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Effects of forest management on haematological parameters, blood parasites, and reproductive success of the Siberian tit (*Poecile cinctus*) in northern Finland

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This study aims to investigate whether forest management has an effect on reproduction, haematological parameters and blood parasites of breeding Siberian tits *Poecile cinctus*. Birds breeding in heavily managed forests had significantly higher heterophil and lower lymphocyte concentrations and a higher heterophil/lymphocyte (H/L) ratio than those breeding in moderately managed forests. Although this suggests the increased level of physiological stress in Siberian tits breeding in heavily managed forests, reproductive parameters of the birds did not differ between the two habitats. Nestlings in moderately managed forests had higher total leukocyte and lymphocyte counts than nestlings in heavily managed habitat. The total count of parasites and *Leucocytozoon majoris* was significantly higher near streams, while the count of *Plasmodium circumflexum* was higher both near streams and lakes. Although blood parasites were detected in the blood of 80% adult birds, this study did not reveal any parasite-related effects on haematological parameters.

Introduction

Free-living organisms face a number of stressors which affect their reproductive potential and survival (Ots *et al*. 1998, Tummeleht *et al*. 2006, Catoni *et al*. 2008). A cornerstone concept of ecological immunology is that immune function, plays a central role in the life-history trade-offs between survival and reproduction (Sheldon & Verhulst 1996, Schalk & Forbes 1997, Zuk & Stoehr 2002). Excessive investment in reproduction may result in parental starvation, physical exhaustion, and susceptibility to predation (Lima & Dill 1990) or parasites (Gustafsson *et al.* 1994). The cost of reproduction is often passed on to offspring because of lower per-capita investment in offspring provisioning, which may reduce nestling growth rates, increase competition among siblings, lower fledging body weight as well as investment in immunity (Nilsson & Gardmark 2001, Pap & Márkus 2003).

Destruction of habitats is considered to be the most important factor causing the current species extinction (Fortuna & Bascompte 2006), because habitat loss that is deleterious to populations may have a threshold level, below which the population goes extinct. Around the globe, previously continuous forests have been turned into managed forests, where small forested patches are usually separated by clear-cuts and young successional forests (Gustafsson & Parker 1992). These changes may result in food shortage for animals (Zanette *et al.* 2000, Krams *et al.* 2001). Lack of food may cause chronic physiological stress in individuals (Romero & Wikelski 2001) which often results in suppressed growth and immune system, decreased resistance against diseases (Suorsa *et al.* 2003), all of which may decrease the survival and reproduction of individuals (Wasser *et al.* 1997, Romero & Wikelski 2001, Griesser *et al.* 2007). To describe the environmental effects on different aspects of an individual's physiology and reproductive output, it is necessary to use condition indices that can be easily measured in free-living birds (Ots *et al.* 1998, Kilgas *et al.* 2006, Tummeleht *et al.* 2006, Mänd *et al.* 2007, Davis *et al.* 2008).

The Siberian tit (*Poecile cinctus*), a small insectivorous passerine, is a keystone species in northern taiga forest. It occurs mainly in coniferous forests up to the timber line in conditions which are tolerated by very few bird species (Virkkala & Liehu 1990, Sekov & Germogenov 2006). During the past decades, the old, natural forests had decreased in area and become fragmented, and the population of the Siberian tit had dropped significantly (Järvinen 1982, Virkkala 1987, Veistola *et al.* 1997). It has been shown that the apparent population decline of Siberian tits resulted from the loss of high-quality wintering and breeding habitats (Virkkala & Liehu 1990, Niemi *et al.* 1998). The Siberian tit is a foliage gleaner (Virkkala 1988), and therefore the forest structure is essential for its survival and reproduction. Since the Siberian tit is among those birds which remain true to their hatching area, it makes this species an excellent model for studies testing the relationships between various fitness traits, individual health indices, and changes in habitat quality on a local and population-wide scale.

