Influence of parasites on fitness parameters of the European hedgehog (*Erinaceus europaeus*)

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For my mother and my sister –
the strongest influences in my life

“Nose-to-nose with a hedgehog, you get a chance to look into its eyes and glimpse a spark of truly wildlife.”

(HUGH WARWICK, 2008)

„Madame Michel besitzt die Eleganz des Igels: außen mit Stacheln gepanzert, eine echte Festung, aber ich ahne vage, dass sie innen auf genauso einfache Art raffiniert ist wie die Igel, diese kleinen Tiere, die nur scheinbar träge, entschieden ungesellig und schrecklich elegant sind.“

(MURIEL BARBERY, 2008)

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Abstract

The European hedgehog *Erinaceus europaeus* is a popular component of rural, suburban and urban habitats and as a synanthropic species it is closely associated with human environments. After the Bern Convention from 1979 the protection of hedgehogs has to be ensured by law by the member states of the Council of Europe. Therefore, studies which consider new aspects of the ecology and behaviour of these animals are of high importance. Unfortunately, no research on this topic has been conducted in Germany so far. Studies from Great Britain from the last two decades, however, report the decline of hedgehog populations by about 7.5% per year. Mainly anthropogenic factors appear to be responsible for the decline, but climatic changes as well as other biotic and abiotic factors also have to be taken into account. Hedgehogs only have a few natural predators, but they harbour a wide variety of different parasites and pathogens. These impose energetic costs on their hosts leading to increased morbidity and mortality and decreased reproductive success. Therefore, it is possible that they play an important role both for the individual as well as for hedgehog populations.

The aim of my work was to obtain basic information on the influence of parasites on the morbidity and reproductive ability of hedgehogs. I approached this goal by focusing firstly at a specific level on the influence of a certain ectoparasite group (ticks), and secondly at a more general level by including the whole macroparasite community of hedgehogs, this representing more natural conditions.

At the specific level, I investigated the influence of ticks on host morbidity using blood physiological parameters by measuring stress levels, reproductive ability and haematological values in an experimental hedgehog population over a period of three years. At the general level, I examined the influence of the whole parasite community on the morbidity and reproductive success of dissected hedgehogs from heavily infected populations from Germany and the UK and lightly infected populations from New Zealand.

The results from the experimental population showed that tick-induced blood loss led to a regenerative anaemia in the hedgehogs, resulting in a reallocation of energy from growth and reproduction to processes of regeneration and immunity. This is a potential life threat for already weakened hedgehogs with a compromised immune system. In combination with biotic and abiotic factors acting as co-stressors, tick-induced blood loss can also be critical for healthy hedgehogs, especially during periods of high stress, such as the breeding season or hibernation, when survival success can be significantly reduced.

At a more general level, hedgehog dissections revealed the negative influence of intestinal *Capillaria* spp. infections on the body condition both in the European and the New Zealand populations including an indirect negative impact on potential reproductive success, measured as the weight of sexual organs. The sexual organ mass was positively correlated with body condition, indicating that healthy hedgehogs can invest more energy in these organs and as a result also more into reproduction.

The effect of the parasites might be increased, especially in combination with environmental alterations like climatic change and anthropogenic influences like habitat fragmentation or destruction. In wild populations this may decrease the survival and also reproductive success and might lead to the decline of hedgehogs in their natural habitats.

Zusammenfassung

Der Europäische Igel *Erinaceus europaeus* ist ein gern gesehener Bestandteil ländlicher, suburbaner und urbaner Habitate und sein Schutz ist in den Mitgliedsstaaten des Europarats gesetzlich verankert. Daher sind Studien, die neue Aspekte der Ökologie und des Verhaltens dieser Tiere berücksichtigen von hoher Bedeutung. In Deutschland wurden solche Untersuchungen bisher nicht durchgeführt, britische Studien der letzten zwei Jahrzehnte haben dagegen ergeben, dass sich die Populationsdichte von Igeln durchschnittlich um 7,5% pro Jahr verringert. Dafür scheinen hauptsächlich anthropogene Faktoren verantwortlich zu sein, aber auch andere abiotische und biotische Parameter werden für den Populationsrückgang in Betracht gezogen. Da Igel nur wenige natürliche Feinde haben, aber eine Vielzahl verschiedener Parasiten beherbergen, die einen negativen Einfluss auf Morbidität, Mortalität und den reproduktiven Erfolg ihrer Wirte haben, ist es wahrscheinlich, dass sie eine bedeutende Rolle für das einzelne Tier aber auch für ganze Igelpopulationen spielen.

