BMC Ecology

BioMed Central

Research article

Patterns in abundance and diversity of faecally dispersed parasites of tiger in Tadoba National Park, central India

Rahul R Marathe[1], Shantanu S Goel[2], Sachin P Ranade[1], Maithili M Jog[1] and Milind G Watve*[1,2]

Address: [1]Department of Microbiology, Abasaheb Garware College, Karve Road, Pune 411 004, India and [2]Life Research Foundation 10, Pranav, 1000/6-c Navi Peth, Pune 411 030, India

E-mail: Rahul R Marathe - rahul_marathe@yahoo.com; Shantanu S Goel - ssgoel@vsnl.com; Sachin P Ranade - ranades@cshl.org; Maithili M Jog - captjog@vsnl.com; Milind G Watve* - watve@vsnl.com

*Corresponding author

Published: 8 May 2002

BMC Ecology 2002, **2**:6

Received: 16 October 2001
Accepted: 8 May 2002

This article is available from: http://www.biomedcentral.com/1472-6785/2/6

Abstract

Background: Importance of parasites in ecological and evolutionary interactions is being increasingly recognized. However, ecological data on parasites of important host species is still scanty. We analyze the patterns seen in the faecal parasites of tigers in the Tadoba National Park, India, and speculate on the factors and processes shaping the parasite community and the possible implications for tiger ecology.

Results: The prevalence and intensities were high and the parasite community was dominated by indirect life cycle parasites. Across all genera of parasites variance scaled with the square of the mean and there was a significant positive correlation between prevalence and abundance. There was no significant association between different types of parasites.

Conclusions: The 70 samples analyzed formed 14 distinct clusters. If we assume each of the clusters to represent individual tigers that were sampled repeatedly and that resident tigers are more likely to be sampled repeatedly, the presumed transient tigers had significantly greater parasite loads than the presumed resident ones.

Background

The importance of parasites in the ecology of large mammals is being increasingly recognized but empirical studies on the ecology of parasites of large mammals are scanty. Parasites can potentially affect population growth of a species as well as interactions between species. Apart from devastating epidemics [1,2] the milder endemic parasites can also play a major role in population regulation [3,4]. Parasites have many other ecological implications in phenomena such as parasite mediated host competition [5], sex and sexual selection [6–10] social behaviour including xenophobia and sexual fidelity [11], foraging strategies [12,13] and predator prey dynamics [14,15].

Parasites are likely to play a significant role in the ecology of tigers for twofold reasons. Watve and Sukumar [16] showed that animals having less predatory pressure have greater parasite loads, tigers showing the maximum loads among the 12 species they examined in the Mudumalai wildlife sanctuary. The estimated parasite densities in some of the tigers in the Mudumalai wildlife sanctuary were up to 1500 flukes in the lungs or a total of 30 meter

length of tapeworms in the intestine [17]. Parasites in such a large amount can certainly have considerable impact on the health, behaviour and reproductive success of individuals. Parasites may be responsible for cub mortality and cub mortality is perhaps the most important factor in the population viability of tigers [18]. Secondly, parasites having the prey species as intermediate host and the predator as a definitive host may alter the predator prey dynamics [19]. Parasites with a predator-prey life cycle constitute a substantial proportion of the parasite community of carnivores and therefore these might have a more significant role in the ecology of predators.

We report here the patterns in the abundance and diversity of faecally dispersed helminth parasites of Tiger in the Tadoba National Park of central India and discuss the possible implications for tiger ecology. We use the fecal densities of parasite eggs, larvae and cysts (referred together as parasite propagules) as indicators of parasite load of an individual. Coprologic studies have been used to study the parasites of wild mammals qualitatively as well as quantitatively [16,17,20–24]. Shaw and Moss [23] found that egg densities were linearly correlated with worm burdens in Red Grouse. Skorping et al [24] showed a positive correlation between worm biomass and egg output. For an endangered predator such as tiger there is no alternative way of collecting sufficient number of samples. Therefore despite the inherent limitations, fecal examination is the only practicable way of collecting data on parasites.

Results and discussion

Out of the 70 samples analyzed 57 were positive for helminth propagules. The mean intensities in the positive samples were high (propagules per gram; mean = 990.07 median = 101.5, maximum = 12,049). The mean for all samples was 792.1. The postmortem examination of a dead old tigress revealed an estimated 32 meter length of *Diphyllobothrium*, 8 meters of *Taenia* sp. and close to 1200 *Toxascaris leonina*. Tapeworm segments were frequently found in fresh or old scats. The parasite prevalence and abundance in tigers of Tadoba were high but substantially less as compared to two other published studies from southern India [17,16] and Thailand [20]. Host species that are free of predatory pressures appear to have higher parasite loads [16] and therefore the high prevalence and abundance in tigers is not surprising. There was considerable variation in the parasite loads of individuals and this could be one of the determinants in the competitive success of individuals. The parasite component therefore should be an essential part of any comprehensive study of tiger ecology.

Parasites from 8 genera were detected in the 57 positive samples (table 1). The conservative estimate of the number of biotypes based on propagule morphology was 12 and a liberal one was 21. The frequency distribution of parasite densities in all the samples was highly aggregated as indicated by the large variance to mean ratio. The variances for all types of parasites were one or two orders of magnitude greater than the mean and tended to increase with the mean. Similar to the observations of McCallum [25] on protozoan parasite densities in fish the double logarithmic plot of means and variances was linear with a slope close to two (fig 1). The variances thus scaled linearly with the square of the mean. A similar pattern was noted by Watve [17] across a range of host species. The consistency of this pattern in the three unrelated situations is curious but as yet we do not know the factors that make the parasite variance scale with the square of the mean.

