Parasite-host relationships of warble fly *(Oedemagena tarandi* L.)[1] and reindeer *(Rangifer tarandus* L.)

A.I. Solomakha

Extreme North Agricultural Research Institute, Norilsk, 663302 USSR

Expanded abstract: Evolutionary adaptation of the warble fly *(Oedemagena tarandi* L.) to parasitism in reindeer has occurred in such a way that survival of the parasite depends completely on the survival of the host. The death ofı the host will thus cause the death of the parasite larvae. Thus the interspecific relations of the warble fly and reindeer have assumed a character of a lenient parasitism. Many researchers note that almost all reindeer are infested by warble fly and reindeer have assumed a character of a lenient parasitism. Many researchers note that almost all domestic reindeer are more heavily infested than wild reindeer. Infestation rates in young domestic reindeer range from 26 to 324 larvae per animal and in young wild reindeer from 15 to 126 larvae per animal (Tables 1, 2) Mature, domestic reindeer are infested with 25 to 417 larvae per animal and in mature wild reindeer the infestation ranges from 38 to 94 larvae per animal (Solomakha 1983). Infestation rates decrease with age. The proportion of young animals which are infested remains in both domestic and wild reindeer constant throughout winter. Young reindeer are, on average, 2 to 4 times more heavily infested than mature animals exept for mature, domestic reindeer treated with ethacide against oedemagenatosis in the previous season in which the rate of infestation may exceed that of juveniles.

Serum antibody titers against warble fly larvae range from 1:4 to 1:16384 in infested reindeer. The intensity of humoral immunity depends upon the age of the reindeer and the developmental stage of the larvae. Antibody titers are higher in reindeer which have endured 3-7 multiple invasions than in juveniles. Antibody titers are lower in mature draught reindeer than in other mature reindeer.

Serum antibody titers ranging from 1:64 to 1:1024 have been discovered before 15 June in newborn calves, which, due to the time of the year, could never have been in contact with warble flies. Serological studies of wild reindeer fetuses have revealed precipitating antibodies against third instar warble larvae in

[1]Editors footnote:
The genus *Oedemagena* has recently been renamed *Hypoderma* (Wood 1987)

Table 1. Infestation rate of warble fly larvae in domestic reindeer.

Year	Reindeer/Age	n	Mean number of larvae
1977	Calves, 8 months	65	119
	Males, 1 year 9 months	29	74
	Males, ≧ 3 year	14	49
	Females, ≧ 3 year	10	76
	Draught reindeer	29	87
1979	Calves, 8 months	10	142
	Males, 1 year 8 months	11	96
	Males, ≧ 3year	4	25
	Females, ≧ 3 year	5	70
	Draught reindeer	4	110
1980	Calves, 8 months	34	34
	Males, ≧3 year	42	29
	Females ≧ 3 year	49	26
1981	Calves, 8 months	7	117
	Males, 1 year 8 months	7	324
	Males, ≧3 year	10	212
	Females, ≧3 year	5	417
1982	Calves, 8 months	6	109
	Males, 1 year 8 months	1	95
	Females, ≧ 3 year	3	163
	Draught reindeer	3	180
1983	Calves, 8 months	16	43
	Males, 1 year 8 months	3	29
	Males, ≧ 3 year	2	50
	Females, ≧ 3 year	10	77

titers varying from 1:40 to 1:5120. Passive hemaglutination tests on milk collected from wild reindeer in June revealed antibodies against water-soluble protein fractions of the hemolymph of third stage larvae with titers ranging from 1:16 to 1:32.

Humoral immune responses can be observed in the zone of contact between larvae and reindeer tissues. Mononuclear leucocytes and cell fragments including nuclei are found in smears made from migrating larvae. At the second stage, when a connective tissue capsule is formed, smears contain principally lymphocytes, plasma cells and macrophages. Some neutrophiles and eosinophiles are also present. At this stage leucocytes accumulate around the larvae and acute granulation tissue containing fibroplasts, macrophages and lymphocytes is

Table 2. Infestation rate or warble fly larvae in wild reindeer.