Das Ziel meiner Arbeit war es, grundlegende Informationen über den Einfluss von Parasiten auf fitnessbezogene Parameter des Europäischen Igels zu erhalten. Dieses Ziel wollte ich auf zwei Wegen erreichen. Zunächst habe ich auf einer spezifischen Ebene den Einfluss einer Parasitengruppen, der Zecken, auf blutphysiologische Parameter untersucht, indem ich Stresslevel, Reproduktionsfähigkeit und hämatologische Werte von Igeln einer experimentellen Population analysiert habe. Zusätzlich habe ich auf einer allgemeineren Ebene, die eher natürlichen Bedingungen entspricht, den Einfluss der gesamten Makroparasitengemeinschaft auf Morbidität und Reproduktionserfolg anhand von Sektionsigeln stark infizierter Populationen aus Deutschland und Großbritannien und schwach infizierter Populationen aus Neuseeland untersucht.

Sowohl bei der experimentellen Population als auch bei den Sektionstieren konnte ich mit meinen Ergebnissen deutlich zeigen, dass Parasiten die Fitness des Igels negativ beeinflussen und dadurch den potentiellen Reproduktions- und Überlebenserfolg reduzieren.

Dieser negative Einfluss von Parasiten kann in Verbindung mit Veränderungen der Umwelt, beispielsweise Klimaveränderungen und anthropogenen Einflüssen wie Habitatsfragmentierung, verstärkt werden. Dadurch verringern sich die Überlebenschancen und der reproduktive Erfolg wilder Igel, was zum Rückgang von Igelpopulationen führen kann.

I. Introduction

1. Parasitism

Parasitism is one of the most successful life models on our planet. At least 50% of all plants and animals are parasitic at some stage during their life cycle (BUSH et al. 2002), and the diversity of parasites exceeds that of free-living species. KURIS et al. (2008) showed e.g. that in three estuaries of the Pacific Coast of California the biomass of parasites is greater than that of the top predators, sea birds, and that the parasitic trematode biomass is comparable to the biomass of birds, fish, burrowing shrimps and polychaetes. Thus it is not surprising that parasites play an important role in the biodiversity of free-living species and their ecosystems by influencing their hosts. This influence can be roughly divided into influence at the individual, the population, and the community level.

At the individual level a parasite can increase mortality and morbidity or decrease the reproductive success of a single host. In the definitive host mortality is often caused by microparasites, parasites that undergo direct multiplication within their hosts like viruses, bacteria and protozoans. In intermediate hosts mortality is increased by parasite-induced changes in fitness, behaviour or phenotype, which enhances the risk of being caught by a predator (LAFFERTY and MORRIS 1996, BAKKER et al. 1997, TARASCHEWSKI 2006a). These effects can also be induced by macroparasites.

Macroparasites like ticks, fleas or helminths tend to cause morbidity rather than mortality in their definitive host (TOMPKINS et al. 2006). This might occur through mechanical damage due to penetration of the hosts tissue (intra- or extracellular) or a body cavity like the intestinal tract, so that the physical presence of the parasite disturbs the local homeostatic balance. Some features of parasites like hooks or biting mouth parts damage the penetrated cell immediately, causing swelling and inflammation (CHERNIN 2000). Penetration might also cause blockages. Heavy infections with the nematode *Ascaris lumbricoides* in children can e.g. block the small and large intestine (CHERNIN 2000). Increased morbidity in combination with co-stressors like environmental (pollutants, habitat fragmentation, extreme temperatures) or social factors (rut, territorial behaviour) can also lead to mortality (TARASCHEWSKI 2006a).

The influence on reproduction can either be indirect or direct. Indirect influence is caused by the reallocation of energy resources. The parasites obtain their essential nutrients directly from their host (blood, lymph, cytoplasm, tissue, fluids, and host-digested food) which then fails in the host in processes like growth, reproduction or other bodily functions (HALL et al. 2007). Therefore, the host is confronted with a trade-off between the maintenance of its

bodily processes (immune response, defence reactions) and reproduction. For example, the diversion of metabolic energy to immune function might reduce the energy available for reproduction and/or secondary characteristics. In addition, testosterone's interaction with immune function may act as an important mechanism for regulating energy allocation between survivorship and reproduction (MUEHLENBEIN 2006). However, the defensive reaction of a host is only worthwhile if the energetic costs are lower than that of the damage caused by the parasite infection (FRIEDRICH and LUCIUS 2006).

An indirect decrease in reproduction can also occur via favourization or antiparasitic sexual mate choice. In this case individuals infected with parasites differ in phenotype or other features, such as smell, from non-parasitized individuals, making them less interesting for the other sex and therefore decreasing their chances for mating (TARASCHEWSKI 2006a).

A direct parasite-induced decrease in reproduction frequently results from parasitic castration. This is normally accompanied by modifications in the expression of secondary sexual characteristics, and variations of physical and behavioural attributes (BAUDOIN 1975). By interfering with host reproduction, castrating parasites might gain advantages from increased host survivorship, host growth or energy availability, caused by redirection of energy resources from reproductive functions into other processes.

