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Review articles

The reasons for helminth infections in hosts[1]

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ABSTRACT. A maximum capacity of the host to parasites is very diverse so intensive infections (hiperinfections) are noticed repeatedly. The reasons for their occurrence can be divided based on the factors related to the biology and ecology of hosts: age, body size, food habits, anatomical and behavioral factors, monoxenous life cycle of parasites, environmental changes, contamination of the environment by the dispersion forms of parasites and new parasite-host relationships.

Key words: infections of helminths, intensive infections, helminths

Regulatory mechanisms that are designed to ensure optimal host population size operate in a host organism, thus limiting the number of individual parasites [1].

More than half a century ago, Wiśniewski [2] introduced the concept of a maximum capacity of the host to parasites as a result of adaptation of both host and parasite. These conclusions were based on studies of helminths in the hosts associated with the aquatic environment. The cestodes of aquatic birds were studied and it was noted that in the case of their high abundance in the intestine of the host, two phenomena may occur: growth inhibition of strobila (reducing size and weight) and inhibition of their maturation (limiting reproduction). The higher the intensity of cestodes, the higher the proportion of immature to mature parasites: this relationship is convenient for both the host and the parasite – as it not only helps the parasite species, but also protects the host against its harmful activity. Exceeding of this capacity within the host may cause damage of the host population as well as decreased parasite measurement and fecundity, and the consequences of the parasites' existence may lead to the death of the host.

The reach of the capacity for individual hosts is extremely variable and depends mainly on the measurement, localization, biology, and pathogenicity of parasites as well as the condition and the efficiency of the immune system of the host. It is commonly believed that intestinal parasites, especially small, are less dangerous to the host, and sometimes even intensive infections do not cause symptoms in healthy immunocompetent individuals. For example, in great cormorants *Phalacrocorax carbo*, shot in the breeding colony at the mouth of the Vistula River, the maximum intensity of the small digenean *Petasiger phalacrocoraxi* (2–3 mm in length) was 3300, and the number of the cestode *Paradilepis scolecina* (less than 7 mm in length) was 5773 individuals. Despite such an intensive infection the examined birds appeared to be in good health [3]. In general, more pathogenic are parasites localized in host tissues. An example might be the blood-feeding nematode *Syngamus trachea* – a parasite of the upper respiratory tract of non-aquatic birds: the length of females can reach 20 mm and males 4 mm. It has been shown [4] that these parasites have contributed to the death of 80% of pheasants at a breeding station in Poland, although the intensity of infection was not very high – fewer than 30 pairs of nematodes in an individual host.

There are many factors affecting the intensity of helminth infections. There are parasites which can

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occur individually, e.g. *Diphyllobothrium latum* in human and *Abothrium gadi* in cod, or as two adult individuals, such as the genus *Gyrocotyle* in the rabbit fish, *Chimera monstrosa* [1]. The number of individuals of a particular parasite species in a single infected host depends, among other things on interspecific competition. The presence of one parasite species in the host makes it impossible for the second to settle. A study conducted by Sulgostowska [5] revealed that in the gut of several species of ducks of the genus *Aythya*, it is only very rarely that two species of cestodes of the genus *Diploposthe* – *D. laevis* and *D. bifaria* occur at the same time. Experimental infections have found that these species contain substances which can exert a toxic effect on *Hymenolepis diminuta* [6]. These results suggest that the secretion of active chemical substances by parasites may regulate the numbers of other parasites in the host. It is thought that interspecific competition is more frequent between generalist parasites and intraspecific competition is more frequent between specialist parasites [7]. Intraspecific competition can be illustrated by intestinal nematodes in the cockroach *Periplaneta americana*, which regardless of the dose of infection, always occur as only one female and one male of *Thelastoma bulhoesi* and *Leydinema appendiculatum* [8].

Even in closely related host species, a high degree of specificity is observed in certain parasites e.g., two sympatric species of intertidal crabs (*Pachygrapsus transversus* and *Panopeus lacustris*). Bush et al. [9] suggest distinct differences exist between the compositions of infracommunities of these two host species. *P. transversus* has a richer fauna and *P. lacustris* has more abundant fauna. Both crabs occur in the same tide pools. The omnivore-scavenger *P. transversus* spends more time out of the water and is more active than the subtidal-intertidal *P. lacustris*. During the day, *P. lacustris* hides submerged under rocks, coming into contact with an abundance of snails and pumping more water, and presumably more cercariae, across its gills than *P. transversus*. Host specificity is probably mediated through a form of biochemical-physiological predisposition for the infections [9].