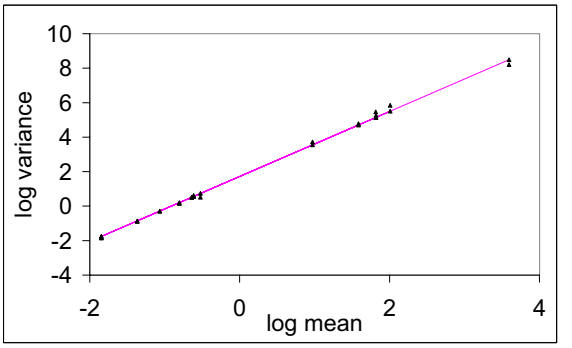

Figure 1
Across all species of parasites the variance in propagule densities increased with the square of the mean densities as indicated by a slope close to two of a double log plot.

The prevalence of a parasite species was positively correlated with the mean density in positive samples (Pearson's $r = 0.85$ $p < 0.01$). Prevalence abundance correlations are seen in other parasite communities [26,17] as well as free-living communities [27]. A simple explanation for this could be that parasites which have higher densities are also more easily detected and hence add to the prevalence. It is also likely to be due to a spill over effect. Parasites that infect individuals with greater intensities produce more propagules and thereby infect a greater proportion of individuals. There was no significant correlation between the propagule densities of any two genera or any pair of operational taxonomic units (OTUs, see methods for explanation). Therefore there was no evidence for competitive exclusion or co-occurrence between any two parasites.

Table 1: The prevalence, propagule densities and other statistics for the genera and families of parasites found. Since identification to the species level from propagules was often not possible, we define OTUs based upon propagule morphological differences. Two strategies are applied for this, the conservative one ignores smaller differences, the liberal makes use of subtle characters for differentiation.

	Conservative	Liberal	prevalence	abundance	mean	var	var/mean
Diphyllobothrium	1	3	0.528	1400.588	740.311	3238786	4374.897
Hookworm	1	1	0.014	0.422	0.006	0.002	0.422
Taenia	3	3	0.014	3119.471	44.563	63212.43	1418.468
Toxocara	1	1	0.028	2.625	0.075	0.205	2.737
Toxascaris	1	4	0.228	22.268	5.089	714.486	140.372
Lungworm	1	1	0.085	22.267	1.908	210.045	110.047
Capillaria	1	1	0.014	0.095	0.001	0.0001	0.095
Paragonimus	1	1	0.028	1.238	0.035	0.081	2.290
Unidentified	3	6	0.057	1.225	0.070	0.166	2.382

Table 2: Brief natural history of tiger parasites. Most of the information is generic and comes from related hosts or captive carnivores. Reliable and specific information on species in tigers and their effects on the host is unavailable at present.

Parasite Name	Family	Description	Lifecycle
Paragonimus	Paragonimidae	These are ovoid with a spiny tegument and are parasitic in the lungs (lung flukes).	The eggs are laid in the cyst in which the worms live and escape in the respiratory system. Animals swallow the cysts along with the mucus which pass in the faeces. The miracidium escapes and penetrates into an amphibian snail. After escaping the snail, the cercariae swim about in the water and on meeting a suitable crab or crayfish, penetrate into it. The final host becomes infected by eating infected crustacea.
Diphyllobothrium Diphyllobothriidae		occurs in the small intestine of man, cat, pig and fish eating mammals. Large tapeworms, The scolex has instead of suckers, narrow, deep, weakly muscular grooves called 'bothria'.	A typical life cycle includes free living *coracidium* (a ciliated embryo), a procerciod occuring in the first intermediate host, copedid crustaceans; a *plerocerciod* found in the second intermediate hosts, fish and definitive hosts (amphibia, reptiles birds or mammals) contain the adult stage. Life cycle of the tiger species (if there is a different one) is not completely known.
Taenia	Taeniidae	Large tapeworms, Gravid proglottids are longer than they are wide, Rostellum with a double row of small and large hooks	Species found in wild carnivores, commonly have herbivores as intermediate hosts. Some of the species form hydatid cysts in the secondary host. Hydatids are frequently found in herbivore viscera of the study area.
Hookworm	Ancylostomatidae	These are hookworms with a well developed buccal capsule with chitinous cutting plates.	Direct. No intermediate hosts involved. Infective larvae enter through water or by active penetration of the skin.
Toxocara & Ascaris	Ascarididae	Relatively large worms with three well developed lips. There is no buccal capsule or pharynx. Cervical alae give their anterior ends an arrow like appearance. For this reason they are sometimes called arrow worms or arrow headed worms.	The infective stage is the egg containing second stage larva. They grow in the intestine of the host.
Lungworm	Filaroididae	Parasites of respiratory system of mammals	Direct. No intermediate hosts involved.
Capallaria	Capillariidae	The worms are closely related to *Trichuris* worms (whip) but they are small and slender and the posterior part of the body is not conspicuously thicker than the anterior part.	The lifecycle may be direct or indirect. The eggs are unsegmented when laid and develop into larval stages which then infect the definitive host if the life cycle is indirect.