Parasite influence on mortality, morbidity and reproduction might regulate host population dynamics and could even lead to the extinction of small populations (PÉREZ et al. 2006). The microsporidian parasite *Steinhausia* sp. caused the extinction of the land snail *Partula turgida* (CUNNINGHAM and DASZAK 1998), while the racoon roundworm *Baylisascaris procyonis* is likely to be the cause for the disappearance of the Allegheny woodrat (*Neotoma magister*) in some parts of its native range (LOGUIDICE 2003).

The mathematical models from Roy Anderson and Robert May (ANDERSON and MAY 1978, MAY and ANDERSON 1978) first described the possibility of parasites being regulating factors in host populations, meaning that every factor that influences birth and death rates (immigration and emigration rates) in a density dependent manner has the potential to regulate a population. Evidence from wildlife for this theory was first provided by HUDSON et al. (1998) who described the prevention of regular population crashes in red grouse (*Lagopus lagopus scoticus*) in Scotland through the use of anthelminthic treatment against the intestinal nematode *Trichostrongylus tenuis*. In this case parasite-induced mortality regulates the bird population. Population regulation through decreased reproduction was shown by ALBON et al. (2002). The fecundity of female Svalbard reindeers (*Rangifer tarandus plathyrhynchus*) is

influenced by the intestinal nematode *Ostertagia gruehneri*. Females treated with anthelmintica were more often pregnant and had more calves than untreated females.

There are almost no studies, which specifically address the influence of parasites on the community structure of an ecosystem, because it is difficult to manipulate parasite abundances in the field and eliminate other influencing factors like food availability and climate (MOURITSEN and POULIN 2002). However, it is suggested that parasite-mediated changes in host behaviour, predator-prey interactions or interspecific competition can also impact communities although, despite the accumulating evidence, the role of parasites in communities is still unclear until (MOURITSEN and POULIN 2002). Nevertheless, evidence suggests that a high biodiversity of parasites improve ecosystem functioning, since parasites can act at various levels to modify mortality as well as predation and competition rates, thus increasing the complexity of the system (HUDSON et al. 2006).

2. The European hedgehog (*Erinaceus europaeus* LINNAEUS 1758)

2.1 Taxonomy and distribution

Hedgehogs were until recently classified as members of the mammalian order of Insectivora (also known as Lipothyphla). This is systematically one of the most complicated taxonomic groups (SYMONDS 2005). BUTLER (1972) described the group as a "waste-basket" since it contains more or less the remains of the mammalian species lacking clearly defined, shared characteristics, besides being insectivorous and small (SYMONDS 2005). In the last 150 years the composition of Insectivora has varied a lot. GRENYER and PURVIS (2003) divided the order into six families (Chrysochloridae, Tenrecidae, Erinaceidae, Soricidae, Talpidae and Solenodontidae). However, hedgehogs are considered to form their own taxonomic order - the Erinaceomorpha (HUTTERER 2005), including the family Erinaceidae with the two subfamilies Erinaceinae or spiny hedgehogs (hedgehogs) and Galericinae or hairy hedgehogs (gymnures and moonrats).

The Erinaceinae are divided in the five genera *Atelerix*, *Hemiechinus*, *Mesechinus*, *Paraechinus* and *Erinaceus*. The species of the genus *Atelerix* occur mainly in Africa, with soothe exception of some introduced species on various islands like the Canaries, the Balearic Islands and the Mediterranean coast of France and Spain (REEVE 1994). The range of the long-eared hedgehogs from the genus *Hemiechinus* extends to the Middle East and Northern Africa but the main distribution is Asiatic (REEVE 1994). *Paraechinus* or "desert hedgehogs" can be found from the Sahara through the Arabian region to India (CORBET 1988), while the

genus *Mesechinus* is common in Central Asia with native ranges in the Russian federation, China and Mongolia.

The genus *Erinaceus* consists of four species, the European hedgehog *Erinaceus europaeus*, the southern white-breasted hedgehog *E. concolor*, the northern white-breasted hedgehog *E. roumanicus* and the Amur hedgehog *E. amurensis*. The range of *E. amurensis* includes two main regions, (i) eastern Manchuria, the Korean peninsula and the Amur basin, and (ii) the Chinese lowland (figure 1B) (CORBET 1988). The two species *E. concolor* and *E. roumanicus* were combined by CORBET (1988) to one species. However, more recent studies from SANTUCCI et al. (1998), BANNIKOVA et al. (2002) and BERGGREN et al. (2005) show that this synonymy is incorrect and the Eastern hedgehog has again been divided into the species mentioned above. *E. concolor* occurs from minor Asia to Israel, including Turkey (figure 2B) while *E. roumanicus* is found in Eastern Europe from Poland to Austria and Slovenia, the Balkan States, Greece and Adriatic islands, Russia, the Ukraine and the Caucasus area (figure 2A) (HUTTERER 2005).

The European hedgehog, on which this thesis is based, occurs in Ireland, Great Britain, southern Scandinavia, and Western Europe to the Czech Republic (figure 1A) where its range overlaps with that of *E. roumanicus* (REEVE 1994). In addition to its native range, *E. europaeus* was introduced in 1974 to the Scottish island of Uist (JACKSON and GREEN 2000) and in the late 19th century to New Zealand (JONES et al. 2005) where this species is treated as a potential threat to the native fauna.