An aggregated parasites distribution means that some hosts „focus” more parasites while others are less infected or not at all. This tendency is related to the biology of parasites that have the ability to reproduce after becoming established in a host e.g., the nematode *Probstmayria vivipara* (Atractidae) is commonly found in horses but also can lead to the significant contamination of the environment such a pasture through the dispersion forms of the parasites. More reasons derive from the host which offers food resources and allows the parasite to avoid immunological defense. There are a few causes of inequality infection of hosts: individual, ecological, social, immunological and genetic [7]. These factors are often interrelated and some of them contribute to the formation of very intensive, almost massive, infections.

The individual factors can be subdivided into: body size, anatomical and behavioral factors, food habits and age of hosts.

Ungulate species such as grazing horses often are infected with small strongyles which are members of the subfamily Cyathostominae. About 40 species cyathostomes (5–20 mm length) parasitize the cecum and colon of horses and it is commonplace to find as many as 15 to 20 of these species infecting an individual host at the same time. Even an apparently healthy horse may be infected with tens or even hundreds of thousands of Cyathostominae [10]. The large dimensions of the organs in which these nematodes live are favourable to massive invasions: colon 6.0–8.0 m long; cecum 0.8–1.3 m long. The heartworm *Dirofilaria immitis* is a species of nematode that frequently occurs in predatory mammals, including dogs. These nematodes can reach up to 30 cm long and occupy usually the right chamber of the heart and the pulmonary arteries of the host. In large animals the intensity of infection can be up to 250 specimens, but in small dogs weighing less than 25 kg, infection with about 50 individuals can have fatal in consequences [11]. Factors related to the anatomy of the hosts can be illustrated by *Aprocta cylindrica* (Spirurida). These nematodes are noticed in the eye sockets and nasal cavity of many Passeriformes (Turdidae, Oriolidae, Muscicapidae and Motacillidae). The birds may well become infected with this parasite on the wintering ground, because *A. cylindrica* in Central and Eastern Europe is found in the hosts usually in the spring months. Numerous studies [12–15] have shown that these nematodes occur in the European robin *Erithacus rubecula* with the highest intensity: up to 36 individuals. The robin is a small migratory bird weighing 16–18 g, mainly insectivorous, with relatively large head and large eye sockets. These anatomical features appear to invite intensive infection by these nematodes. It is hard to imagine, that so many animals can be housed in the organs of this host.

Some species of helminths are found only in young animals because the immune system of host matures with age. These include the nematodes *Parascaris equorum* and *Strongyloides westeri*, noted only in young horses [16]. A special type of infection route is the possibility of transplacental and transmammary transmission of parasites, which can result in intensive infections of to several hundred individuals of *Toxocara canis* in puppies and *T. cati* in kittens. The behaviour of the animals (e.g., food habits) is age related and plays a role in prevalence of infections with endoparasites. Research conducted in the vicinity of Geneva [17] revealed a relationship between red foxes infected with *Echinococcus multilocularis* and both the of hosts and their environment. A few juvenile foxes collected from rural and residential areas, harboured very high burdens up to more than 120000 worms and were significantly more heavily infected than adults, with 64 juveniles harbouring 93.8% and 51 adults harbouring 6.2% of the total worm burden. All foxes infected with more than 55000 worms were juveniles from two to five and a half months-old. The differences in the intensity of infection were found to be associated with the frequency of eating rodents, intermediate hosts of *E. multilocularis*, by foxes.

The diversity of infections of hosts with respect to their age can be demonstrated in the aquatic environment on the example of fish. Borowik [18] notes that the prevalence and intensity of infection of bleak (*Alburnus alburnus*) increases with the age of fish. While metacercaria (e.g. *Posthodiploplostomum cuticula*) predominated in the fry and annual fish, intestinal trematodes (e.g. *Sphaerostomum globiporum*) predominated in two-year olds.

Some passerine birds (Passeriformes), feeding on invertebrates such as snails can be intensively infected with *Leucochloridium* spp. (Digenea). Our previous study [19] revealed the infection of chaffinches (*Fringilla coelebs*) with *L. perturbatum* and blackbirds (*Turdus merula*) with 386 and 734 specimens, respectively. These infections were probably the cause of death of these birds. It is known the Passerines become infected with this parasite by eating the colorful swelling tentacles of *Succinea* sp. snails, where sporocysts are present [1].