The parasite community was dominated by parasites with indirect life cycles. This would be expected for hosts that occur in low densities so that direct transmission between individuals is difficult. Further the short monsoon and low soil moisture perhaps makes the survival of direct lifecycle parasites more difficult. Therefore unlike the prolonged monsoon habitat of Mudumalai wild life sanctuary [17], hookworms were not common in Tadoba National Park. Particularly common were *Diphyllobothrium* and *Taenia* sp. Unlike the findings of Watve [17] and Patton and Robinowitz [20]*Paragonimus* and *Capillaria* were not common. *Diphyllobothrium* was the most prevalent and was detected in 37 samples and densities up to 12049 / g were found. The species of *Diphyllobothrium* in domestic carnivores have a lifecycle involving fish as the intermediate host. The definitive host is known to get infected by consuming infected fish. However, the contents of over 100 tiger scats (data not shown) did not reveal scales or any other evidence of fish eating in the study area. Dubay [28] also analyzed 140 tiger scats in the same area during 1994 to 1997 but did not report fish scales in the scat. If *Diphyllobothrium* infection were acquired by eating fish the cost of fish eating for a tiger would be large as compared to the nutritional benefit. No specific information is available on the pathological effects of *Diphyllobothrium* on tigers. However, since *Diphyllobothrium* are very large worms the energy cost of their growth or even the space occupied in the intestine can be a significant cost to the host individual. Therefore fish eating would not be an evolutionary stable behaviour for tigers in areas with adequate ungulate prey density. It is possible therefore that the species of *Diphyllobothrium* seen in tigers has a different life cycle that does not necessarily involve fish eating by the definitive host. The definitive host could be small aquatic animals which are ingested accidentally by tigers. Alternatively the infective stages may leave the alternative host and enter the definitive host through water or by active penetration of the skin. The life cycle needs to be investigated. The life cycles of other parasites can be currently assumed to be similar to those in the domestic carnivores (table 2). It is hard to obtain data on the pathological effects of parasites on the host individual in the wild. Tapeworms, hookworms or lung fluke are known to be debilitating when in large numbers [29]. If the same applies to wild tigers parasites can potentially be an important population regulating factor in tigers. This needs serious investigations.

Although the 70 samples analyzed revealed between 12 to 21 possible species, it is likely that many more species remain undetected. This is particularly likely because a number of species were encountered only once. We used the non-parametric bootstrap estimator of the total number of species including the ones that were not detected [30,16]. Using the conservative morphotype number the estimate was 16.44 (s.d = 1.07 n=100) and a liberal estimate was 33.34 (s.d. = 1.45, n = 100). The helminth community of tigers therefore was highly diverse despite the host population being small and fragmented.

A possible source of bias in the above analysis is that the 70 samples must have come from a much smaller number of individuals. Many individuals therefore must have been sampled repeatedly and each individual sample cannot be considered as independent. In an attempt to correct for repeated sampling we subjected the 70 samples to cluster analysis. The predominant helminth species of tigers are large and long-lived. Therefore we do not expect the parasite species composition to change rapidly. If this is true a cluster analysis of all the samples should yield definite clusters that probably represent individual tigers. We used a log transform of abundance data on each parasite taxon in each sample and subjected all samples to cluster analysis using Euclidean distance and group average strategy for clustering [31] (fig 2). The number of clusters decreased with distance with two distinct plateaus (Fig 3). Defining clusters at a plateau is natural as well robust [32]. The first plateau occurred at a distance of 0.27 resulting into 31 clusters. Clusters at this level are unlikely to represent individual tigers for two reasons. The samples analyzed contain four from a male and three from a female tiger that were identified anecdotally from sightings and distinctive pugmarks. Both of them belonged to two distinct clusters (fig 2). The maximum distance between two samples of an identified individual was 0.83 that is considerably greater than the position of the first plateau but slightly less than that for the second plateau downstream. It seems reasonable therefore to assume that the distinct clusters obtained with the second plateau beginning at a distance of 0.88 represent different individual tigers. The first plateau gives us 31 clusters, which is unrealistically large for the study area. The second plateau gives us 14 distinct clusters. This number is within the limits of the reported tiger densities from comparable habitats [33].

The broad statistical patterns observed remained unchanged after clustering. The double logarithmic plot of means and variances was linear with a slope of 1.93. The prevalence abundance correlation remained positive but was non-significant. No association was found between any two parasites after clustering.

Out of the 14 clusters recognized 4 were represented by a number of samples and 10 were single samples. The territory holding resident tigers are very likely to be sampled repeatedly whereas the non-resident transients that may have visited the study area occasionally could have been sampled only once. If the larger clusters represented resident tigers the study area could have 4 resident tigers and

