Epidemiology of an intestinal parasite (*Spirometra* spp.) in two populations of African lions (*Panthera leo*)

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SUMMARY

Infection with the cestode *Spirometra* spp. was studied in 2 populations of lions in the Serengeti and the Ngorongoro Crater in Tanzania, East Africa. These 2 lion populations lived in different habitats and were known to differ genetically: lions in the Serengeti were outbred, whereas lions in the Ngorongoro Crater were inbred. Faecal samples were collected from 112 individually known lions between March 1991 and November 1992. Over 60 % of lions were infected and the median intensity of infection was 975 eggs per g of faeces. The distribution of egg counts was overdispersed. There was variability through time, though this was unrelated to seasons delimited by rainfall. There were no significant differences in levels of infection between age classes; cubs less than 9 months were already heavily infected. Sex and reproductive status did not have a significant effect. However, there were significant differences in intensities of infection between the Crater and the Serengeti populations – *Spirometra* spp. showed a higher level of infection intensity in the Crater population – with some variation between prides within these populations. Allozyme heterozygosity scores were available for a subset of 28 lions but were unrelated to levels of *Spirometra* infection. It was not possible to ascribe differences in levels of parasite infection to genetic rather than ecological factors.

Key words: wildlife disease, spatial heterogeneity, cestode, Tanzania.

INTRODUCTION

Macro- and microparasites in natural populations have mainly received attention in the aftermath of serious epidemics (Roelke-Parker *et al.* 1996; Thorne & Williams, 1988; Scott, 1988). Despite an increasing knowledge of human diseases and theoretical studies suggesting the importance of parasites for maintaining genetic diversity and regulating host populations (Anderson, 1978; May, 1985; Scott & Dobson, 1989), surprisingly little is known about the ecology of endemic diseases in natural populations. Part of the problem lies in the practicalities/logistics of monitoring the dynamics of wildlife diseases. There are not many wild populations with sufficient long-term data on the hosts which allow the study of disease at the individual and population level. However, interest in diseases as part of the ecological system and the increasing interest in the conservation of natural animal populations have resulted in recognition of the importance of this area of research (May, 1988; Scott, 1988; Grenfell & Gulland, 1995).

This study examines the interactions of wild lions (*Panthera leo*) with their most prevalent parasite *Spirometra* spp. (Müller-Graf, 1995) in 2 populations in the Serengeti and the Ngorongoro Crater in Tanzania, East Africa. Faecal samples were obtained from individual lions that were subjects of long-term demographic and ecological studies (Schaller, 1972; Bertram, 1978; Packer, 1986; Packer *et al.* 1988, 1991*b*; Hanby, Bygott & Packer, 1995). This allowed parasite infection to be related to known characteristics of individual animals. The 2 host populations were chosen because they differed in genetic structure and habitat. The Serengeti lions are part of a large outbred population, whereas the Ngorongoro Crater population is small, isolated and inbred (O'Brien *et al.* 1987; Yuhki & O'Brien, 1990; Gilbert *et al.* 1991; Packer *et al.* 1991*b*). Crater lions had a significantly lower degree of genetic diversity in the isozymes tested (Yuhki & O'Brien, 1990; Packer *et al.* 1991*b*). As a result, the 2 populations might be expected to show different levels of parasitic infection. Higher levels of genetic uniformity might

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reduce resistance to parasites (May, 1988; O'Brien & Evermann, 1988), thus a comparison of the 2 lion populations might indicate whether these inbred lions are more susceptible to *Spirometra* spp. However, levels of infection of the 2 populations may also differ because of the ecological differences between the habitats, including differences in prey availability (Packer *et al.* 1988; Hanby *et al.* 1995). Allozyme data from individual lions in the Crater and the Serengeti were used to examine whether differences in infection were linked to genotype. Variation in parasite burden may, however, also be influenced by several other factors, which were also investigated. Samples were collected over 5 seasons, and parasite dynamics may change according to season (Dogiel, 1964; Cheng, 1986; Esch, Bush & Aho, 1990), especially as seasons are related to the movement of prey, which are the intermediate hosts for several lion parasites including *Spirometra* spp. Infection can vary with host age because of different exposure, innate or acquired immunity (Bundy, 1988*a*; Anderson & May, 1991). Host sex may influence intestinal parasite burden (Bundy, 1988*b*); furthermore, female reproductive status can alter susceptibility to infection with pregnant or lactating females likely to exhibit higher parasite egg output (Jackson, Angus & Williams, 1988; Behnke, 1990). Differences in host group size may account for variations in infection depending on the type of parasite involved (Freeland, 1976; Møller, Allander & Dufva, 1993; Coté & Poulin, 1995).