Ecological factors play a role when the presence or frequency of occurrence of a parasite depends on the environmental conditions under which the developmental cycle proceed. Johnson and McKenzie [20] studied the effect of environmental factors on the occurrence of infection of amphibians by the digenean metacercariae *Ribeiroia* sp. (Echinostomatida). The first intermediate hosts in the life cycle, aquatic snails in the genera *Planorbella* and *Biomphalaria*, become infected when the eggs hatch into miracidia and invade the tissues of snails. Inside the snail, the miracidia develop into rediae, reproduce asexually, and produce large numbers of mobile cercariae. *Ribeiroia* cercariae preferentially infect and penetrate the tissue surrounding the limbs of amphibian larvae, often causing improper formation of the developing limb bud [21]. These malformations may benefit the parasite by increasing the vulnerability of infected amphibians to definitive host predation: parasite manipulation. These parasites are widespread and sometimes extremely abundant (~1000 metacercariae per frog), generally with a high corresponding frequency of severe malformations in the population [20]. Other authors focused on how environmental change can increase the abundance of these parasites. Johnson et al. [22] found that eutrophication enhanced *Ribeiroia* infection in green frog larvae through two related mechanisms: nutrient- mediated increases in algal growth enhanced both the density of *Ribeiroia* infected snails and the per-snail production of *Ribeiroia* cercariae. Collectively, these changes caused a three- to five-fold increase in metacercerial abundance in co-occurring tadpoles. Furthermore a diverse mixture of pesticides can suppress immune function in amphibians and their exposure may increase the susceptibility of amphibian larvae to infection by cercariae [20].

Gelnar [23] demonstrated experimentally that the growth rate of *Gyrodactylus gobiensis* micropopulations is markedly affected by the physical condition of the host (*Gobio gobio*). A comparison of the mean increase in the number of gyrodactylids parasitizing unfed fish in water with different oxygen concentrations showed that number of parasites increased much more rapidly under conditions of oxygen deficiency than under control conditions.

The reasons of intensive infections of helminths can be biological, ecological and behavioural. Animals associated with an aquatic environment usually are infected with helminths which have heteroxenous life cycles. Quite often they are found in massive invasions of endoparasites due to the availability of intermediate and paratenic hosts. For example, Borgsteede et al. [24] found 25 dead eider ducks (*Somateria mollissima*) on the coast of the North Sea or the Wadden Sea. Extremely intensive infections of helminths were noticed: nematodes – *Amidostomum acutum* (up to 1500 individuals), *Capillaria nyrocinarum* (up to 1700), digeneans – *Cryptocotyle concavum* (up to 10000), *Psilotrema simillimum* (10000), cestodes – Hymenolepididae (4000) and acanthocephalan *Profillicolis botulus* (up to 4000). The authors were uncertain whether the cause of these mass duck deaths was the parasites or perhaps water contamination. The reason for the intensive infections of helminths in these birds could be biological and behavioural factors: the birds feed mainly on bivalve molluscs, particularly cockles (*Cardium edule*) and mussels (*Mytilus edulis*), the ability to dive to 10 meters, and gathering in large groups in marine waters.

An example of the role played by spatial segregation is the degree of helminth infection of European perch *Perca fluviatilis* fry [25]. The authors found a marked difference in infection rates in the 3 spatially segregated subpopulations of perch fry: epipelagic, bathypelagic and littoral perch fry. Parasites were found almost exclusively in the littoral perch fry, which were heavily infected (overall prevalence = 30%) compared with the other studied subpopulations. Kuchta et al. [25] state that these differences are associated with various composition of plankton, the intermediate hosts of parasites, at different depths of the sea.

Due to maladjustment of the parasite and host populations, an uncontrolled increase in the number of parasites and their increased pathogenicity occurs in young evolutionary systems [26]. An example of a new parasite-host relationship is a blood-sucking abomasal nematode *Ashworthius sidemi* – a typical, natural parasite of the Asiatic deer, *Cervus unicolor*, although it is mainly a parasite of sika deer *Cervus nippon*, through which it was introduced into many European countries. *A. sidemi* was first found in Poland in February 1997 in four European bisons from the Bialowieża-Caucasus line, living in the wilderness in the Bieszczady Mountains. In 1999, the parasite was noticed in wild ruminants such as red deer, roe deer and European bison, in the Bieszczady Mountains. In 2000 infection by this parasite was confirmed in bison in the Białowieża Forest. The degree of infection over the years gradually increased and in 2004, the prevalence was 100% with a maximum intensity of 11913 individuals. In subsequent years, the intensity of the infection increased and in 2007, its maximum value was 44310 [27].

The acquisition of new parasites from other hosts, especially in such a unique environment as the zoo, may result in death of animals. A parasitological section of a female Cape giraffe (*Giraffa camelopardalis giraffa*) from a zoo in Spain was performed by Garijo et al. [28]. A total of 2724 nematodes were found. Of the helminths recovered in this study only *Trichuris giraffae* and *Camelostrongylus mentulatus* were reported as occurring in giraffes. The other nematodes occur commonly in mouflons, fallow and red deer, which can usually be found in the same paddock as the giraffes in Aitana Zoo.

Opportunistic infection caused by bacteria, protozoa, fungi and helminths have been recorded in patients with immune deficiency caused by cancer, chronic diseases, immunosuppressive drugs or HIV infection. An example is strongyloidiasis induced by the nematode *Strongyloides stercoralis*. In immunocompetent patients, strongyloidiasis is usually asymptomatic but patients with AIDS may develop hiperinfection of parasite, leading to the consequent death of the host [29,30].

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