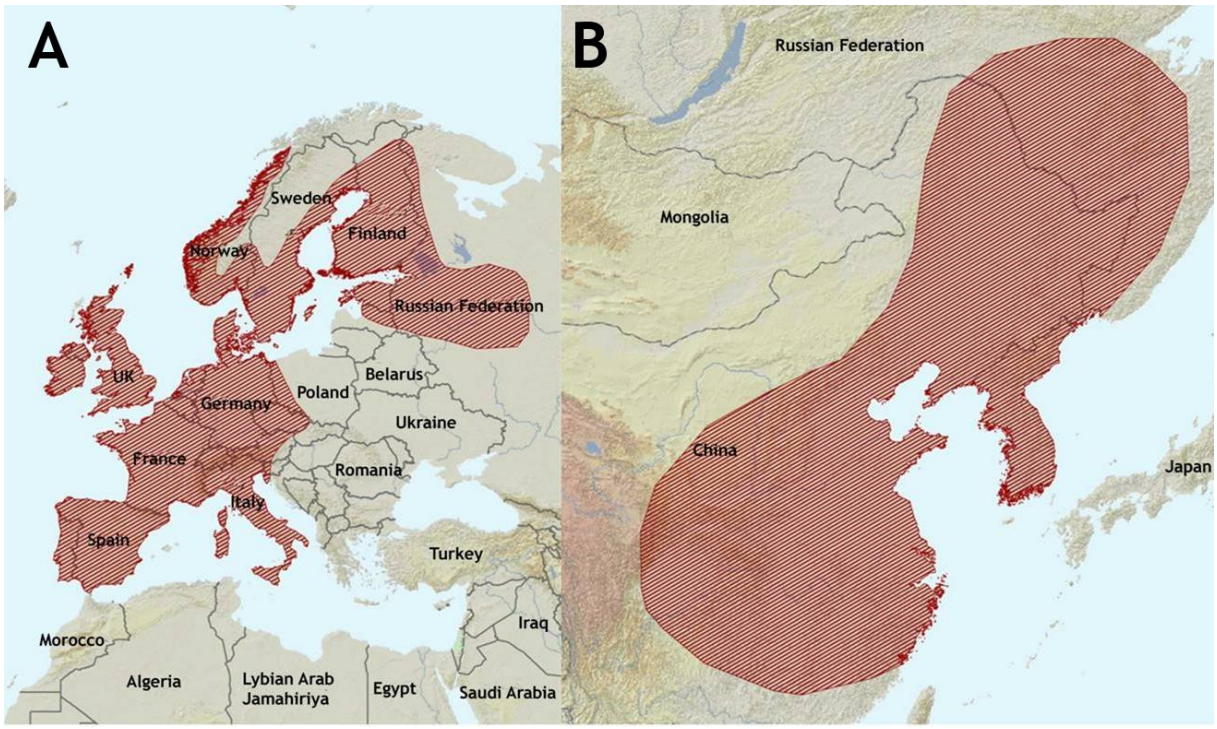

Figure 1: Natural distribution of *Erinaceus europaeus* (A) and *E. amurensis* (B). Red shaded areas show the native range of the different species (modified after IUCN Red List 2009).