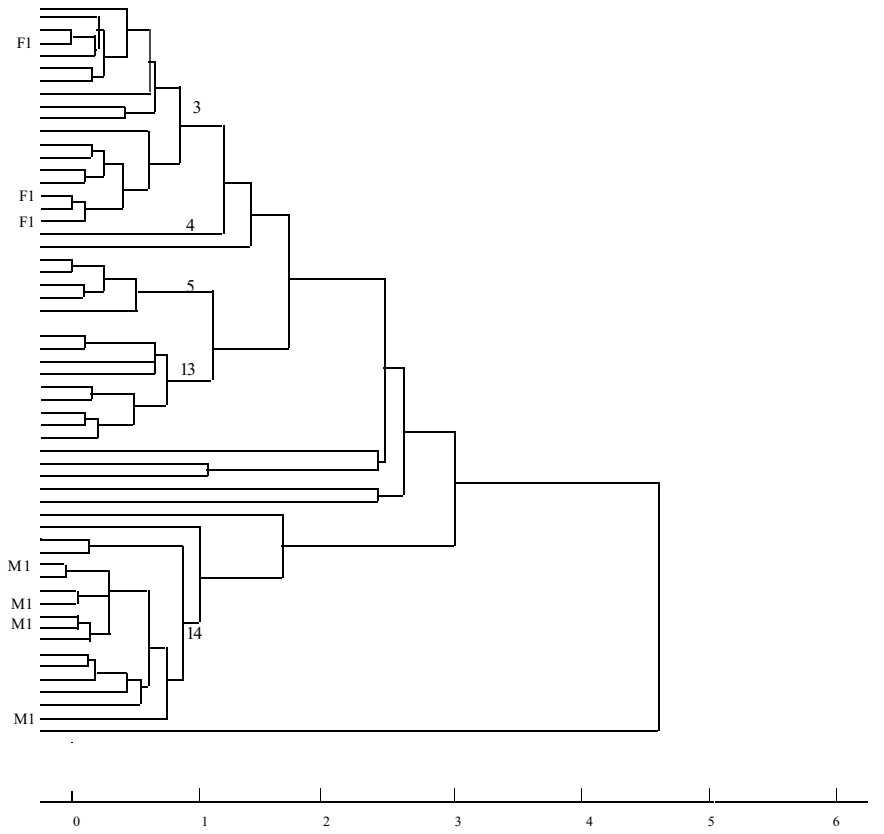

Figure 2
Cluster analysis of the parasite composition of all samples. If the parasite composition of individual tigers is fairly consistent, samples coming from different individuals should form different clusters. The clustering was robust since three different clustering strategies gave very similar clusters (data not shown). The larger clusters that would presumably reflect repeated sampling of resident individuals are numbered. One identified mail (M1) and one identified female (F1) that were sampled repeatedly are indicated. Both of them belong to one cluster each.

an unestimated but certainly a larger number of non-resident tigers. Out of the four large clusters, cluster 3 consisted of zero or low density (< 5/g) of propagules. The propagules however belonged to three different parasites in different samples namely ascarid, *Taenia* and lungworms. Therefore the cluster might represent up to three individuals raising the possible number of resident tigers to 6. The cluster 5 consisted of samples having between 5 to 20 *Diphyllobothrium* eggs per gram and no other parasite. The cluster 13 consisted of between 50 to 350 *Diphyllobothrium* eggs and occasional ascarid eggs and the cluster 14 consisted of a large number (500–4000) of *Diphyllobothrium* eggs with a low to moderate number of *Taenia* and Ascarid or lungworm. If the areas over which each of the four large clusters was sampled (fig 4) were considered as home ranges of individual tigers, the home range sizes were 49.25 Km^2 for cluster 3, 46.75 Km^2 for cluster 14, 31.2 Km^2 for cluster 13 and 15.75 Km^2 for cluster 5. The presumed home range sizes are close to the sizes of tiger home ranges in radio telemetry studies [34]. There was a considerable overlap in the distribution of the collection sites of the samples in different clusters. Very similar overlaps have been seen in radiotelemetry studies [34].

Interestingly the presumed resident tigers had significantly lower parasite loads than the presumed non-resident ones (Median test $X^2 = 7.4$, $p < 0.01$). This can happen if tigers which are parasite resistant and therefore healthier are more likely to be successful in establishing territories. Alternatively transient tigers may be under greater stress

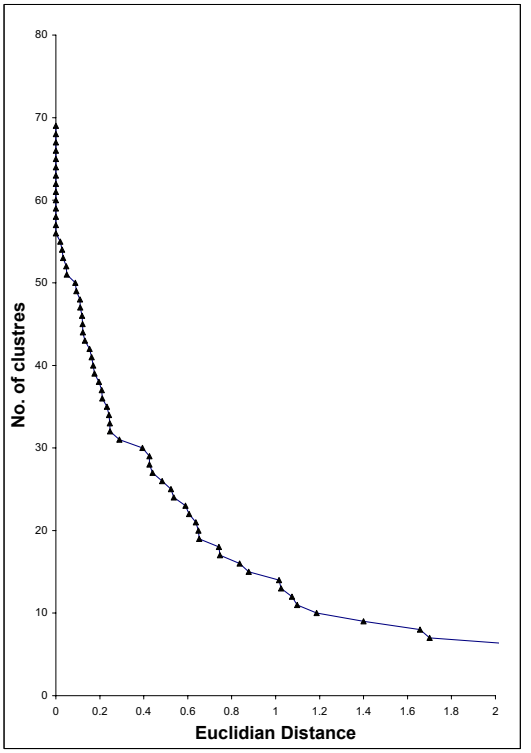

Figure 3
The number of clusters reduced with the distance discontinuously to give two distinct plateaus. We suspect the second plateau to appropriately represent individual tigers since the distance matches with that seen in known individual tigers and the number of clusters is close to the plausible number of tigers in the study area.

and therefore more susceptible to parasites. Ranging over a larger area might also result in acquiring more parasites since the range covers more microhabitats that may harbor different intermediate hosts and different survival conditions for parasite infective stages. It cannot be ignored, however, that such a pattern can arise as an artifact of cluster analysis. If the variance in parasite densities within scat samples of a single individual increased with the mean it is likely that the distances become larger for samples with higher parasite loads. A log transformation of the data would substantially reduce this effect. In any case, the suggestion obtained from the observed pattern needs validation that can be done by monitoring the parasite compositions of identified or radio-collared tigers over a considerable time period.