Age of reindeer (years)	n	Mean number of larvae
1	33	98
2	14	123
3	41	72
4	39	61
5	45	56
6	28	59
7	16	38
8	9	52
9	5	94
10-14	5	80

survival. There are two main types of hemocytes in *O. tarandi* larvae. They differ in their structure and in their ability to stain with azure-eozine. Basophilic hemocytes absorb stain well and their cytoplasm colours blue or bright blue. These hemocytes make up 0.5 - 1.0% of the hemolymph of the first and second stage larvae and 4 - 5% in hemolymph of third stage larvae.

The majority (99.0%) of hemolymph cells in first and second stage larvae and 95 - 96% of the hemolymph cells in the third stage larvae are plasmocytes. These cells have phagocytic and secretory functions. They have characteristic honeycomb structures int the cytoplasm and small nuclei. Small plasmocytes predominant the early stages of the development stages of the larvae. Large plasmocytes are dominant at late stages. These cells are abundant in the hemolymph before the parasitic stage of the flies life cycle in the host organism is complete. Production of large plasmocytes decreases after the larvae have emerged from the fistulae and during the larvae pupation. The plasmocytes disappear totally after seven days. The protective function of the hemocytes is connected with the phagocytosis of the heterogenio-

Table 3. Titers of hemolysins and hemoglutinins in the larval hemolymph.

Date	Number of reindeer	Larval develop-mental stage	Hemolysis or hemoglutination of reindeer erythrocytes by larval hemolymph						
			1:0	1:2	1:4	1:8	1:16	1:32	1:64
23.10 1982	5	I	5	5	5	3	2	—	—
13-15.02 1979	82	II	43	20	1	—	—	—	—
28.06 1980	48	III	48	48	48	46	23	14	7
Protein-free hemolymph	10	III	0	0	0	0	0	0	0

formed. At the third stage, before the end of the parasitic stage, the content of cells in smears consits mostly of polynuclear leucocytes. Simultaneously, an infiltration of leucocytes occurs into the hemolymph of some of the larvae. About 60% of these leucocytes are lymphocytes.

Resistance against the acticve influence of the host immune system is important for larval us substance which penetrates the larvae. Hence, the number of hemocytes increases under the influence of unfavourable factors. In this case, phagocyting hemocytes may be exhausted and thus, the total number of cells in the hemolymph decreases.

In addition to hemocytes, larval defence includes hemoglutinines and hemolysins which agglutinate and hemolyze reindeer erythrocytes. The titer of hemoglutinines and hemolysins in migrating larvae does not exceed 1:16. The titer in third stage larvae reaches 1:64 (Table 3) corresponding with the maximum level of precipitating antibodies against hemolymph antigens in reindeer blood. The secretional function of larval hemocytes increases through both increased size and quantity of secretion drops produced. Increased secretion by the hemocytes is connected with trophic needs and is one of their protection factors. In vitro treatment of the larvae with ethacide results in a decrease of the number of secretion drops produced by the hemocytes within a few hours followed by their complete disappearance.

Serum titers of antibodies increase with increasing age in reindeer. "Camouflage" of the parasite capsule by antigen-antibody complexes promotes survival of the larvae. In addition, larvae have proteolytic enzymes which may destroy immunoglobins with which they come into contact. It is quite probable that larvae may exert an inhibitory effect on their hosts' immune system, thus initiating a sequence of responses promoting the survival of the parasite. In the process of evolution, the host-parasite relationship between reindeer and warble fly larvae has been formed in the way that an interrelation in the larvae-reindeer system developed. For example, warble fly larvae in the subcutaneous tissue excrete products which induce production of specific precipitating antibodies in the host. However, the larvae have the ability to resist the protective factors of the host and to maintain their integrity at the expence of their own cellular and humoral system. After between three and seven invasions the relationship favours the reindeer and the number of infesting larvae decrease with increasing age of the host.

This investigation has revealed previously unknown aspects of the host-parasite relationships between warble fly larvae and reindeer. The results may be useful when the immunobiological relations of the host-parasite system are used for the control of warble flies.

References

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