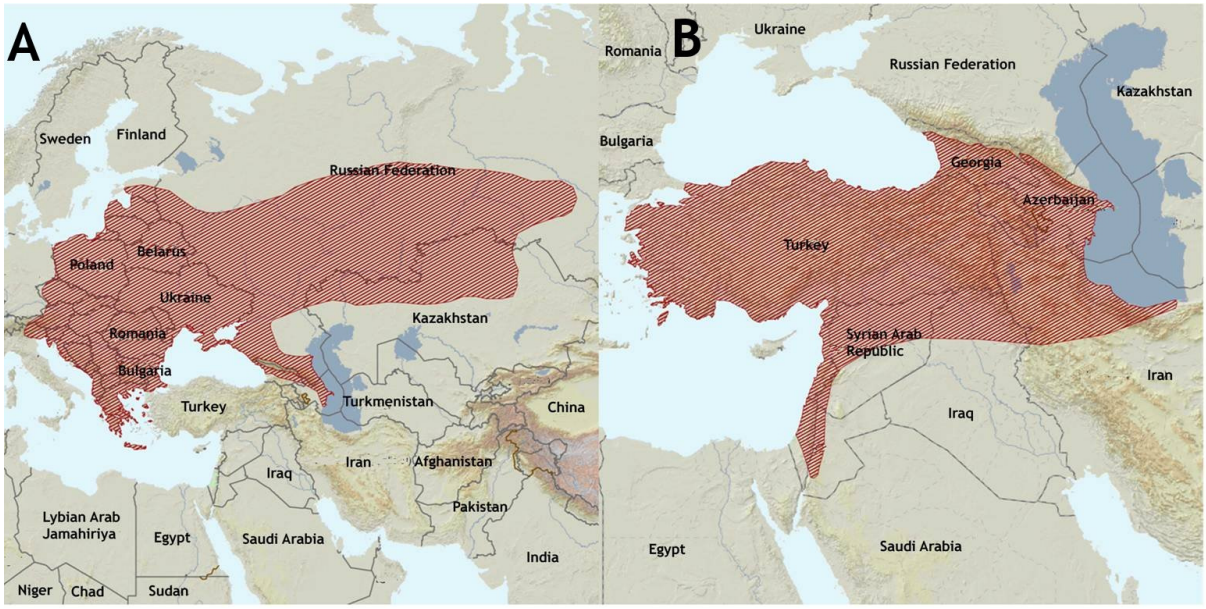

Figure 2: Natural distribution of *Erinaceus roumanicus* (A) and *E. concolor* (B). Red shaded areas show the native range of the different species (modified after IUCN Red List 2009).

2.2 Ecology

Hedgehogs are quite primitive mammals, featuring several plesiomorphic characteristics in their morphology, physiology and behaviour. They are nocturnal, terrestrial, insectivorous, build nests and the dominant senses are hearing and olfaction. These are attributes that are very similar to those of ancestral mammals (REEVE 1994). But although being conservative, they show various specializations such as their spines and the highly developed back muscles, which enable the hedgehog to roll up (figure 3).

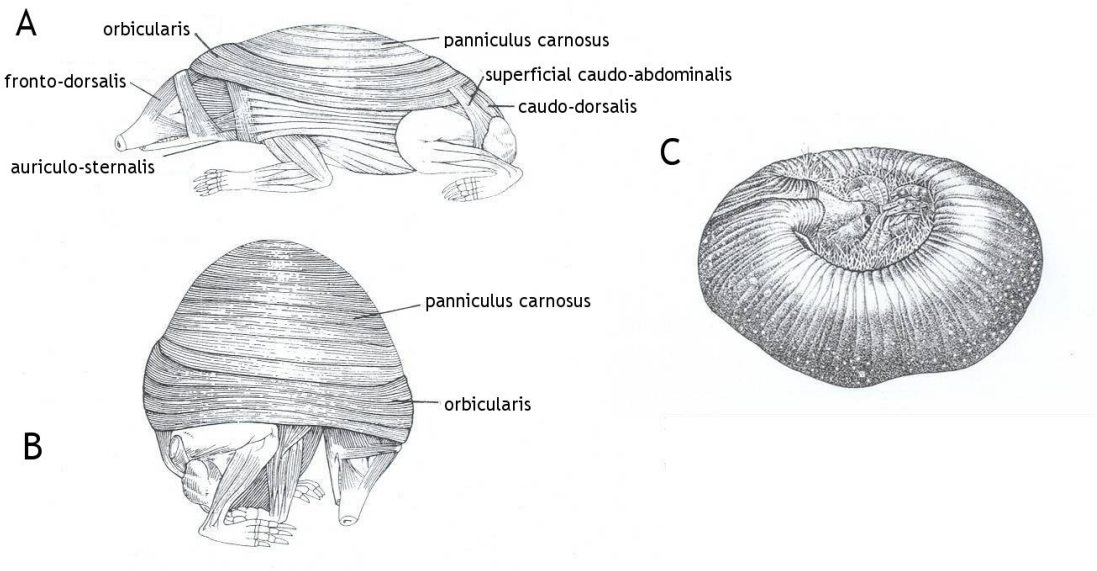

Figure 3: (A) Overview of the muscles of a hedgehog showing the main muscles involved in rolling up. (B) Hedgehog partly rolled up. Muscles overlay the forehead, shoulder and tail. (C) Partly rolled up hedgehog. In a fully rolled up hedgehog neither head nor feet are apparent (modified after Reeve 1994).

The specialized back muscles and the spines (3,500-7,000 modified hairs which replace the normal hair on the back of the body) are features serving as a highly effective defence mechanism against predators. When the hedgehog feels threatened it first becomes very wary and erects its spines. Most of the time it only shows passive defence (freezing and rolling up) but sometimes it also shows active behaviour like jumping with erected spines. The spines might be the reason for the hedgehog having only few natural predators of which the most important one is probably the badger (*Meles meles*). Studies by DONCASTER (1992, 1994) and MICOL et al. (1994) from the UK indicate that hedgehog population density and mortality are influenced by badger populations. Thus, it seems that badgers can either be a major threat to hedgehogs due to predation, or they compete with them for food and habitat. Additionally,

owls, martens, foxes and dogs occasionally kill hedgehogs, but there seems to be no evidence that they are a real threat to hedgehog populations.