Conclusions

Tigers have rich and diverse parasite communities that are dominated by indirect life cycle parasites. Parasite community of tiger shares certain statistical patterns with other parasite communities, notably the positively skewed distribution, prevalence-abundance correlation and scaling of variance with the square of the mean.

Of particular interest are the clusters, the "territories" occupied by each of the clusters and the apparently higher parasite loads of the presumably "non-territorial" ones. These findings need to be validated by long term parasite monitoring of identified individual tigers. In the absence of such a validation the above results are only suggestive. They leave no doubt however about the need to include parasites in any comprehensive study of tiger ecology. Since the frequency of locating fresh scats is usually high in most of the tiger areas, parasite compositions in scats can be a useful tool in monitoring tigers particularly in areas where tiger sighting is rare. Besides a number of questions regarding individual health, prey choice, territorial behaviour, movement patterns and reproductive success in relation to parasite loads can be worth investigating.

Materials and Methods

Study Area

The Tadoba-Andhari Tiger Reserve (TATR) (between 20^0 - 04'.53" N to 28^0 - 25'.51" N latitude to 79^0 - 13'.13" E to 79^0 - 33'.34" E longitude) lies in the Chandrapur district of Vidarbha Region of Maharashtra and is spread over 625.40 Sq. Km. As per the Biogeographic classification of India by the Wildlife Institute of India, Dehradun, it falls under 6B Central pleateau Province of Deccan Peninsula Zone. This area of TATR is comprised of the Tadoba National Park (Area 116.55 Sq. Km.) and the Andhari Wildlife Sanctuary (area 508.85 Sq.Km.) It is composed of two geomorphological units. The northern part comprises of a hilly region known as the "Chimur Hillocks" and covers almost the entire Tadoba National Park. The rest is a more or less plain area of the Moharli & Kolsa Ranges which constitute the Andhari Sanctuary. The area has a perennial river and a number of lakes. TATR supports a diverse mammalian assemblage including tiger (*Panthera tigris*), leopard (*Panthera pardus*), hyena (*Hyaena hyaena*), sloth bear (*Melursus ursinus*), dhole (*Cuon alpinus*), jackal (*Canis aureus*) and jungle cat (*Felis chaus*) as the carnivores, the common langur (*Semnopithecus entellus*) is the most numerous primate and the ungulates include barking deer (*Muntiacus muntjak*), gaur (*Bos gaurus*), sambar (*Cervus unicolor*), chital (*Axis axis*), wild boar (*Sus scrofa*), nilgai (*Boselapheus tragocamelus*) and chousinga (*Tetracerus quadricornis*). Dubay [20] estimated the densities (no./sq. km) of major prey species in the study area as Chital 17.23 (Coefficient of variation%=10.59), Sambar 5.1 (CV%=9.16), Wild boar 4.36 (CV%=8.16), Gaur 2.75

