SHORT COMMUNICATION

Sarcocystosis of chital (*Axis axis*) and dhole (*Cuon alpinus*): ecology of a mammalian prey–predator–parasite system in Peninsular India

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The question as to whether predators preferentially kill sick or disabled individuals has been addressed by many ecologists working with different predator-prey systems. Rau & Caron (1979) showed that heavily infected moose were more susceptible to hunting. Kruuk (1972) observed that hyenas appeared to select sick animals in the Serengeti. Vorisek et al. (1998) demonstrated that voles infected with a species of Frenkelia were taken more frequently by buzzards. As a broad generalization, wherever prey capture is difficult and involves large energy expenditure a greater proportion of sick animals seems to be captured (Fitzgibbon & Fanshawe 1989, Holmes & Bethel 1972, Temple 1987). In a host-parasite association where the prey species is an intermediate host and the predator is the definitive host, the capture of the prey is often an essential part of the life cycle. Therefore any mechanism which makes the prey susceptible to predation would enhance the parasite's fitness. In such relationships the susceptibility induced by the parasite can be very specific to the predator host (Levri 1998). Freedman (1990) suggested that a mutualistic association between the predator and parasite might exist. A mutualistic relationship can be said to exist between a predator and a parasite if the cost of harbouring the parasite is less than the benefit of greater success in catching the prey. There is perhaps no demonstrated example of such a mutualism in natural populations since it is difficult to weigh the parasite cost against the predation benefit.

We studied the relationship between dhole or Indian wild dog (*Cuon alpinus*) and a protozoan parasite (*Sarcosystis* sp.) with chital or spotted deer (*Axis axis*) as the prey-host. Chital is a medium-sized, highly gregarious

species of deer. They are sedentary animals, having small home ranges estimated to be between $2-10 \text{ km}^2$ (Barette 1991). The dhole, a central and southern Asian canid, is a social animal hunting in packs usually by day (Johnsingh *et al.*, in press). In the study areas, its main prey is chital (Dubay 1999, Venkataraman *et al.* 1995). Dhole use a 'rush and chase' strategy for prey capture. The distance over which an animal is chased is short to moderate, rarely going above 500 m (Johnsingh *et al.*, in press). Dhole hunting therefore can be placed at an intermediate position in the courser–stalker dichotomy of Fitzgibbon & Fanshawe (1989).

Sarcocystis axicuonis is a coccidian with an obligatory two-host life cycle. The sexual cycle takes place in the intestinal mucosa of dhole and results in the formation of sporocysts that are shed in the faeces. The asexual cycle which leads to the development of sarcocysts in skeletal or heart muscles occurs in chital, the intermediate host (Jog et al. 2003). The sarcocysts in the heart do not elicit an inflammatory response or any other pathological consequences (Watve 1992). However, even if the large number of cysts merely compete with the heart muscles for oxygen, this can make chital more susceptible to predation. There is no evidence of any pathological effects of this species on the carnivore host either (Watve 1992), however, the large number of sporocysts shed in dhole scat indicate that dhole might have to pay some energy cost in harbouring the parasite.

The study was carried out in two sanctuaries in Peninsular India, namely Mudumalai Wildlife Sanctuary and Tadoba National Park. Two packs of dhole in this area were identified and studied by Venkataraman *et al.* (1995). We sampled these two packs repeatedly and at least three more unidentified packs in the adjoining area during 1989–1992 and again in 1999–2000. The

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Tadoba National Park (116 km²) is a part of the Tadoba Andhari Tiger Reserve (TATR 625 km²) that lies in the Chandrapur District of Vidarbha Region of Maharashtra, India. Dhole in Tadoba during the sampling period (1998–2001) occurred in small packs of 2–6 individuals, although large packs in adjoining Kolasa area were recorded. One pair and one pack of four were identified and sampled repeatedly. In addition at least four other different packs were sampled during 1998–2001.

We collected fresh faecal samples of dhole from the study areas. Dhole often use a communal defecation site where fresh samples of all individuals in a pack can be collected. On 15 occasions entire packs could be sampled. These 15 pack samples come from at least seven different packs. The samples were processed immediately: 10% formalin was used for preservation if delays of several hours were unavoidable. For estimating the density of sporocysts in the scats, a quantitative sedimentationflotation technique (Watve 1992, Watve & Sukumar 1995) was used, with 4-5g of sample mixed with water to make a slurry. This slurry was filtered through muslin cloth to remove coarse debris. The filtrate was centrifuged at 2000 rpm for 5 min. The supernatant was then removed and 5 ml of ZnSO4 solution (sp. gr. 1.18) was added and mixed well with the sediment. This was centrifuged again at 2000 rpm for 5 min. Using an L-shaped wire with a 6-mm-diameter loop the contents of the surface layer were transferred on to a slide for observation. All parasite propagules on the slide were counted.

Skeletal and heart muscles of chital killed by dhole were collected for histopathological examination whenever fresh kills were detected. Chital dead due to other causes including tiger kills (8), leopard kills (3), domestic dog kills (2), accidents (1), poaching (1), disease (2) and unknown cause (6) were sampled in a similar way. They were used as a control group. Often only small amounts of muscles could be obtained since the kills were almost entirely eaten by predators. Heart muscles were not available in many kills. Skeletal muscles were collected from various parts of the body whenever possible. All the samples were fixed and stained with haematoxylin and eosin or unfixed sections were stained with iodine and the mean number of cysts per cm² of section area counted.

Sarcocystis sporocysts were widely and consistently detected from dhole scats throughout the duration of the study. Individuals were often free of infection but whenever all or a majority of individuals from a pack were sampled a large number of sporocysts were shed by at least some individuals in a pack – 5 000–10 000 sporocysts g^{-1} were commonly obtained in these individuals and occasionally 26 000 sporocysts g^{-1} were recorded. Out of the 29 occasions when the entire packs were sampled, 25 showed sporocysts. All packs with five or more individuals were always positive. The protozoan therefore

seems to be intimately and consistently associated with dhole.