The home range of a European hedgehog varies according to the area where it lives. In urban and suburban areas the home range is normally smaller than in rural landscapes. REEVE (1981) reports home range sizes for males of 32 ha and for females of 10 ha in the UK, while KRISTIANSSON (1984) reports home ranges of 47 ha for males and 20 ha for females in Sweden. The home range itself varies from day to day (MORRIS 1988) since hedgehogs travel about three to four kilometres in one night (REEVE 1994). Therefore, home ranges of different individuals often overlap and there is no territorial behaviour, because the defence of home range seems to be uneconomical (KRISTIANSSON 1984).

Due to their large areas of movement hedgehogs have more than one nest in which to spend the daytime in to rest. Males change nests more often (every three days) than females (every ten days) (REEVE and MORRIS 1985), which is associated with their larger home ranges. Nest types can be classified into summer or day nests, breeding nests and winter nests or hibernacula. The different nest types do not differ much in their construction. They are carefully made structures, 30-60 cm in diameter and consist of packed dry leaves forming walls up to 20 cm thick. Hedgehogs build their nests by gathering up dry leaves until they have created a pile under supporting vegetation. The hedgehog then uses a burrowing and rolling action to form a nest chamber with tightly packed and stable walls. The inner part of the nest is often lined with softer vegetation like hay, moss or leaves (HERTER 1968). Figure 4 shows in schematic form the construction of a hedgehog nest.

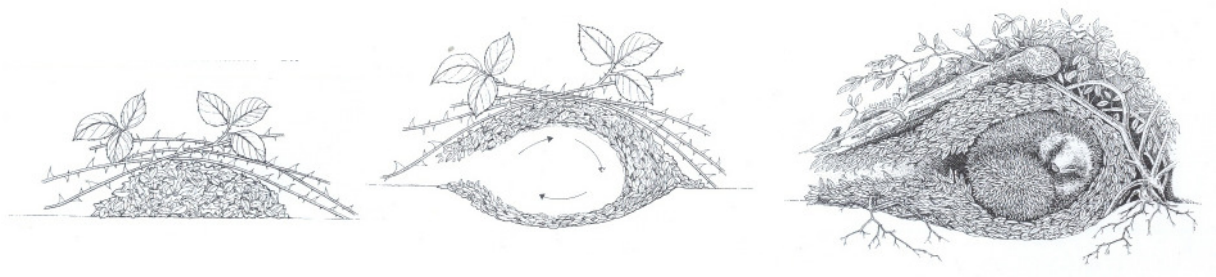

Figure 4: Method of nest construction by a European hedgehog. A pile of leave is placed under supporting vegetation. The animal forms a nest chamber which is lined with moss, leaves or hay. The finished nest has tight and firm walls, protecting the animals against environmental factors (after REEVE 1994).

Summer nests are often more loosely built than winter nests. Breeding nests have to ensure enough space and protection from environmental factors for the breeding female and her

offspring. Therefore, it is as densely built as a hibernaculum but larger than both summer and winter nests (MORRIS 1983). Importantly, nests may be of significance in the ecology of certain parasites (REEVE and MORRIS 1985) (see chapter I.2.4). Winter nests are of major importance for hedgehogs during hibernation, since they are protecting the animals against environmental factors while helping to maintain a constant inside temperature of 1-5 °C (MORRIS 1983). This buffers the animals from thermal variations (WALHOVD 1979) and prevents them from arousal if temperatures increase outside over 10 °C for short time.

The hedgehog is a real hibernator, which mainly depends on the availability of food during winter. Its diet consists mostly of insects, snails and slugs, earthworms, woodlice and sometimes also of small vertebrates (frogs, toads, snakes, birds and their eggs and small mammals) (HERTER 1963). A substantial proportion of the animals in its diet serves as intermediate hosts for endoparasites (see chapter I.2.4) and is not available during the cold season.

Hibernation is a period of lowered metabolism, during which hedgehogs decrease their heartbeat from 200-280 to 5 beats/min and their breathing rate from 50/min to 13/min. During this phase hedgehogs depend on the fat reserves they built up in late summer and autumn, which are needed to maintain the minimal metabolism. Throughout hibernation it can come to a weight loss of 35% (LIENHARDT 1979). The minimum weight to survive hibernation varies from author to author. SCHICHT-TINBERGEN (1995) mentions a minimum weight of between 500-600 g, while ESSER (1984) indicates 450-600 g. The weight of an adult hedgehog averages between 700-1,400 g (SCHICHT-TINBERGEN 1989).

The hibernation cycle starts, depending on the latitude and area, between September and November and lasts till March-May (FOWLER and RACEY 1990a, REEVE 1994). In males, hibernation is induced by several endogenous factors like photoperiod and lowered testosterone and increased melatonin levels (REEVE 1994). In females hibernation is more linked to changes in ambient temperature and food availability (SABOUREAU 1986). In addition, hibernation patterns are different according to sex and age, meaning that males start and stop hibernation earlier than female and juvenile hedgehogs (SABOUREAU 1986). These differences are associated with the deficits in fattening, since females need to raise their offspring first, before they can build up fat reserves.