MATERIALS AND METHODS

Study area

The study deals with the *Spirometra* infection of 2 lion populations located in a 2000 km² area in the Serengeti National Park (coordinates of Seronera, the research station in the centre of the Serengeti, 34° 50′ E, 02° 30′ S) and the 250 km² floor of the nearby Ngorongoro Crater (35° 35′ E, 03° 10′ S), part of the Ngorongoro Conservation area, 120 km southeast of Seronera in Tanzania, East Africa (Fig. 1).

The Serengeti ecosystem is dominated by 2 main vegetation types, grassy plains with scattered rocky outcrops (kopjes) and open woodlands. The Ngorongoro Crater is an extinct volcanic caldera with a primarily open grassland floor that includes a number of swamps and marshes (Schaller, 1972; Sinclair, 1979; Packer *et al.* 1988). The Serengeti ecosystem is characterized by the migration of the herbivores according to season, whereas in the Crater there is only minor seasonal variation in herbivore distribution and prey is consistently abundant (Kruuk, 1972; Packer *et al.* 1988; Hanby *et al.* 1995). Here, the resident biomass of the lions' preferred prey species is the highest in Africa (Packer *et al.* 1988). Crater lions have a higher food intake than the

lions of the Serengeti plains (Hanby *et al.* 1995) which are subjected to greater nutritional stress during certain times of the year. The lions in the Serengeti woodlands have better access to prey than the lions in the plains during times when migratory prey is rare, but they are nevertheless subject to seasonal variation (Scheel & Packer, 1995). The Crater contains a smaller, but denser lion population (Packer *et al.* 1988; Hanby *et al.* 1995). The average pride size is the same in both habitats.

Seasons

The dry season typically starts in June and lasts until October while the rains normally begin in November and continue until May (Schaller, 1972; Sinclair, 1979). However, there is considerable variation in the date of onset of the wet season. Serengeti rainfall data from 1990 until 1993 were used to classify each season with precision (Fig. 2). Rainfall was read regularly each month at gauges in the Serengeti woodlands near Seronera. Comparison with readings from previous years at several gauges in the Serengeti, suggests that these rain gauge readings provide a good indication of the overall rainfall patterns as plains rainfall is highly correlated with woodland rainfall (Packer *et al.* 1988). Rainfall patterns in the Ngorongoro Crater are similar to the Serengeti (Packer *et al.* 1988) and data from the Serengeti were used for the Crater as well.

Seasons in the sampling period were classified as follows: the first wet season from August to June 1990/91, the first dry season July to September 1991, the second wet October 1991 to May 1992, second dry June 1992 to September 1992 and the third wet October 1992 to April 1993 (see Fig. 2).

The lion population

Lion prides normally consist of 2–9 related females (range 1–18), their dependent offspring and a coalition of 2–6 adult males (range 1–9) (Packer *et al.* 1991*b*). The resident males are either closely related or unrelated to each other (Packer & Pusey, 1982; Packer *et al.* 1991*a*). Overall pride size averages 15 members (range 1–37) (Schaller, 1972). Prides are 'fission-fusion' social units. Pride members do not remain in constant association, but form subgroups throughout the pride-range and spend some time alone (Pusey & Packer, 1987; Cairns, 1990; Packer, Scheel & Pusey, 1990). A small number of females live alone in stable ranges and some males are nomadic and live alone.