Post mortem examination of chital revealed that 14 out of 24 heart samples and 16 out of 42 skeletal muscle samples had sarcocysts (Jog et al. 2003). The density of cysts was greater in heart muscles than skeletal muscles. However in all the 14 cases where heart and skeletal muscles from different parts of the body were sampled from the same individual, the heart muscles had 2-100 times greater density of cysts than the skeletal density whereas skeletal muscles from different parts of the body did not differ significantly. Substantial proportions of the chital kills in Mudumalai were young fawns below 4-6 mo of age. Sarcocysts are unlikely to be observed in very young fawns since the infective stages enter the body through forage and establishment of a cyst in the heart or skeletal tissue takes several weeks. Therefore we excluded fawn data while looking at differences between dhole kills and other causes of death.

Logistic regression analysis on the presence/absence of cysts revealed that the probability of finding one or more cysts was not significantly associated with location of the muscle, sex or area. However, the probability of finding one or more cysts in dhole kills was significantly greater than in other causes of death ($\beta = -1.57$, P < 0.05). With pooled data on adult kills from both sanctuaries, the sarcocyst density in heart muscles of dhole kills (median = $9.15 \,\mathrm{cm}^{-2}$) was significantly greater than in chital with other causes of death (median = 0 cm^{-2}) (Wilcoxon two-sample rank test T = 155, $n_1 = 14$, $n_2 = 14$, P < 0.05). The skeletal muscle sporocyst density did not differ significantly (dhole kills median = 0 cm^{-2} , mean = 1.68 cm^{-2} , non-dhole kills median = 0 cm^{-2} , $mean = 1.2 \text{ cm}^{-2}$) (Wilcoxon two-sample rank test T = 674, $n_1 = 26$, $n_2 = 29$, P > 0.05). If we assume that Sarcocystis axicuonis does not alter the probability of death due to other causes, the difference indicates that dholes are more likely to kill chital with sarcocysts. If sarcocysts increase the chances of death due to other causes as well, the effect on susceptibility to dhole predation must be significantly greater than the effects on other causes of death. A selective susceptibility to predation by the definitive host is important for the parasite. If the parasite makes the prey host generally weak and susceptible to predation by other predators or death due to other causes, it is a loss to the parasite, which cannot complete its life cycle in any other predator or scavenger. Other predators of chital in the study area are tiger and leopard that are more stalkers than coursers (Prater 1971). These predators rarely shed sporocysts in the study areas. High densities of cysts in the heart muscles can make the prey susceptible particularly to coursers (Fitzgibbon & Fanshawe 1989). Dhole are more coursers than stalkers although the chases are much shorter in the deciduous forest habitats than the typical

savannah coursers (Johnsingh *et al.* in press). If dholes kill disproportionately larger number of infected chital, they can be said to be benefited by the parasite. However, they have to pay a cost of harbouring the parasite in the intestine in order to disseminate it effectively. We do not have a quantitative estimate of the cost at present. Many identified individuals that shed large numbers of sporocysts when sampled did not show any detectable symptoms or lethargy. Diarrhoeic or otherwise abnormal scats were not associated with large numbers of sporocysts shed. The protozoan therefore appears to be non-pathogenic to dhole. However there can be some energy cost of growth of the parasite in the intestine.

All the packs consistently showed a parasite density distribution in which one or two individuals carried most of the parasite load, one or two individuals were always free of the parasite and others had intermediate loads (Figure 1). The distribution could be described by a simple relationship in which the parasite load of individuals arranged in decreasing order reduced by a constant fraction β . The parameter β decreased with increasing



Figure 1. Distribution of sporocyst densities within dhole packs. Only three groups out of 15 sampled are shown. X axis represents pack members arranged in decreasing order of sporocyst densities.



Figure 2. Correlation of pack size and β . Correlation is significantly negative for empirical data.

pack size and had a significantly negative correlation (Figure 2). In order to test that this is a peculiar distribution and not a statistical generality, sets of different pack sizes were randomly generated from the pooled data on parasite loads of dhole. The same equation was fitted to the randomly generated packs. It was observed that the random sets do not show a significant correlation between pack size and β . This indicates that the pattern seen in every pack was not a statistical generality but a consistent pattern in which in all packs at all times there were a few individuals that were free of infection.

If the energetic cost of carrying the parasite affects the hunting efficiencies of individuals, it is likely that the parasite-free individuals could do most of the hunting. We do not have adequate data to test whether the uninfected individuals play a major role in hunting, but the peculiar and consistent parasite distribution leaves a possibility of division of labour. If individuals spreading the infection are different from the ones more active in hunting, the cost of harbouring the parasite could be nil or negligible for the pack. Achieving this kind of division of labour is not very difficult. Chital tissues differed substantially in the densities of sarcocysts, the maximum density being in the heart. Therefore, individuals eating the heart could acquire a large number of cysts and those eating body parts such as the abdominal viscera would acquire the least or nil. A consistent distribution of the kill among the individuals of the pack can both generate as well as sustain this pattern. This may be a simple key to keeping the cost of harbouring parasites to a minimum.

The absence of a parasite-free dhole–chital system as a control makes it difficult to estimate the actual costs of harbouring parasites. Therefore we are still some way short of demonstrating that the benefits of the parasite to dhole are greater than its costs. However, the invariable presence of the protozoan infection in dhole, the proportionately greater capture of infected prey and the apparent division of labour make it a very likely case of a mutualism between a predator and a parasite with a prey-predator life cycle.

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