Mortality is highest in winter. HOECK (1987) reports winter mortality rates for adults of 20-40% and for juveniles of 70-80% in Germany. Studies from Sweden showed winter mortality rates of 26-43% (average 33%) for adults and of 6-94% (average 33%) for juveniles (KRISTIANSSON 1990). The total annual mortality from this study was 47% for adults and 34%

for juveniles. In England annual mortality rates for adults are about 40% and for juveniles 65-80% (ESSER 1984).

The reproductive period varies between populations according to the duration of hibernation and latitude. Sexual behaviour starts soon after hibernation, but the majority of sexual activity takes place between May and July and lasts in general until August (REEVE 1994). Courtship and pregnancy (four to five weeks) can occur through the whole active season (DEANESLY 1934, REEVE 1981). The mating period is the only time in the year during which hedgehogs are not solitary. Hedgehogs are promiscuous, so females mate with more than one male and conversely. The males are not involved in raising the offspring. After ALLANSON (1934) and ISENBÜGEL (1976), sexual maturity starts at an age of nine months, FONS (1988) assumes an age of at least one year while females in Fennoscandia mature not until an age of two years (REEVE 1994).

In Germany one litter per year is common, but there are reports of two litters in some regions (ESSER 1984, NEUMEIER 2001). In France SABOUREAU and DUTOURNÉ (1981) report two litters, one in spring and one in late summer. The litter size is normally 4-6 young (MORRIS 1961). Females are very sensitive during birth and disturbance can lead to their abandoning or killing the young. After the birth, the females stay at least 24 h in the nest before starting foraging again (REEVE 1994). The young are born naked, with closed eyes and ears, the spines are buried under the skin but appear soon after birth (BURTON 1969, MORRIS 1977). Females wean their offspring at about 40-45 days (SCHICHT-TINBERGEN 1989) and during this time the birth weight of 8-25 g increases to 200-235 g (REEVE 1994). After this the young are independent and disperse to gain weight for hibernation.

In the literature, information on the life expectancy of the European hedgehog varies. In the UK and Sweden the mean life expectancy is about two years (KRISTIANSSON 1981, REEVE 1994), while SCHICHT-TINBERGEN (1989) reports ages from three to seven years from Germany. ISENBÜGEL (1976) reports an age of ten years in captivity and eight years in the wild while LIENHARDT (1979) uses more plausible assumptions in his estimate of an average life span of three years.

2.3 Hedgehog populations

According to the Bern Convention on the Conservation of European Wildlife and Natural Habitats from 1979 (appendix III of the convention), the protection of the European hedgehog has to be ensured in the member states of the Council of Europe (COUNCIL OF EUROPE, 1979). In addition, after the Bundesnaturschutzgesetz (Federal Nature Conservation Act) § 20 and

the Bundesnaturschutzverordnung § 1 (Federal Nature Conservation Decree, appendix I of the decree) the European hedgehog belongs to the legally protected animals in Germany. To ensure its protection it is necessary to study the ecology and behaviour of these animals and the factors which drive their population dynamics. Unfortunately, there are no detailed research findings dealing with the population dynamics of hedgehogs in Germany. There is only one study from the middle of Saxony (Dresden and the administrative districts of Pirna, Dippoldiswalde, Meissen, Döbeln, Freiberg, Mittweida, Riesa-Grossenhain and Kamenz), in which the roadkills on certain roads were counted by one person over a period of eleven years (KAPISCHKE 2006). In this study, 81% of all animals found were hedgehogs. This high proportion is thought to be dependent on the spiny carcasses which are more seldom eaten by scavengers. KAPISCHKE's results indicate that the population of hedgehogs fluctuates in a 3-4 year rhythm, although more comprehensive studies nationwide are required to confirm this finding.

Results from roadkill surveys conducted by the People's Trust for Endangered Species (http://www.ptes.org/index.php?cat=64, 20.9.2009) and from hedgehog sightings carried out by HogWatch (http://www.hogwatch.org.uk/Downloads%5CHogWatchSurveyReport.pdf, 20.9.2009), outlining data from 1991 and from 2001-2008, indicate that hedgehog populations in the UK are in decline with a decrease of 7.5% hedgehogs/year in England and Wales and up to 50% in some other regions (1991-2001). From the perspective of conservation biology these findings are alarming; foremost the factors responsible for this decline are as yet unknown. Some suggested hypotheses for these declines are increasing urbanisation and "tidier" gardens, lacking natural habitats for hedgehogs, and habitat fragmentation or destruction is also mentioned as a factor in rural areas. Arable fields are becoming bigger and bigger, leaving no space for the animals (hedgehogs naturally avoid open fields and tend to occur at field margins). Badgers are also taken into account. As mentioned in chapter I.2.2, hedgehog population densities seem to be lower in areas with large badger populations. It is known that badgers and hedgehogs compete for both food and habitat and that badgers also prey on hedgehogs. In some areas badgers might be responsible for the decline of hedgehog populations, although this may also occur because of the smaller habitat patches available for both species, so that hedgehogs are not able to avoid potential predators. However, results from the UK also showed that hedgehog populations are decreasing in regions where badger populations are very low (http://www.hogwatch.org.uk/Downloads%5CHogWatchSurveyReport.pdf, 20.9.2009).