Our study focused on Siberian tits during the nestling period in managed and semi-natural taiga forests in northern Finland. Our aim was to investigate the reproductive success of these birds and its association with several haematological condition indices as well as composition, prevalence (proportion of infected individuals) and parsitemias (the intensity of infection) of blood parasites. In habitats deteriorated by extensive forestry we expected higher indices of stress in adults and nestlings as well as lower reproductive success. We also tested whether the prevalence of blood parasites and intensity of infections differs between habitats, and whether the parasite load affects the function of the immune system as indicated by the inflammation response.

Material and methods

Study site, study animals, and habitat quality

Our study was conducted in 2007 in the vicinity of Kuusamo (66°N, 29°E) in northern Finland. The dominant tree species in the area is the Scots pine *Pinus sylvestris* which on sandy spoils may occur in mixed stands with the Norway spruce *Picea abies* and on peat spoils with the Downy birch *Betula pubescens*. Siberian tits bred in wooden nest-boxes arranged in lines. All the nest-boxes were checked for several times during breeding season within a long term project carried out by the University of Oulu investigating the ecology of Siberian tits. The total size of our study area was about 100 km^2. Nest-boxes were checked by MH every third day in order to record basic breeding parameters such as clutch size, brood size and the number of fledglings. Breeding adult Siberian tits were captured within their nest boxes (n = 23) from 17 June to 21 June 2007 when their nestlings were at the age of 9–12 days and reaching their maximum rate of growth. Nest boxes containing younger (1–5 days old) blind nestlings were not included in this study. No nests were deserted due to our activities. All of the breeding individuals were banded with metal and individual plastic rings. Sex and age of marked birds was known from previous seasons or was accessed by the presence of incubation patch in females.

We studied Siberian tits in two main patches of northern taiga which differed in structure and conservation status due to management practices: (i) moderately managed forests, and (ii) heavily managed areas. The heavily managed areas had been thinned heavily, leaving only middle-sized 40–60 years old pines with no understorey. The moderately managed areas included both areas thinned at least a decade ago and patches of old growth coniferous forests (Virkkala 1990) consisting of pines, spruces and an admixture of birches. The moderately managed forests (n = 12) also comprised many dead trees which increased the quality of habitat for Siberian tits (Virkkala 1990, Orell *et al*. 1999) while dead trees were almost absent in the heavily managed forests (n = 11). Both habitat types were represented by forest massives or patches of at least 45 ha in size. Due to the low density of Siberian tits, the nest boxes occupied by the birds were at least 1 km apart, and we never used more than one nest box in the same forest massive or patch. Since the distribution of Siberian tits was uneven because of clear-cut areas, bogs and agricultural land, and the average distance between two neighbouring nest boxes was 3.94 ± 1.56 (mean ± SE) km, we considered each nest box as an independent data point. All of the spatial data were collected by GPS (Global Positioning Systems, Trimble).

Haematological parameters

The blood samples were taken from 45 Siberian tits (23 males and 22 females) by following the recommendations of Bennett (1970). For identification of blood parasites and leukocytes, from each individual Siberian tit a drop of blood was obtained by puncturing the tarsal vein and then smeared on three individually marked microscope slides. The blood samples were also taken from nestlings in both habitats. We randomly selected 1–3 nestlings in each nest box and obtained samples from 25 nestlings in the moderately managed habitat and from 26 individuals in the heavily depleted habitat.

Smears were air-dried in the field and immediately fixed with methanol and subsequently stained using Gimsa stain. Proportions of different types of leukocytes were assessed on the basis of examination of a total of 100 leukocytes from each of the three slides under oil immersion at 1000× magnification. The total white blood cell count (WBC) was estimated by counting the number of leukocytes per approximately 10 000 erythrocytes (Ots *et al*. 1998). For this purpose, all leukocytes were counted in 100 microscope fields, counting both leukocytes and erythrocytes. Concentration of leukocytes per number of red blood cells was obtained by multiplying proportions of different leukocytes with WBC. The repeatability of leukocyte concentrations obtained from repeated scannings of the same blood smear by DC and TK were high (r = 0.92, 0.91, 0.90, and 0.89 for heterophil concentration, heterophil/lymphocyte (H/L) ratio, WBC, and lymphocyte concentration, respectively; all p's < 0.001). Similar methods for estimating leukocyte concentration have been used by Saino *et al*. (1997).