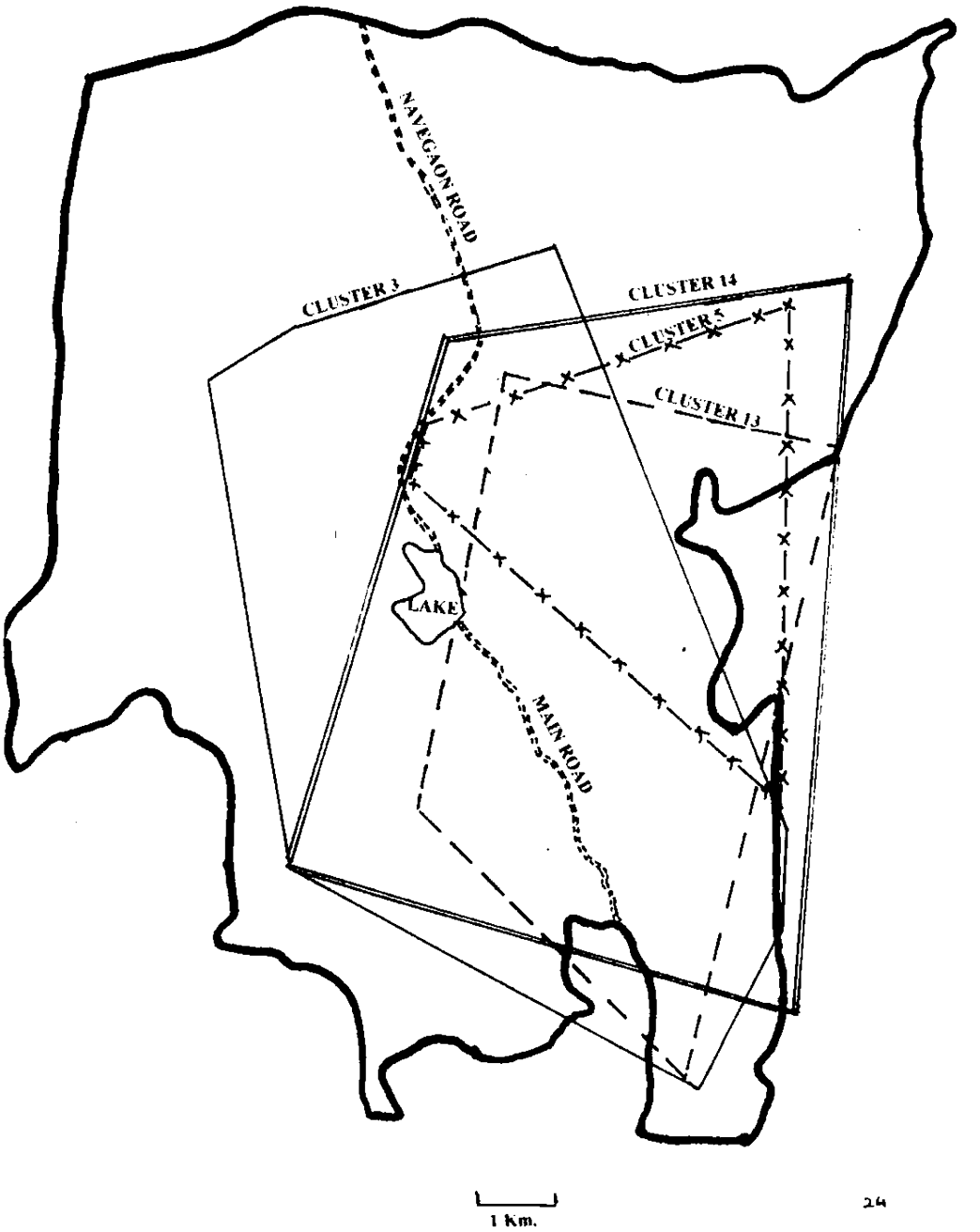

Figure 4
The areas over which samples from individual clusters were collected were marked using the principle of minimum convex polygon. The sizes of the resultant ranges and their overlaps are comparable to those of individual tigers obtained by radiotelemetry (Karanth and Sunquist 2000).

Table 3: Parasite propaule densities in samples (raw data).

sample no.	total	No. of species	*Diphyllobothrium*	Hookworm	*Taenia*	Toxocara	*Ascarid*	Lungworm	*Capillaria*	*Paragonimus*	Unidentified
1	45.00	1	45.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	285.63	2	285.21	0.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	661.46	2	656.93	0.00	4.53	0.00	0.00	0.00	0.00	0.00	0.00
5	0.60	1	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.00
6	1.29	3	0.16	0.00	0.00	0.00	0.97	0.16	0.00	0.00	0.00
7	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9	5575.00	2	5500.00	0.00	75.00	0.00	0.00	0.00	0.00	0.00	0.00
10	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	51.60	2	50.00	0.00	0.00	0.00	1.60	0.00	0.00	0.00	0.00
12	35.33	3	35.14	0.00	0.00	0.00	0.00	0.00	0.10	0.10	0.00
13	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
14	53.15	3	50.56	0.00	0.39	0.00	2.19	0.00	0.00	0.00	0.00
15	14.50	1	14.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16	10.95	2	0.00	0.00	0.00	0.00	8.57	0.00	0.00	2.38	0.00
17	2870.31	1	2870.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
18	138.38	2	135.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00
19	169.23	1	169.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
20	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
21	218.36	1	218.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22	11.46	1	0.00	0.00	11.46	0.00	0.00	0.00	0.00	0.00	0.00
23	669.74	1	669.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24	1768.11	1	1768.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25	12049.16	3	12048.19	0.00	0.00	0.00	0.84	0.00	0.00	0.00	0.12
26	0.54	2	0.00	0.00	0.00	0.00	0.43	0.11	0.00	0.00	0.00
27	939.97	2	937.97	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00
28	3451.01	1	3451.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
29	1.68	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.68
30	4.50	1	0.00	0.00	0.00	0.00	4.50	0.00	0.00	0.00	0.00
31	3.00	1	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00
32	2.75	1	0.00	0.00	0.00	0.00	2.75	0.00	0.00	0.00	0.00
33	3095.29	1	3095.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
34	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
35	3168.64	1	3165.64	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00
36	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
37	1406.95	1	1406.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
38	566.03	2	562.78	0.00	3.25	0.00	0.00	0.00	0.00	0.00	0.00
39	245.96	2	0.00	0.00	151.36	0.00	94.60	0.00	0.00	0.00	0.00
40	204.54	2	0.10	0.00	0.00	0.00	204.34	0.00	0.00	0.00	0.10
41	9.50	1	0.00	0.00	0.00	0.00	9.50	0.00	0.00	0.00	0.00
42	12.00	1	0.00	0.00	0.00	0.00	12.00	0.00	0.00	0.00	0.00
43	7.00	1	0.00	0.00	0.00	0.00	7.00	0.00	0.00	0.00	0.00
44	20.50	2	11.75	0.00	0.00	0.00	0.00	8.75	0.00	0.00	0.00
45	914.52	1	914.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
46	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
47	1832.13	3	1688.34	0.00	22.70	0.00	0.00	121.09	0.00	0.00	0.00
48	506.50	1	506.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
49	3869.11	1	3869.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
50	4748.46	2	3869.11	0.00	879.34	0.00	0.00	0.00	0.00	0.00	0.00
51	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
52	15.50	1	0.00	0.00	15.50	0.00	0.00	0.00	0.00	0.00	0.00
53	64.87	1	64.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
54	2.50	1	2.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
55	905.34	2	879.34	0.00	26.00	0.00	0.00	0.00	0.00	0.00	0.00
56	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
57	3.50	1	0.00	0.00	3.50	0.00	0.00	0.00	0.00	0.00	0.00

Table 3: Parasite propaule densities in samples (raw data). ***(Continued)***

58	14.50	1	14.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
59	3.25	1	0.00	0.00	0.00	3.25	0.00	0.00	0.00	0.00	0.00
60	880.84	2	879.34	0.00	1.50	0.00	0.00	0.00	0.00	0.00	0.00
61	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
62	1969.73	1	1969.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
63	1922.83	1	0.00	0.00	1922.83	0.00	0.00	0.00	0.00	0.00	0.00
64	8.00	1	8.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
65	7.60	1	7.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
66	3.50	2	0.00	0.00	1.50	2.00	0.00	0.00	0.00	0.00	0.00
67	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
68	0.50	1	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	
69	0.00	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
70	2.00	1	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	

Figures indicate estimated density of propagules per gram.