Lions not only kill their own prey but also scavenge from other predators and eat animals that have died from disease and other causes (Schaller, 1972). They kill almost any animal they can catch, but in most areas prey from a few species predominates. The Serengeti lions feed mainly on wildebeest (*Connochaetes taurinus*), zebra (*Equus*
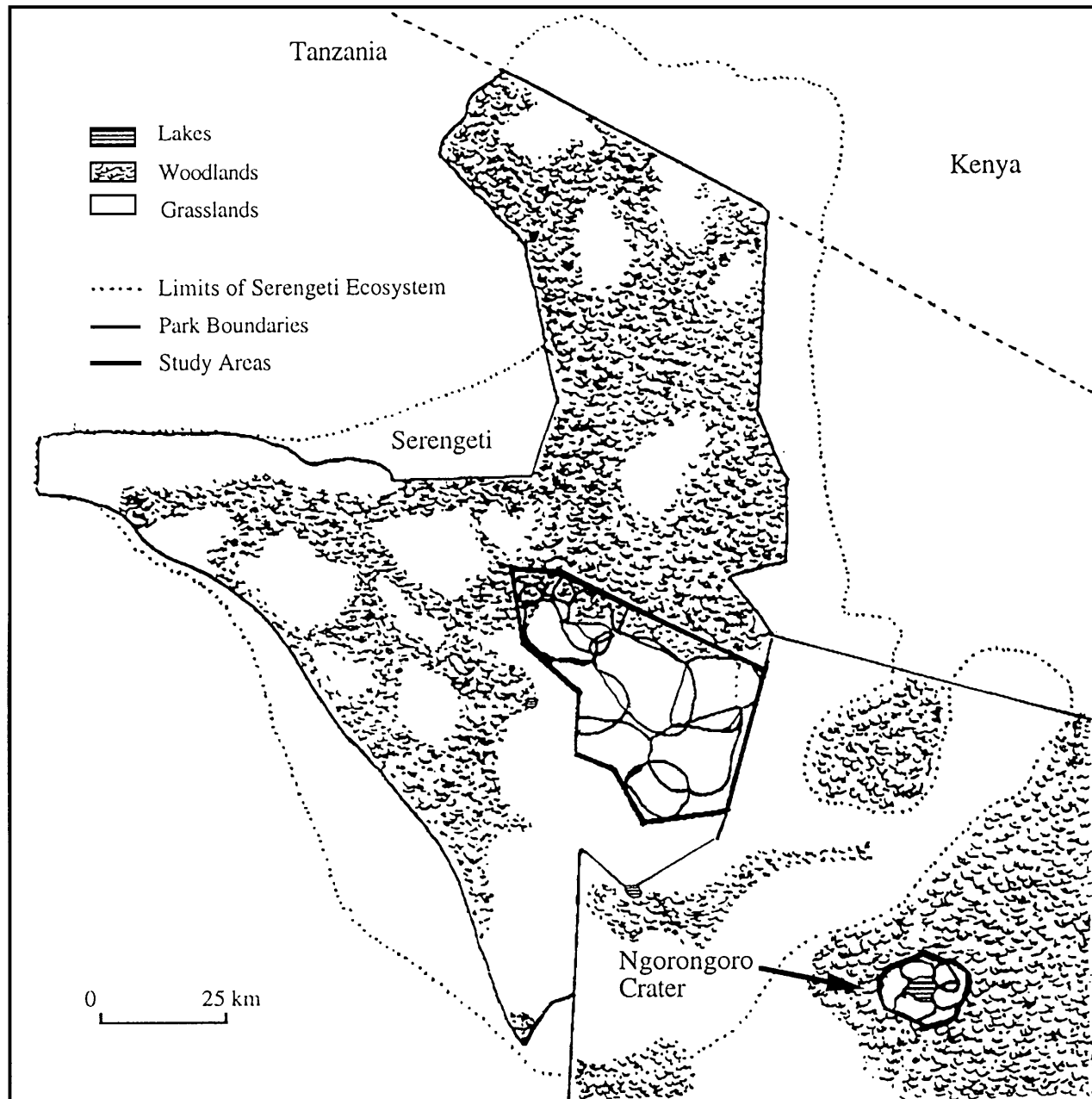
Fig. 1. Study areas in the Serengeti National Park and Ngorongoro Conservation Area. Approximate pride ranges are drawn in the study areas. The woodland prides are those whose ranges are primarily in the woodlands habitat at the northern edge of the study area. Map after Packer *et al.* (1988).