Total white blood cell count (WBC) is the number of leukocytes per approximately 10 000 erythrocytes. Elevated leukocyte number is symptomatic of stress syndrome and inflammatory processes (Davis *et al*. 2008). Usually, leukocytosis is caused by an elevated concentration of heterophils and/or lymphocytes (Dein 1986, Ots *et al*. 1998). Lymphocytes are immune cells that assist in the recognition and destruction of many types of pathogens. The lymphocyte concentration in peripheral blood can be used as an indirect measure of cell-mediated immunity (Davis *et al*. 2008, Fahey & Cheng 2008). Although sometimes its value is difficult to interpret, decreased lymphocyte concentrations may signal stress-induced immunosupression (Hõrak *et al*. 1999), or may indicate the lack of parasite infections (Ots & Hõrak 1998). Heterophils are non-specific phagocytosing cells that enter the tissues during inflammatory processes. The production of reactive oxidants by heterophils during inflammation can be harmful to host tissues (Davis *et al*. 2008). Heterophil concentrations increase during inflammatory processes, stress and infections (Ots *et al*. 1998). The heterophil/lymphocyte ratio (H/L ratio) is a widely used indicator of stress and it increases in response to various stressors like infectious diseases, starvation and reproductive effort (Ots & Hõrak 1998, Moreno *et al*. 2002, Davis *et al*. 2008). Eosinophil number increases sharply in certain diseases (Davies *et al*. 2008). Eosinophils are cytotoxic, releasing the content of their granules on the invader.

In this study, we did not collect any data on the wing and tarsus lengths of adult Siberian tits. Since we also did not analyze bird blood for hematocrit and such haemato-serological indices as total plasma protein, triglycerides, free fatty acids, uric acid and plasma carotenoids, we have no data on an individual body condition of Siberian tits (Ots & Hõrak 1998).

Blood parasites

After being scanned for total number and proportion of different types of leukocytes, smears were screened with a light microscope under oil immersion at 1000× magnification for *Haemaproteus* and *Plasmodium* and at 500× magnification for *Leucocytozoon*, *Trypanosoma* and *Microfilaria*. Parasites were enumerated from 100 fields by moving the slide to areas where blood cells formed a monolayer for *Lecocytozoon* and from more than 200 fields for *Haemaproteus* and *Plasmodium*. Slides were screened by T.K. and T.I. Individuals were classified as infected when smears were positive for at least one hemoparasite taxon.

Statistical analysis

Values of blood cell concentrations in nestlings were not distributed normally and were log-transformed. All other trait values such as blood cell concentrations of adult birds and parasite counts were normally distributed (one-sample Kolmogorov-Smirnov test) which allowed us to use parametric statistical procedures.

Leukocyte concentrations and parasites loads in male and female Siberian tits in both habitats were analysed by using GLM models. The inclusion of number of nestlings as a covariate in the models did not change the results and, since that covariate itself remained always non-significant, we dropped it from final models. In our study, most of the birds in moderately (10 males and 11 females) and in heavily managed habitats (9 males and 11 females) were yearling individuals, thus we did not investigate any age-related effects. While collecting blood smears from nestlings, we occasionally sampled more than one nestling per a nest. To avoid pseudoreplication we analyzed the data with a mixed-model design with habitat as fixed factor and nest identity as random factor.

