubin & Lucker (1956) was determined by examining small aliquots of the larval suspension. Each calf was drenched orally with two consecutive doses of about 250 L3 each on 28 and 29 September (days 0 and 1, respectively).

With the availability of lungworm larvae from a roe deer on 19 October 1999, four more calves (5127, 5128, 2329 and 2331; group 2) about 2 months of age with a mean (± SD) BW of 77 (± 15) kg were purchased. However, only one animal (no. 5128) was inoculated on 2 November 1999 because only about 250 viable L3 were present. When more roe deer lungworm L3 were available, this calf and the other calves were infected with two consecutive doses of about 200 L3 each on 25 and 26 November (days 0 and 1, respectively). Calves 5127 and 2329 were negative for infection on day 52 post-inoculation (PI) based on faecal examination and they were re-infected on 19 January 2000 with about 250 Dviv-Se L3 each. The L3 used were collected and cultured from faeces of group 1 calves which became patent after infection with Dviv-Se L3. On the other hand, calves 5128 and 2331 were given about 800 roe deer-derived *D. capreolus* larvae each on the same day.

The two groups of calves were kept in two pens with one pen in between throughout the duration of the study. Straw bedding was provided and changed daily. Some calves were fed with milk until they were 9 weeks old, then on dried forage and concentrate according to the Swedish feeding standards. Drinking water was given *ad libitum*.

Group 1 and 2 calves were slaughtered on 4 December 1999 and 4 March 2000, respectively. The animals were kept and slaughtered in accordance with the national

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guidelines for ethical permission (Swedish permit no. C296/97).

Faecal and blood collection

Faecal samples from each animal were collected directly from the rectum just before infection (day 0), then weekly for the first 3 weeks PI, and every other day beginning from the first day of patency until slaughter. Blood was collected by venipuncture from the coccygeal vein into a vacutainer without anticoagulant at day 0 and weekly thereafter until days 67 and 97 PI, for group 1 and 2 calves, respectively. Sera were separated, collected, and stored at −20°C.

Faecal and serological examination

Faecal samples from each animal were examined by the Baermann technique (Anon., 1986) using two subsamples of about 25 g of faeces from each animal. The sediment drawn from the bottom of each funnel after overnight incubation was placed in a small Petri dish with grids and larvae were counted under 20–30× magnification using a dissecting micrsocope. The formula for obtaining the mean number of larvae per gram of faeces for each animal was: (count 1/25 + count 2/25)/2.

Levels of serum antibodies to *D. viviparus* were measured by an ELISA that had been tested according to international ISO 5725–1986 standards the Ceditest (ID-DLO, Lelystad, the Netherlands). The coating antigen in this test could be a sperm antigen, which means that larval uptake is not detected. Values are expressed as % positivity in relation to control sera that was included on all plates. The cut off limit was 15% (Cornelissen *et al.*, 1997).

Clinical signs and post-mortem examination

After slaughter, the thoracic organs of each animal were removed *in toto* and brought to the laboratory. The trachea and bronchi were dissected and examined for the presence of adult worms. About 500 g of lung tissue from all lobes was removed and cut into small pieces and processed according to the technique of Borgsteede and co-workers (personal communication) for the recovery of inhibited worms.

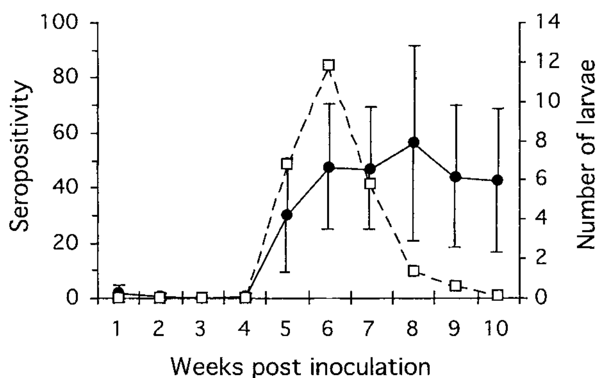

Fig. 1. Comparison between larval shedding and antibody response to patent *Dictyocaulus viviparus* (Swedish isolate) infection in calves as measured by ELISA. ● % seropositivity ±SD; □ Number of L1 g^{-1} faeces.

Identification of lungworms

To ascertain serologically the presence of *D. viviparus* infection in the herd where the dead calf came from, blood samples were collected from the remaining calves at the farm one week after necropsy. Sera were analysed by the Ceditest as mentioned above. Larvae collected from calves that were experimentally infected with *D. viviparus* and an adult lungworm saved from the roe deer that served as the source for the cervid larvae were identified by a DNA hybridization assay according to Divina *et al.* (2000).