burchelli), wart-hog (*Phacochoerus aethiopicus*), buffalo (*Syncercus caffer*), Thomson's gazelle (*Gazella thomsoni*) and topi (*Damaliscus korrigum*) (Schaller, 1972; Scheel, 1993). Season and location, however, have a significant influence on prey choice (Schaller, 1972; Scheel, 1993; Scheel & Packer, 1995).

Individual lions were identified by their earmarks and whisker spots (Pennycuick & Rudnai, 1970; Packer, 1992; Packer & Pusey, 1993). During this study, 26 prides of lions were monitored, 18 prides in the Serengeti (containing 190 lions) and 8 prides in the Ngorongoro Crater (containing about 70 lions).

Although genetic data are not available for each individual in this study, the 2 lion populations are known to differ genetically. The Serengeti population is more outbred than the population in the Crater. The Crater lions were reduced from 72 to 10–15 individuals following an outbreak of biting flies (*Stomyxys calcitrans*) in 1962 (Packer *et al.* 1991*b*). The present Crater population is descended from only 10–15 founders and most individuals can be traced back to 4 female ancestors (Packer, 1992). There has been no immigration into the Crater since 1969 (Packer *et al.* 1991*b*).

In contrast, male lions disperse throughout the Serengeti ecosystem and mating partners are typically unrelated (Packer *et al.* 1991*b*). Empirical data from previous studies reveal that, in comparison to the Serengeti, lions in the Crater show a lower
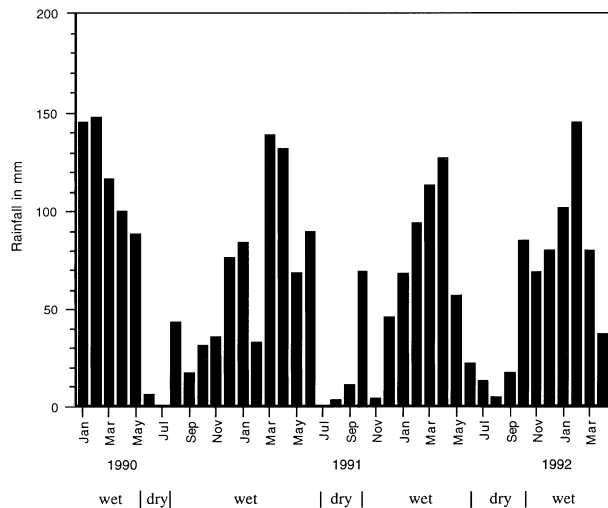
Fig. 2. Rain was measured in mm at rain gauges in the Serengeti woodlands near Seronera. Bars show monthly totals of rainfall. Seasons are indicated.

degree of genetic diversity in isozymes (Packer *et al.* 1991*b*). Furthermore, a striking lack of diversity in restriction fragments of the major histocompatibility complex (MHC) class I gene (Yuhki & O'Brien, 1990), which appears to play a role in the immune response to parasitic infections, was observed.

Genetic data were available for a subset of the sampled lions from both populations ($n = 28$; Serengeti $= 21$, Crater $= 7$). Genotypes at 8 polymorphic allozyme loci were tested for each individual and an overall score of heterozygosity, indicating the proportion of tested loci that were heterozygous, was calculated for each individual (see O'Brien *et al.* 1987; Packer *et al.* 1991*b*).