Results

Reproductive success

We did not find any differences between moderately (n = 12) and heavily managed habitats (n = 11) in the clutch size, number of nestlings and number of fledglings (Table 1). In the heavily managed habitat one nest box was destroyed by local people, and nestlings starved or froze to death in another nest box, while in the moderately managed habitat nestlings starved or froze to death in one nest box and in another nest box

Table 1. The reproductive success of pairs of Siberian tits breeding in moderately managed (n = 12) and heavily managed forests (n = 11).

	Eggs					Nestlings					Fledglings				
Habitat	Mean	SD	df	*F*	*p*	Mean	SD	df	*F*	*p*	Mean	SD	df	*F*	*p*
Moderately managed	8.50	1.09	1	0.35	0.56	8.33	0.98	1	0.31	0.086	6.92	3.42	1	0.021	0.89
Heavily managed	8.50	1.17				8.25	1.06				6.83	2.95			

only two out of seven nestlings survived due to disappearance of the male. All these cases occurred during the last four to five days of the nestling phase.

Leukocytes of adults

The main effects of habitat, sex and total parasite count on the total counts of white blood cells were not significant indicating that the number of leukocytes was similar in Siberian tits breeding in moderately managed and heavily managed forests (Tables 2 and 3). However, Siberian tits breeding in heavily managed forests had more heterophils than those breeding in moderately managed forests. Sex, total count of parasites, habitat and sex, habitat and parasite interactions had no effect on heterophil concentrations (Table 3). Although lymphocyte concentrations differed between the two contrasting habitats (Table 2), we did not find a significant effect of sex, total parasite count, habitat and sex, habitat and parasite interactions (Table 3). However, the main effects of habitat and sex were highly significant on the H/L ratio. As a measure of environmental stress, this ratio was found to be higher in heavily managed habitats and it was significantly higher in females than in males (Tables 2 and 3). The habitat and sex interaction also was found to be highly significant on the H/L ratios (Table 3).

We found a significant difference in eosinophil concentrations between habitats and sexes (Tables 2 and 3). We also found a significant habitat and sex interaction indicating sex-related differences in concentration of eosinophiles in different habitats. The concentration of eosinophiles was found to be considerably higher in 3 males and 1 female breeding in heavily managed forest suggesting a possible effect of an infectious disease in these individuals.

Leukocytes of nestlings

Nestlings from moderately managed forest had significantly higher counts of white blood cells than nestlings from heavily managed forests (mixed-model ANOVA: $F_{1,21} = 8.62$, $p = 0.008$,

Table 2. Haematological parameters of adult Siberian tits caring for their nestlings in moderately managed and heavily managed habitats.

Sex/Habitat	Total white blood cell count (WBC)			Heterophils			Lymphocytes			Heterophils/ lymphocytes (H/L)			Eosynophils		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
Males															
Moderately managed	16.56	13.88	12	7.08	4.17	12	82.92	7.68	12	0.08	0.05	12	8.58	9.00	12
Heavily managed	12.68	5.67	10	14.30	5.79	10	57.80	16.12	10	0.25	0.17	10	21.70	20.13	10
Females															
Moderately managed	11.96	14.42	12	6.67	3.68	12	79.67	6.78	12	0.09	0.05	12	9.33	5.73	12
Heavily managed	16.5	12.29	11	36.40	9.14	11	50.80	12.43	11	0.64	0.43	11	13.00	8.39	11

Table 3. The effects of habitat, sex and total count of parasites on haematological parameters of breeding Siberian tits (a mixed-model GLM with habitat as fixed factor and nest identity as random factor).