(CV%=8.84), Barking deer 1.41(CV%=39.25), Langur 19.07 (CV%=13.80), Chowsingha 0.33 (CV%= 26.37), Nilgai 1.04 (CV%=22.94). Tiger densities have not been estimated except for the pugmark based estimate by the forest department of 36 tigers in TATR and 15 in the Tadoba National Park. No standard deviations are available with these estimates.

Sample collection and analysis

Fresh faecal samples of tigers were collected by following fresh tiger trails in the early morning hours from the Tadoba range over a period of two years. Samples were collected from the ground, avoiding the part contaminated with soil. Weighed quantities of the samples (typically 4 grams) were analyzed using the quantitative zinc sulphate sedimentation flotation technique [17,16] to estimate parasite propagule densities per gram of faeces. The sample was mixed with water and filtered to remove debris. The filtrate was centrifuged at 2000 rmp for 5 minutes. The supernatant was then removed and 5 ml of $ZnSO_4$ solution (sp. Gr. 1.18) was added and mixed with the sediment. This was again centrifuged at 2000 rpm for 5 minutes. Using an L shaped wire loop with a 6 mm diameter loop the contents of the surface layer were transferred on to a slide for observation. All the propagules were counted and the count converted into density per gram of sample. Watve (1992) compared different methods of fecal analysis and found that Zinc Sulfate flotation was more sensitive in detecting low densities of propagules although at high concentrations it tended to underestimate the numbers. The counts thus obtained were used for calculation of prevalence and mean densities. The prevalence was defined as the proportion of samples showing the presence of parasite. The mean densities for all the samples were calculated separately and mean intensities in positive samples were calculated ignoring the negative samples.

Adult worms and tapeworm segments were collected from faeces whenever present and from autopsy of a dead tigress. The 70 samples collected came from a much smaller number of individuals. Many individuals therefore must have been sampled repeatedly. For seven of the samples the individual sampled was identified by sighting or by a distinctive pugmark.

Parasite identification

Parasites were identified to the genus or family level from the propagule morphology. Since extensive taxonomic accounts of the helminth species of tigers in the wild are not available, we do not claim to have identified all species. Whenever morphological differences in the propagules, including distinct bimodality in size, were present within a genus distinct operational taxonomic units (OTUs) were recognized. Attempt to identify the species was made only when the adult stages were collected. Due to the unavoidable tentativeness in identification, while analyzing parasite diversity we used two strategies. A conservative one in which closely resembling morphotypes were merged into a single OTU and a liberal one in which OTUs were split based on small but distinguishable differences. Due to the limitations of faecal analysis the terms prevalence and intensities have somewhat different meanings [17,16] than the classical definitions of Margolis [35].

Statistical analysis

Parasite distributions are typically highly skewed. Therefore we use non-parametric methods throughout. Species richness estimate by Bootstrap – The method uses a computer simulated subsampling from the data and calculates the species richness using Smith and van Belle equation,

$$B(S) = S + \Sigma (1-p_i)^n$$

Where,

B = bootstrap estimate of species richness

S = Observed number of species in original data

p_i = proportion of the n bootstrap quadrats that have species i present. The simulation is repeated 100 times to get the mean estimate and its standard deviation.

Clustering by parasite species composition

Parasite abundance data for each taxon was log transformed. The log transformed data for each taxon were used for cluster analysis using CLUSTER.BAS [31] with Euclidean distance and group average strategy. Thus both species richness and relative abundance are considered during clustering.

Acknowledgements

We are grateful to the Department of Science & Technology, Govt. of India for giving financial assistance for this work. We thank the Chief Conservator of forest (Wild life), Conservator of Forest and Deputy Conservator of Forest, TATR, Maharashtra State for their cooperation during our work in Tadoba Andhari Tiger Reserve. Active assistance in parasite identification by Dr. Kolte, Dept. of Parasitology, Nagpur Veterinary College is acknowledged. We thank. Dilip Tiwade, Suresh Khobragade, Narayansingh Gharkele, Sudhakar Dhadmal, and Aesambre for their help in fieldwork.