The parasite

Both *Spirometra* (order: Pseudophyllidea; class: Eucestoda) eggs and proglottids were found in the lion faeces. Identification was made on the basis of egg morphology (egg size length: 54·7–76·0 μm, mean: $64·9 \pm 1·0$ s.e.; width: 30·4–44·4, mean: $37·5 \pm 0·6$) (Müller-Graf, 1994, 1995). Eggs were compared with a sample of eggs from a mature and gravid *Spirometra pretoriensis*. The proglottids were identified as belonging to *Spirometra* spp. (A. Jones, personal communication). *Spirometra* had already been found to infect lions in previous studies (Nelson, Pester & Rickman, 1965; Dinnik & Sachs, 1969). According to Round (1968), the species in lion is *Spirometra theileri*, whereas the species found in hyenas is generally accepted to be *S. pretoriensis*. However, the morphology of a fragment of *Spirometra* found in a lion faecal sample was consistent with *S. pretoriensis*. This suggests that both species may occur in lions.

Not much is known about the life-cycles of *S. theileri* and *S. pretoriensis*. They have an indirect life-cycle involving 2 intermediate hosts. Baer (1971)

reported that upon hatching from eggs in water, the coracidia infect cyclops. The second intermediate host which becomes infected with the larval stages (procercoid) is a mammal, which acquires the infection by drinking water contaminated with infected cyclops. Amphibians and reptiles seem to play no role in the transmission cycle (Schmid & Watschinger, 1972; Opuni & Muller, 1974) as in other species of the genus *Spirometra*. Plerocercoids (spargana) of *Spirometra* have been recovered from big game animals like antelope, buffalo, zebra, wildebeest and wart hogs (Sachs & Sachs, 1968; Dinnik & Sachs, 1969) in Tanzania and Kenya. The final host, a carnivore, picks up the parasite when feeding on prey. Man can act as an intermediate host as well (Nelson *et al.* 1965; Khalil, 1991).

Collection of faecal samples

Faecal samples from individually identified lions were collected opportunistically between March 1991 and November 1992 and preserved in 50 ml vials with 10 % formalin on site or at the research station. More samples were collected in the Serengeti ($n = 129$) than in the Crater ($n = 39$) and more in the wet season ($n = 114$) than in the dry season ($n = 53$; date unrecorded $n = 1$). Overall, 168 samples were examined from 112 individuals. Faecal samples were sieved with a large mesh sieve to remove large contaminants and centrifuged to obtain 1 g of faeces from the pellet and screened for parasite eggs with the formol-ether method (Cheesbrough, 1987; Müller-Graf, 1994). Egg counts were made from 1 g of the pellet from the faeces.

Statistical analysis

Intensity describes the number of *Spirometra* spp. eggs in a faecal sample. Mean intensity is calculated for both infected and uninfected host individuals.

Egg counts were $\log(x+1)$ transformed. To avoid bias due to the repeated sampling only 1 sample per individual was used and individuals were as evenly spread across the seasons and locations and habitats as possible. The number of individuals from the wet and dry season in the 2 habitats of the Serengeti (woodlands and plains) and the Crater did not differ significantly ($\chi^2_2 = 0·76$, $P > 0·5$). Intensity was analysed using a general linear model (SAS statistical software, 1990) with the variables seasons, sex, age, location (Crater/Serengeti) and pride nested in location. Age was used as a continuous variable. The analysis was repeated on a subset of the data from the Serengeti alone using habitat (woodlands *vs.* plains) as an independent variable. Further variables of overall pride size and reproductive status were separately added to the previous model and tested for significance. The result was confirmed in a second model where only the tested variable and the