	Total white blood cell count (WBC)				Heterophils				Lymphocytes				Heterophils/ lymphocytes (H/L)				Eosinophils			
	df	MS	*F*	*p*	df	MS	*F*	*p*	df	MS	*F*	*p*	df	MS	*F*	*p*	df	MS	*F*	*p*
Habitat	1,28	413.01	3.12	0.09	1,28	2178.56	31.58	0.001	1,28	2318.76	31.04	0.001	1,28	0.51	15.00	0.01	1,28	603.16	5.87	0.02
Sex	1,28	1.67	0.01	0.91	1,28	50.10	0.73	0.41	1,28	51.28	0.73	0.40	1,28	0.06	4.43	0.03	1,28	567.88	5.53	0.026
Parasites	4,28	405.49	2.81	0.08	4,28	17.14	0.25	0.91	4,28	16.82	0.24	0.91	4,28	0.01	1.22	0.97	4,28	323.64	2.99	0.06
Habitat × sex	1,28	391.19	2.96	0.10	1,28	49.07	0.71	0.41	1,28	50.40	0.72	0.41	1,28	0.45	5.02	0.02	1,28	699.52	6.81	0.01
Habitat × parasites	3,28	187.53	1.61	0.36	3,28	19.63	0.29	0.84	3,28	19.15	0.27	0.85	3,28	0.01	0.10	0.96	3,28	43.35	0.42	0.74

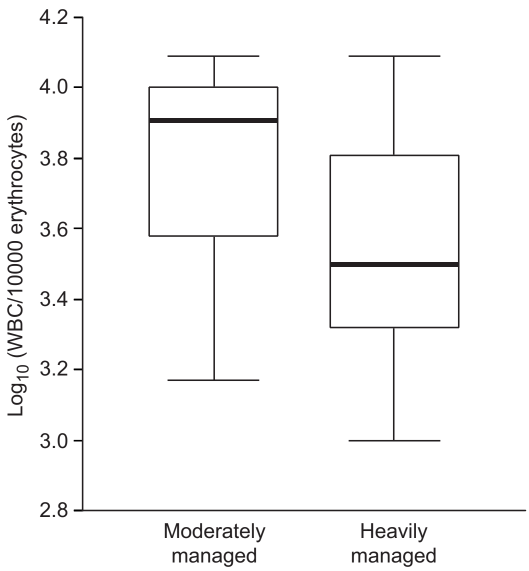

Fig. 1. Box-and-whisker plot (thick bar = median, box = interquartile range, whiskers = full value range) of total counts of white blood cells of Siberian tit nestlings at the age of 9–12 days in moderately managed and heavily managed habitats.

Fig. 1). Concentrations of lymphocytes was higher in nestlings from moderately managed habitat (mixed-model ANOVA: $F_{1,21} = 9.27$, $p = 0.006$, Fig. 2). Conversely, heterophil concentration of nestlings (1.55 ± 0.88 *vs*. 1.21 ± 0.89 $\log_{10}$(heterophils/10^4 erythrocytes, mean ± SD) and the nestling H/L ratio (–1.94 ± 0.85 *vs*. –1.95 ± 1.03 $\log_{10}$(H/L, mean ± SD) did not differ between the contrasting habitats (mixed-model ANOVA: $F_{1,21} = 2.62$, $p = 0.12$ for heterophil concentration, and $F_{1,21} = 0.001$, $p = 0.99$ for H/L).

Blood parasites

In our samples we found the following blood parasites: *Leucocytozoon majoris*, *Plasmodium circumflexum*, *Trypanosoma* spp., *Haemaproteus majoris*, *Hepatozoon* spp. (Table 4). The majority ($n = 32$) of the birds were infected by *Leucocytozoon majoris* and most of the infected individuals (26 out of 36 individuals) had single infections. In 6 cases, Siberian tits sustained double infections and triple infections in 4 cases (Table 4). Females and males did not differ in the levels of double (3 males and 3 females) and triple (2 males and 2 females) infections. *Trypanosoma* never occurred in single infections and in all cases (n = 9) they were found together with *Leucocytozoon majoris* suggesting the same vector for both parasites.