Results

All four calves that were given Dviv-Se L3 larvae became patently infected. Larval shedding started on day 21 PI (5258) and ceased on about 64 days PI (fig. 1). There was individual variation in larval output both between sampling occasions and experimental animals (table 1). Calves 5258 and 5259 showed peak shedding on 30 days PI but it was only on the 38th and 52nd days PI when calves 5260 and 5261, respectively, reached their peak larval output. Thus, the mean peak of larval shedding occurred at 37.5 ± 10.4 (s.d.) days PI. Incidentally, calves 5228 and 5259 which reached their peak of larval shedding earlier had also stopped shedding larvae earlier, on days 56 and 58 PI, respectively. At necropsy, calf 5260 harboured three adult worms but no inhibited larvae. Neither adult worms nor inhibited larvae were found in any of the other calves.

Raised serum antibody levels against adult lungworm were only seen in calves from group 1. Seroconversion was first detected in three calves (5258, 5259, 5260) at day 35 PI, whereas the fourth calf (5261) seroconverted on day 42 PI (fig. 1). The highest seropositivity (99%) was observed on day 56 PI in calf 5260. On day 67 PI, calf 5258 turned negative whereas the remaining calves were still seropositive. Group 2 calves, which were given lungworm L3 from roe deer did not become patently infected even after re-infection with a higher dose than the first infection dose. Neither immature nor adult worms were found at necropsy and seroconversion against *D. viviparus* was not detected. The two calves that were previously given *D. capreolus* and later challenged with Dviv-Se L3 did not become patently infected as shown by faecal and post-mortem examinations, and serology.

Sera collected from 14 of 18 (78%) animals from the farm that served as the source of *D. viviparus* larvae in this study had elevated antibodies. With the DNA hybridization assay, we were also able to confirm that the Dviv-Se infected calves shed *D. viviparus* larvae and that adults and larvae from the roe deer were *D. capreolus*.

Because there have been many studies describing detailed clinical and pathological consequences of lungworm infection in cattle, this aspect was not included in the present study. However, the Dviv-Se-infected calves exhibited occasional excess nasal discharges, mild

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Table 1. Experimental infections of calves with *Dictyocaulus viviparus* (Swedish isolate).

Animal no.	Pre-patent period (days)	Duration of larval shedding (days)	No. of larvae/g of faeces (mean ± S.D.)	Duration of seropositivity (days**)
Group 1				
5258	23	34	1.1 ± 1.4	29
5259	25	36	6.6 ± 8.1	> 33
5260	25	44 (or more)*	14.3 ± 16.2	> 33
5261	25	42	2.0 ± 4.0	> 33
Mean ± S.D.	24.5 ± 1.0	39 ± 4.8 (or more)	6.0 ± 6.0	> 32

* Larval shedding was still being observed on day 44 PI and adult worms were recovered at necrospy on day 67 PI.
** All animals were still seropositive at slaughter.

diarrhoea and coughing during the patent period, which were observed during sample collections. In spite of these signs, animals showed a good appetite and were alert. At post-mortem, some small focal areas of hepatization and emphysema were seen on the lungs of all infected animals. The main bronchi appeared normal but small amounts of yellowish mucoid plugs were observed in some bronchioles.

Discussion

This study is the first reported successful experimental infection of calves with *D. viviparus* in Sweden. It is also the first attempt of a cross-transmission experiment using roe deer-derived *D. capreolus*. Based on clinical and post-mortem observations on animals infected with Dviv-Se, these indicate that they were mildly infected using a total dose of 500 L3 or about 12 L3 kg^{-1} BW. Schnieder & Daugschies (1993) studied the effect of 30 and 3 L3 kg^{-1} BW infection doses in calves. The group that received the higher dose showed severe clinical signs whereas those that were given a low dose remained clinically healthy. Using an infection dose of 88 L3 kg^{-1} BW, Corrigall *et al.* (1988) observed signs of tachypnoea, harsh lung sound, coughing and dullness in infected cattle.

The mean prepatent period and the duration of larval excretion observed in this study were close to or within the ranges of figures previously reported for *D. viviparus* in cattle (Rubin & Lucker, 1956; Jarrett *et al.*, 1960; Presidente *et al.*, 1972; Corrigall *et al.*, 1988; Seesee & Worley, 1993). However, Schnieder & Daugschies (1993) obtained a prepatency of 18–22 days, which is a slightly shorter time than in the present study. Variable prepatency periods indicate differences in the infectivity of different isolates and/or in host susceptibility. In this context, the storage conditions for larvae prior to inoculation are important. The time that lapsed between larval inoculation and peak in shedding obtained here agrees with the result of Boon *et al.* (1984). The absence of worms in most animals at necroscopy 10 weeks after infection shows that lungworms were eliminated rapidly. This agrees with a previous study that also showed that almost all lungworms were expelled after the post-patent phase of dictyocauliasis, which normally occurs at 55 to 90 days PI (Urquhart *et al.*, 1973). The time of slaughter of calves in this study falls within this period. The mechanism behind this is somewhat obscure but it is generally known that cattle infected with *D. viviparus* develop a high degree of immunity manifested by resistance to reinfection. With regard to the ELISA results in comparison with observations on larval shedding, the latter started 1–2 weeks before the calves seroconverted. This observation, which includes the time at PI when *D. viviparus*-specific antibodies were first detected, conforms to previous studies (Tenter *et al.*, 1993). In general, there was good agreement between the results of both diagnostic methods except that antibody levels remained positive even after larval shedding started to cease. This observation is in agreement with Tenter *et al.* (1993) and Cornelissen *et al.* (1997).