significant terms from the first model were added. An initial analysis controlled for the following variables that can influence the egg counts: volume of sediment left after centrifugation and sand in each sample. The presence of sand can obscure the presence of cysts and parasite eggs. Samples were classified by eye into 3 categories: sandy, less sandy and not sandy. The degree of dilution of the sediment, after the last centrifugation for extraction from the tube, can influence egg detection as fewer cysts and parasite eggs may be detected if they are less concentrated. The dilution of the sediment was quantified according to the gradient on the Eppendorf tube between 0 and 1·7 ml. As these potentially confounding factors did not show any significant influence in the overall model, they were removed from the analysis. Samples for which information was missing were removed from the analysis (number of samples used in the GLM = 94). A correlation between isoenzyme heterozygosity, using an overall score calculated from 8 loci (Packer *et al.* 1991*b*), and *Spirometra* spp. intensity was tested non-parametrically using a Spearman-rank correlation. The difference in heterozygosity scores between the Crater and the Serengeti was tested using a Wilcoxon-2-sample test (SAS, 1990). In all the analyses the significance level was set at the 5 % level. The figures and the overall prevalence are taken from all the samples which were collected (in contrast to the statistical analysis where repeated samples were not taken into account to avoid any bias due to repeated sampling). Here, if the same animal was sampled repeatedly, mean intensity was taken.

RESULTS

Prevalence of infection

Spirometra spp. had the highest prevalence of all the lion parasites (Müller-Graf, 1995) with a prevalence of 63 % and a median intensity of 975·0 epg (eggs per g of faeces). The distributions of *Spirometra* spp. and the other individual parasite species were over-dispersed, many individuals harboured few parasites and few hosts harboured large numbers of parasites as shown in Fig. 3.

Spatial variation

There was a significant difference between the Serengeti and the Ngorongoro Crater in the mean intensity of infection ($F_{1,67} = 8·42$, $P = 0·005$) with the infection significantly higher in the Crater (adjusted mean intensity Crater = 310·0 epg [mean = 91·55 ± 2·14 s.e.), adjusted mean intensity Serengeti = 12·25 epg (mean = 25·36 ± 1·56 s.e.]). Furthermore, a trend was found for individual prides to differ within location ($F_{19,67} = 1·74$, $P = 0·051$).

However, when analysing the effect of habitat within the Serengeti, no significant effect was observed overall ($F_{1,50} = 0·73$, $P = 0·40$) or at the level of prides within each habitat ($F_{13,50} = 0·96$, $P = 0·50$).

Temporal variation

Infection differed between the seasons ($F_{4,67} = 3·34$, $P = 0·015$). This was particularly due to the first dry season (July 1991–September 1991), which differed significantly from the other seasons ($F_{1,67} = 7·48$, $P = 0·008$). The means adjusted for the other variables in the model for all the seasons were: 1st wet season = 24·7 epg; 1st dry season = 1112·0 epg; 2nd wet season = 18·3 epg; 2nd dry season = 11·8; 3rd wet season = 149·5.

Other factors

There was no significant linear relationship between age and levels of parasite infection ($F_{1,67} = 0·34$, $P = 0·57$). An age–intensity profile describing the relationship between intensity of individual parasite taxa and the age of the host is shown in Fig. 4. Parasite intensity for *Spirometra* spp. was highest in the unweaned cubs, and lower and approximately the same for the other age classes. When comparing the cubs with the other age classes together, a significant difference was found (Mann-Whitney U-test Z corrected for ties = −2·573, $P = 0·01$).

There was no significant difference in *Spirometra* spp. burden between the two sexes ($F_{1,67} = 0·77$, $P = 0·38$). Reproductive status (lactating, pregnant or not) likewise had no influence on the intensity of *Spirometra* spp. ($F_{2,43} = 0·25$, $P = 0·78$; $n = 69$), nor did group size show an impact on levels of infection ($F_{1,66} = 0·11$, $P = 0·74$; $n = 92$). However, the number of females that were pregnant ($n = 5$) or lactating ($n = 11$) may have been too small to reveal significant effects. The model including location, age, sex, seasons and prides within location only explained about half ($r^2 = 0·49$) of the observed variation.