Blood parasites were detected in the blood of 80% of 45 parent Siberian tits (36 infected and in 9 individuals infections were undetected) while the level of parasitemia was low in all of our samples. Although among 36 infected birds there were 21 males (58.3%) and 15 females (41.7%), total parasite prevalence did not differ between sexes (χ^2 = 3.75, p = 0.11, Yate's correction, Table 5). We did not detect blood parasites in 7 females (77.8%) and in 2 males out of 9 individuals (22.2%). However, this did not make sexes different with the respect to parasite absence because of 2 × 2 table design where frequencies for male/female infected/undetected infections were tested.

A GLM analysis revealed that the total count of parasites, *Leucocytozoon majoris* and *Plasmodium circumflexum* counts were not affected by habitat and sex (Table 5). However, the risk of being infected by *Leucocytozoon* significantly increased with the decreasing distance to the nearest stream (Table 5). We found the same effect in the case of the total parasite count, while the risk of infection by *Plasmodium* significantly increased with decreasing distance both to streams and lakes (Table 5). Other factors and their interactions did not have a significant effect on the total count of parasites and counts of *Plasmodium* and *Leucocytozoon*. The prevalence of *Haemaproteus majoris*, *Trypanosoma* spp and *Hepatozoon* spp. was too low to perform a GLM analysis.

Discussion

Despite the low sample size, which is a characteristic of studies on the Siberian tit (e.g. Haftorn 1973, Järvinen 1982, Virkkala 1990), our results clearly show that Siberian tits breeding in heavily managed forests have a higher concentration of heterophils, lower lymphocyte concentrations (Fig. 2), higher stress-related H/L ratios and higher eosinophily (Table 2) than individuals breeding in moderately managed forests. While the elevated level of the H/L ratio serves as a reliable indicator of stress (Davis *et al*. 2008), higher eosinophily usually indicates a presence of infection diseases (Dein 1986). This shows that Siberian tits breeding in moderately managed forests may be in a better health condition as compared with the individuals breeding in heavily managed forests, suggesting a link between habitat use and level of physiological stress. In this respect, our findings support the

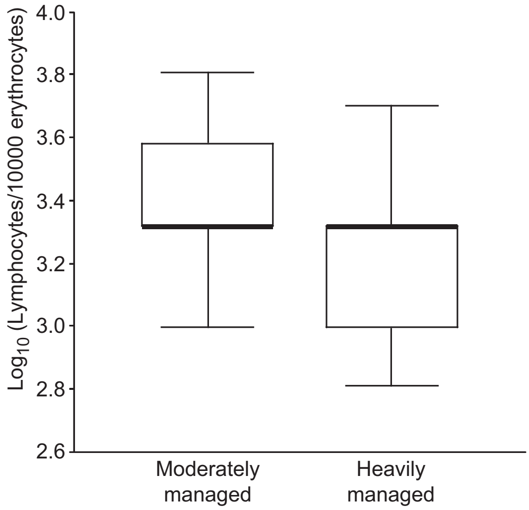

Fig. 2. Box-and-whisker plot (thick bar = median, box = interquartile range, whiskers = full value range) of lymphocyte concentrations of nestlings of Siberian tits at the age of 9–12 days in moderately managed and heavily managed habitats.

Table 4. Prevalence of single, double and triple infections of blood parasites in Siberian tits regarding to individual's sex.

Single/combined infections	Males	Females
Leucocytozoon	13	9
Trypanosoma spp.	0	0
Plasmodium circumflexum	1	1
Haemaproteus majoris	0	0
Hepatozoon spp.	2	0
Leucocytozoon × *Trypanosoma* spp	4	1
Leucocytozoon		
× *Haemaproteus majoris*	0	1
Leucocytozoon		
× *Trypanosoma* spp.		
× *Plasmodium circumflexum*	1	3
Total	21	15