Infection of calves, dosed with *D. capreolus* from roe deer (group 2), did not result in a patent infection indicating that this species does not establish in cattle. On the other hand, it is possible that the number of L3 given was either too low or too high to produce an infection. In the case of calves dosed with too many larvae, this may have resulted in poor establishment due to a sudden and massive stimulation of the host immune response. Similar findings were observed in pigs experimentally infected with a high dose of *Ascaris suum* (Roepstorff *et al.*, 1997). In the current study, however, calves were dosed with approximately the same number as in previous cross-infection trials in which they were able to transfer lungworms from one host species to another (Bienioschek *et al.*, 1996). Although the experimental dose of larvae given in this study might have been too small, a similar dose resulted in patent infection when calves of similar size and age were given *D. viviparus*. It has been shown in cross-transmission experiments that cattle are less susceptible to infection with deer-derived *Dictyocaulus* than deer to infection with *D. viviparus* (Corrigall *et al.*, 1988; Bienioschek *et al.*, 1996). Calves that are reared and infected in isolated units also appear to resist the effects of an infection more easily than those housed together (Jarrett *et al.*, 1960). Keeping calves in an isolated pen may be another contributing factor to why patency was not reached. Again the calves were susceptible to *D. viviparus* under exactly the same conditions.

Two early studies suggested that larval dose is not the most important determining factor for successful cross-infection and that it is more a question of variation in host

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specificity of various parasites to different recipient hosts. Concerning the infective dose, 6000 to 12,000 lungworm L3 from the American moose, *Alces alces americana* (Gupta & Gibbs, 1971) or from the Rocky Mountain elk or red deer, *Cervus elaphus nelsoni* (Presidente *et al.*, 1972) were tested to infect cattle but neither of these larval sources resulted in a patent infection. Divina *et al*. (2000) and Höglund *et al*. (1999) provided clear evidence that roe deer and moose in Sweden are parasitized by a genetically distinct lungworm species. Consequently, this genetic difference seems to be reflected by differences in host specificity from that of *D. eckerti*. It has been identified as the species infecting wild cervids in other parts of Europe (Enigk & Hildebrandt, 1965, 1969; Corrigall *et al.*, 1988; Bienioschek *et al.*, 1996), and also proven to be infective to cattle based on experimental studies (Enigk & Hildebrandt, 1965; Bienioschek *et al.*, 1996). The complete absence of this novel lungworm species in samples of cattle obtained from the field (Divina *et al.*, 2000), further supports the existence of such biological differences from *D. eckerti* and especially in terms of host specificity.

Patency was readily established in the parasite-naive calves that were primarily infected with *D. viviparus*. However, two of the calves, which were previously infected with *D. capreolus* without reaching patency, remained uninfected even after being challenged with *D. viviparus* L3. One probable explanation for this is that prior infection of the calves with L3 of *D. capreolus* could have elicited the development of cross-immunity that was effective against *D. viviparus*. Therefore this opens up the possibility of controlling bovine dictyocauliasis using roe deer-derived lungworm L3 for vaccination. However, a complicating factor is that the calves were 3 months older when they were challenged with *D. viviparus* L3. Consequently, age resistance might be involved and this might be the reason why the booster infection with *D. viviparus* failed to establish. It is also important to note that larvae used in this study were never subjected to outdoor conditions. Because the larvae were exposed to laboratory conditions only, they were not primed for larval arrestment inside the host, from which no immature worms were recovered at necropsy.

The results of the present study indicate that the course of primary infection with the Dviv-Se in Swedish Red Breed calves is basically similar to that of *D. viviparus* in other countries. On the other hand, patency in calves did not occur with *D. capreolus* from roe deer. This suggests that the roe deer lungworm is not transmissible to cattle and therefore, co-grazing of the two animal hosts poses no danger in terms of the occurrence of bovine dictyocauliasis. Further work is needed to determine whether infection of calves with roe deer lungworm L3 is likely to be a potential control measure against bovine dictyocauliasis.

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