Genetics

The available genetic data were tested for an association with parasite infection. No correlation between the overall score for heterozygosity and *Spirometra* intensity could be observed ($r_s = −0·034$, $P > 0·5$, $n = 28$; Fig. 5). However, even though the Crater individuals show significantly lower levels of heterozygosity than those in the Serengeti (Packer *et al.* 1991), the heterozygosity scores we used for this study were not significantly different between the Serengeti and the Crater (Wilcoxon 2 sample test with continuity correction: Z = −0·783, $P > 0·43$) due to the low number of individuals ($n = 28$) for which parasite and genetic data together had been obtained.
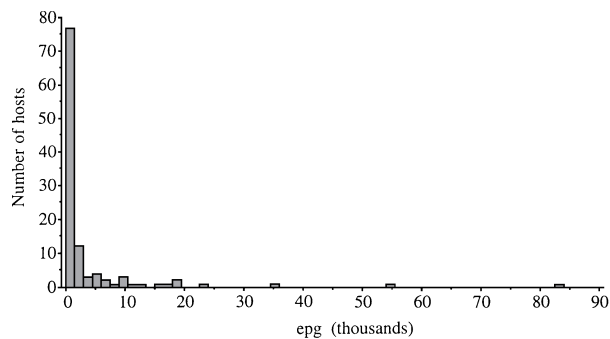
Fig. 3. Frequency distribution of egg output (epg = eggs per g of faeces) of *Spirometra* spp. (arithmetic mean = 3632 epg, s.d. = 10 548). Zero counts are included in the first bar (total number of hosts including uninfected and infected $n = 112$). Bar intervals describe 1500 epg.
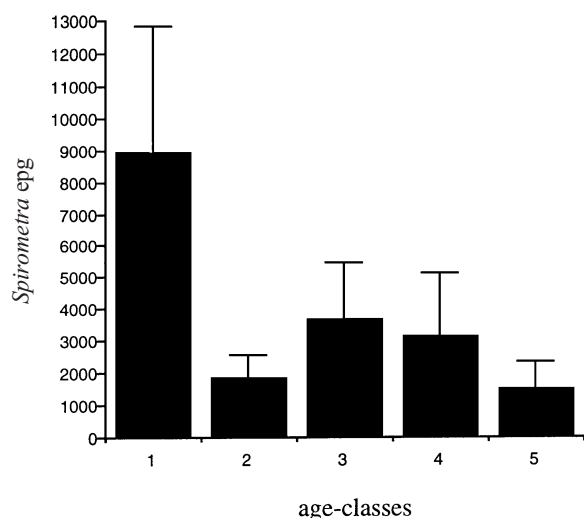

Fig. 4. Age–intensity profile of *Spirometra* spp. Lions were divided into 5 age categories: 1 = unweaned cubs (birth to 8 months, $n = 4$), 2 = subadults (9 months to 2·5 years, $n = 27$), 3 = young adults (2·6 years to 5·5 years, $n = 22$), 4 = middle aged adults (5·6 years to 10·5 years, $n = 28$) and 5 = old individuals (> 10·5 years, $n = 14$). Bars represent standard errors of the mean.
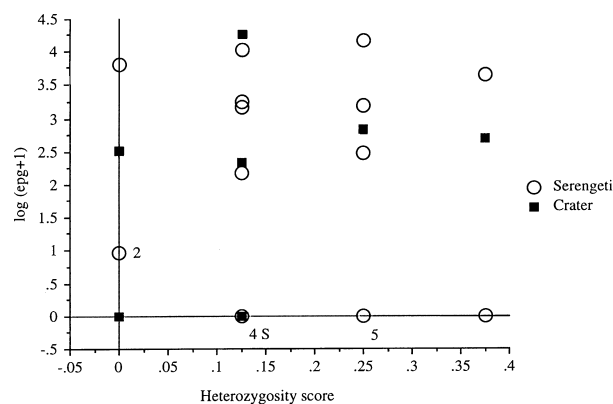

Fig. 5. Heterozygosity scores in relation to *Spirometra* spp. intensity in the Serengeti and the Ngorongoro-Crater. Numbers next to the symbols indicate when more than 1 individual showed the same score ($n = 28$).