results of those few studies which used haematological parameters to examine adult condition variation in relation to forest loss or fragmentation. These studies revealed a negative impact of habitat deterioration on a health condition and reproductive success of breeding individuals in areas affected by modern forestry (Saari *et al*. 1994, Suorsa *et al*. 2003, 2004). However, while heavily managed areas are supposed to be suboptimal habitat in terms of offspring production, nesting success and fledgling size (Virkkala 1990), we did not find significant differences in breeding success between Siberian tits breeding in the moderately managed forests and the heavily managed forests (Table 1). This result could be explained by the fact that the climate conditions were rather mild and stable during the course of our study which supposedly reduced physiological stress and improved reproductive success in heavily managed habitats. However, we found that the condition of adult Siberian tits was passed on to offspring which resulted in a better condition of nestlings in moderately managed habitat as indicated by higher lymphocyte concentration (Hõrak *et al* 1999). Overall, the results of this study show that Siberian tits have to sacrifice their health in order to reproduce in such sub-optimal habitat as highly managed forests (Wiersma *et al*. 2004) yet, at least in mild weather conditions, the lower habitat quality does not necessarily result in reduced reproductive success.

Higher stress-related H/L ratios, the increased eosinophily in adults and lower lymphocyte concentration in nestling Siberian tits in highly managed forests might be due to lower availability of food resources in this habitat. Jansson *et al* (1981) and Krams *et al*. (2001) observed that for willow tits (*Poecile montanus*) and crested tits (*Lophophanes cristatus*) food abundance was crucial for winter survival, and that it also limited the size of the breeding population in spring. In the breeding season Siberian tits prefer areas having more birches and large coniferous trees (Virkkala & Liehu 1990) which were abundant in patches of moderately managed forests. These preferences are probably due to more arthropods available to the foliage-gleaning Siberian tit (Hågvar 1976, Virkkala 1988, Virkkala & Liehu 1990). Since the winter and breeding densities of Siberian tits are low in managed pine forests (Virkkala 1987), it is possible that a year-round shortage of feeding resources restricts tits nesting in heavily deteriorated forests. The future studies should deal with availability of food resources of Siberian tits and the role of food in the interplay among reproductive effort, adult physiological stress, nestling condition and survival under different climate conditions.

We found that the H/L ratio and eosinophils showed remarkable variation between sexes indicating different stress levels among males and females (Table 3). The H/L ratio of males was significantly higher in heavily managed forest than in moderately managed forests while the H/L ratio of females was found to be twofold higher than that of males in heavily managed forests (Table 2). Thus, females in this study seemed to be in a poorer health condition than males (Hõrak *et al* 1999, Ots *et al*. 1998). It is possible that these differences are related to egg laying and incubation costs in females, and that either different endocrine profiles between sexes or the greater contribution of females to offspring rearing are behind the observed sex differences in the H/L ratio (Sanz *et al*. 2000,

Table 5. The effects of habitat, sex, distance to the nearest lake and distance to the nearest stream on the blood parasite abundance of breeding Siberian tits (GLM analysis). The closest distance from bogs and streams was calculated by using GPS (Global Positioning Systems).

	Total parasite count				*Leucocytozoon majoris*				*Plasmodium circumflexum*			
	df	MS	*F*	*p*	df	MS	*F*	*p*	df	MS	*F*	*p*
Habitat	1,13	0.24	0.59	0.45	1,13	0.01	0.11	0.75	1,13	0.14	3.69	0.08
Sex	1,13	0.19	0.45	0.51	1,13	0.15	1.14	0.31	1,13	0.02	0.58	0.46
Distance to lake	2,13	0	0.0001	1.00	2,13	1.33	2.69	0.07	2,13	0.33	8.67	0.004
Distance to stream	6,13	1.56	3.79	0.02	6,13	1.71	13.3	0.001	6,13	0.22	5.78	0.004

Visser & Lessells 2001, Wingfield & Kitaysky 2002, Kilgas *et al*. 2006). The reason for the elevated concentration of eosinophils found in the samples of three males may be explained by the fact that males, as compared with females, are generally considered to have reduced immune responses (Poulin 1996, Moreno *et al*. 2002, Zuk & Stoehr 2002). Since we found a significant effect of sex and habitat and sex interaction on concentration of eosinophils, this reveals a significant impact of habitat on immunity of breeding Siberian tits. In future, it should be tested whether habitat-related immune responses could be linked to the species decline in habitats deteriorated by the modern forestry.