References

1. Sinclair ARE: **Dynamics of the Serengeti ecosystem, process and pattern.** *In: Serengeti – dynamics of an ecosystem. (Edited by: Sinclair ARE, M Norton Griffiths) Chicago, London.: University of Chicago Press.* 1979
2. Sumpton KJ, Flowerdew JR: **The ecological effects of the decline of rabbits (*Oryctolagus cuniculus*) due to myxomatosis.** *Mammal Rev.* 1985, **15:**151-186
3. Anderson RM: **Parasite pathogenicity and the depression of the host population equilibria.** *Nature* 1979, **279:**150-152
4. Anderson RM: **Depression of host population abundance by direct lifecycle macroparasites.** *J. Theor. Biol.* 1980, **82:**289-311
5. Price PW, Westoby M, Rice B: **Parasite mediated competition: some predictions and tests.** *Am. Nat.* 1988, **131:**544-555
6. Freeland B: **Arms races and covenants: the evolution of parasite communities.** *In Community ecology, patters and processes. (Edited by: Kikawa J, Anderson DJ) Melbourne: Blackwell scientific publication.* 1986
7. Hamilton WD: **Sex versus non-sex versus parasites.** *Oikos* 1980, **35:**282-290
8. Hamilton WD: **Pathogens as causes of genetic diversity in their host populations.** *In Population biology of infectious diseases. (Edited by: Anderson RM, May RM) Berlin, Heidelberg, New York.: Springer Verlag.* 1982
9. Hamilton WD, Zuk M: **Heritable true fitness and bright birds: a role for parasitism?** *Science* 1982, **218:**384-387
10. Hamilton WD, Axelrod R, Tenese R: **Sexual reproduction as an adaptation to resist parasites (a review).** *Proc. Natl. Acad. Sci. USA,* 1990, **87:**3566-3573
11. Freeland WJ: **Pathogens and the evolution of primate societies.** *Biotropica* 1976, **8:**12-24
12. Milinski M: **Parasites determine a predator's optimal feeding strategy.** *Beh. Ecol. Sociobiol.* 1984, **15:**35-37
13. Lozano GA: **Optimal foraging theory: a possible role for parasites.** *Oikos* 1991, **60:**391-395
14. Hudson PJ, Dobson AP, Newborn D: **Do parasites make prey vulnerable to predation? Red grouse and parasites.** *J. Anim. Ecol* 1992, **61:**681-692
15. Temple SA: **Do predators always capture substandard individuals disproportionately from prey populations?** *Ecology.* 1987, **68:**669-674
16. Watve MG, Sukumar R: **Parasite abundance and diversity in mammals: correlates with host ecology.** *Proc. Natl. Acad. Sci, USA.* 1995, **92:**8945-8949
17. Watve MG: **Ecology of host-parasite interactions in a wild mammalian host community in Mudumalai, southern India.** *Ph. D. Thesis, Indian Institute of Science, Bangalore.* 1992
18. Karanth U, Stith BM: **Prey depletion as a critical determinant of tiger population viability.** *Riding the Tiger: Tiger conservation in human-dominated landscapes. (Edited by: J Seidensticker, S Christie, P Jackson) Cambridge, UK: CambridgeUniversity Press.* 1999
19. Freedman HI: **A model of predator prey dynamics as modified by the action of a parasite.** *Mathematical Biosciences* 1990, **99:**143-155
20. Patton S, Rabinowitz R: **Parasites of wild Felidae in Thailand: A Coprological survey.** *J. Wildlife Diseases,* 1994, **30:**472-475
21. Freeland WJ: **Primate social groups as biological islands.** *Ecology,* 1979, **60:**719-728
22. Appleton CC, Henzi SP, Whitehead SI: **Gastrointestinal helminth parasites of the chacma baboon, *Papio cyanocephalus ursinus,* from the costal low lands of Zululand, South Africa.** *Afr. J. Ecol.,* 1991, **29:**149-156
23. Shaw JL, Moss R: **The role of parasite fecundity and longevity in the success of *Trichostrongylus tenuis* in low density Red Grouse populations.** *Parasitology* 1989, **99:**253-258
24. Skorping A, Reed AF, Keymer AE: **Life history covariation in intestinal nematodes of mammals.** *Oikos* 1991, **60:**365-372
25. McCallum HI: **Infection dynamics of *Ichthyophthirius multifillis*** *Parasitology.* 1982, **85:**475-488
26. Aho JM: **Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes.** *In: Parasite communities: patterns and processes. (Edited by: GW Esch, AO Bush, JM Aho) London, New York: Chapman and Hall.* 1990
27. Hanski I: **Dynamics of regional distribution: the core and satellite species hypothesis.** *Oikos* 1982, **38:**210-221
28. Dubay Y, Mathur VB: **Establishing computerized wildlife database for conservation, monitoring and evaluation in Tadoba-Andhari Tiger Reserve, Maharashtra.** *Final project report.* 1999
29. Soulsby EJL: **Helminths, arthropods and protozoa of domesticated animals** *E.L.B.S./Bailliere Tindall* 1982
30. Krebs CJ: **Ecological Methodology** *New York: Harper & Row* 1989
31. Ludwig JA, Raynolds JF: **Statistical ecology: a primer on methods and computing.** *John Wiley* 1988
32. Watve MG, Gangal RM: **Problems in measuring bacterial diversity and a possible solution.** *App. Env. Microbiol.* 1996, **62:**4299-4301
33. Karanth UK: **Counting tigers, with confidence.** *In: Riding the Tiger: Tiger conservation in human-dominated landscapes. (Edited by: J Seidensticker, S Christie, P Jackson) Cambridge, UK. CambridgeUniversity Press* 1999
34. Karanth UK, Sunquist ME: **Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India.** *J. Zool., London.* 2000, **250:**255-265
35. Margolis L, Esch GW, Holmes JC, Kuris AM, Schad GA: **The use of ecological terms in Parasitology (Report of an AD HOC committee of the American Society of Parasitologists.** *J. Parasitol* 1982, **68:**131-133