DISCUSSION

Infection with *Spirometra* spp. was common in the lion populations, with overall prevalence exceeding 60 % and maximum intensities of infection of tens of thousands of eggs per g of faeces. Across these populations, the distribution of *Spirometra* spp. was overdispersed, a characteristic pattern of most macro-parasite infections, indicating differences in exposure, innate and/or acquired immunity (Anderson, 1978; Anderson & Gordon, 1982; Anderson & May, 1991). Since these may be related to host factors such as age, sex, reproductive status and genetics or to environmental factors such as seasonal changes, the influence of each of these variables was studied. Significant differences in levels of infection between the populations in the Serengeti and the Crater were shown to be most important in the analysis and there was also a trend for prides to differ within localities. Membership to a particular pride accounted for 28 % of the observed variation in intensity and the difference between Serengeti and Crater accounted for 7 % (when sex and age were excluded). The second important factor was temporal variation across the seasons.

Spatial differences

The lions in the Crater showed a higher intensity of *Spirometra* than the lions in the Serengeti. This was a trend in the predicted direction if genetic diversity has an impact. On the other hand, there was no significant relationship between individual levels of allelic heterozygosity and *Spirometra* intensity. However, the number of lions for which genetic and parasitological data were available was smaller than the overall sample size used in this study and a larger sample size is necessary to confirm this result. Furthermore, the scores on heterozygosity used in this study only measure overall heterozygosity for a small set of blood enzyme loci and these may not directly reflect heterozygosity for any locus/loci involved in resistance against these parasites. *Spirometra* – the most common parasite – was further-more the only parasite species which showed a higher intensity in the Crater (Müller-Graf, 1994).

The difference in *Spirometra* infection between the 2 lion populations may also be the result of environmental factors and different habitats. For instance, the higher occurrence of swampy areas in the Crater could provide more transmission oppor-tunities (as the first intermediate host is a copepod) or the high year-round availability of prey (Kruuk, 1972; Packer *et al.* 1988; Hanby *et al.* 1995), which may transmit infection, could lead to a higher transmission rate in the Crater than in the Serengeti.

There was also a trend that prides differed in rates of infection. Differences between prides may be related to habitat or group size (Coté & Poulin,

1994). The effects of group size could not be demonstrated here. *Spirometra* is acquired from prey, so that differences in prey among prides may be reflected in differences in parasite burden among lion prides, since prides share habitats and prey.

Temporal variation

Temporal variation in *Spirometra* was observed between the sampling seasons, but could not be associated with seasonal patterns. Temporal variation may be correlated with other events, such as changes in the population dynamics of the intermediate hosts. Seasonal categories based on rainfall data may not be sensitive enough to detect a pattern of variation and, for example, prey movement may be more important. The longevity of parasites – and therefore continuous high egg production also in the seasons with lower transmission – could further mask seasonal effects.

Other factors

The age–intensity curve showed some association between age and infection. *Spirometra* had a high intensity and prevalence in unweaned cubs. Rapidly rising prevalences imply high transmission rates. Unweaned cubs first eat meat at the age of about 4–6 weeks (Schaller, 1972). Peak parasite burden in cubs may be caused by acquired immunity or lower adult innate susceptibility. However, this result has to be treated with caution because the low number of unweaned cubs may influence the results. Across all ages, there was no correlation between parasite burden and age.

Neither sex nor reproductive status seem to play a role in *Spirometra* distribution. Although male lions have higher testosterone levels (see also Festa-Bianchet, 1990; Zuk, 1990; Folstad & Karter, 1992), a higher white blood cell count and have higher chances of parasitic contact due to greater food intake rates, males did not show higher levels of parasite infection than females.

This study shows that the distribution of parasites in individual lions was overdispersed and thus that there was variability between *Spirometra* spp. egg output between individual lions. Some of this variability was accounted for by differences between the Serengeti and Ngorongoro Crater, and some by differences between prides. It is not possible to distinguish between the influences of ecological and genetic factors in explaining these differences, but, for a subset of lions, there was no detectable influence of allozyme heterozygosity on egg counts. To find out whether there is a systematic difference between natural outbred and inbred populations in terms of parasite infections and in determining whether

Spirometra was influenced more by habitat than inbreeding, there would have to be a wide array of study populations that varied not only in the level of inbreeding but also in aspects of the physical environment that might spread the parasite.

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