It is usually considered that blood parasites provoke chronic infections in the wild with relapses during stressful situations for the hosts (Atkinson *et al*. 1988, Bennett *et al*. 1995) especially during breeding season (Merino *et al*. 2000, Shutler *et al*. 2004) which is energy- and time-demanding. Food limitation and exhaustion while provisioning food for nestlings require greater investments in each breeding attempt on the northern latitudes (Virkkala 1990, Sanz *et al*. 2000, Rytkönen & Orell 2001, Rytkönen & Krams 2003). Therefore, northern birds are expected to be more stressed during breeding season, which may result in suppressed immune function (Silverin *et al*. 1997) because of prolonged corticosterone exposure which in turn may lead to higher intensity of parasite infection (Sheldon & Verhulst 1996, Boonekamp *et al*. 2008). However, the findings of our study, which is the first parasitological study on the Siberian tits, do not suggest any direct link between haematological parameters, habitat and blood parasite counts in Siberian tits breeding in northern Finland. This is a surprising result especially given the high densities of parasite vectors in northern Finland. It can be admitted that blood parasites of Siberian tits do not reduce parental working capacity of the birds while feeding nestlings as in other tit species (Merino *et al*. 2000). On the other hand, it is usually considered that it is easier for blood parasites to invade the peripheral blood of individuals whose immunity is impaired. However, we did not find such a relationship in the Siberian tit suggesting that the activated immune system of the breeding birds may considerably decrease parasite numbers in the peripheral blood.

Recent studies have shown higher blood parasite prevalence in mature and well preserved forests rather than in degraded or heavily managed forests suggesting that habitat structure may affect the density of different parasites or their vectors (Bonneaud *et al*. 2009, Chasar *et al*. 2009). Our results, however, clearly show that the total abundance of blood parasites and *Leucocytozoon* counts are more related to the distance to the nearest streams (Table 5) where the parasite vectors, such as simuliid flies (Diptera: Siimulidae), reproduce (Hellgren *et al*. 2008). *Plasmodium* counts were found to be higher in the vicinity of lakes and small streams where blood-sucking mosquitoes (Diptera: Culicidae), vectors of malaria parasites in birds, reproduce. Thus, the results of this study do not support the notion that mature and less degraded forests support higher prevalence of blood parasites. It is likely that the numbers of simuliid blackflies and mosquitoes are much more dependent on availability of their breeding sites rather on the age or structure of forest habitat.

Finally, there are many reports from all over the world revealing noticeable differences in bird blood parasite geographical prevalence (Merilä *et al*. 1995, Rintamäki *et al*. 2000, Altizer *et al*. 2004, Valkiūans 2005, Sehgal *et al*. 2006). Although the diversity of blood parasites of birds has been found to be higher in tropical areas, the prevalence seems to be highest at higher latitudes (Valkiūans 2005). The fact that *Leucocytozoon* and *Trypanosoma* parasites always occurred together (Table 4) enables us to assert that both types of blood parasites may be transmitted by the same vector, supposedly by the blood-sucking simuliid blackflies (Hellgren *et al*. 2008). *Trypanosoma* infection can also be transmitted by other vectors such as biting midges (*Culicoides* spp.) and blood-sucking mosquitoes which are vectors of *Plasmodium* and *Haemaproteus* parasites (Valkiūans 2005). All of these vectors are abundant in northern Scandinavia (Alder *et al*. 1999), thus, the parasite prevalence found to be as high as 80% is not surprising in Siberian tits. Overall, the first parasitological study on the Siberian tits did not reveal any direct link between haematological parameters, habitat and blood parasite counts in birds breeding in northern Finland, which suggests a more complex relationship between the immune system and parasites deserving a more detailed research in the future.

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