Another factor might be climatic changes with warmer winters and drier summers (http://www.hogwatch.org.uk/Downloads%5CHogWatchSurveyReport.pdf, 20.9.2009), but this also remains unclear. Road traffic is a potential factor which seems to be the predominant reason for summer mortality (KRISTIANSSON 1990). Various data from the Netherlands estimated 113,000-340,000 hedgehogs/year killed by cars. This represents 6.1-9.0% of the total population (BERGERS and NIEUWENHUIZEN 1999). HUIJSER and BERGERS (2000) stated that roads may reduce hedgehog density up to 30% in specific areas, which might affect the survival probability of local populations. These studies indicate the importance of anthropogenic factors on hedgehog populations.

In a survey carried out by REEVE and HUIJSER (1999) based on records from wildlife rescue centres in the UK and the Netherlands which dealt with the specific causes of death of hedgehogs, it was found out that 41% of the deaths could be attributed to anthropogenic factors. The additional 59% were attributed to natural causes like parasites or diseases with 64% of the investigated hedgehogs being infected with endoparasites and 87% infested with ectoparasites. This shows how important parasites and pathogens are, and that they should be considered as possible regulating factors when studying hedgehog population dynamics.

2.4 Parasites of the hedgehog

Hedgehogs are hosts for a wide variety of different parasites and pathogens. In the following chapters I will mainly focus on parasites and pathogens found on and in *E. europaeus* in Europe with some additionally information from other hedgehog species.

2.4.1 Ectoparasites

Fleas (Siphonaptera):

To a greater or lesser extent every hedgehog is infested with the hedgehog flea *Archaeopsylla erinacei* BOUCHÉ, 1835 (BECK and CLARK 1997, BECK et al. 2005). In a few cases other flea species, like the cat flea *Ctenocephalides felis felis*, the dog flea *C. canis*, the rat flea *Nosopsyllus fasciatus* and others occur (ISENBÜGEL 1976, CARLSON 1980, SAUPE 1988, RÜMPLER 1995, BECK et al. 2005). *A. erinacei* (figure 5) is about 3 mm long with an oval head and a laterally compressed body which permits an easy movement through the hair and spines of its host. It has genal ctenidia (comb) with 2-3 short spines and pronotal ctenidia with 5-6 spines (KUTZER 1992, BECK and CLARK 1997).

Figure 5: Female and male hedgehog fleas (*Archaeopsylla erinacei*). Scale bar represents 1 mm (courtesy of Pro Igel e.V.).

Habitat preferences on the host are the front legs, the neck, the head, the chest and the belly (SGONINA 1935, SAUPE 1988). A study by BRINCK and LÖFQVIST (1973) on the Baltic island of Öland indicates that *A. erinacei* is a nest-dwelling species reproducing only in the nests of breeding female hedgehogs. The larvae, which live in the nest and are not directly parasitic on the host, feed on the excrement of the adult fleas. Adults emerge in August, so that young hedgehogs are infested before they leave the nest. BRINCK and LÖFQVIST (1973) also mention that flea dispersal by the hedgehog population is more extensive than in other flea species and their host populations.

High infestation rates with *A. erinacei* can lead to pruritus, weakening and anaemia (BECK 2003, BECK et al. 2005). Additionally, *A. erinaceus* seems to be a vector of *Rickettsia felis*, the agent of the flea-borne spotted fever rickettsiosis (GILLES et al. 2008), but it is not known how this affects hedgehogs.

The prevalence of flea infestation in hedgehogs is very high. VISSER et al. (2001) found prevalences of 84.2% in Germany while BAKER and MULCAHY (1986) found prevalences of 100% with an abundance of 56 fleas per animal on hedgehogs from Dublin, Ireland. SAUPE (1988) reported 982 fleas in total on a young hedgehog from Germany.

Mites (Acari):

A number of mite species are found on European hedgehogs. One of these is *Demodex erinacei* HIRST, 1917. *Demodex* mites are found in the hair follicles or sebaceous glands of their hosts and feed on subcutaneous tissues, especially sebum (SERVICE 2006). They are highly specialized and specific for various host species (IZDEBSKA 2004). Symptoms of infestation with *D. erinacei* are crusty thickenings and papulous alterations of the skin (SAUPE

1988, CARLSON 1990, KUTZER 1992). Infestations with *D. erinacei* seem to be rare in hedgehogs (FISHER et al. 2007).

Heavy infestations with the mange mite *Caparinia tripilis* MICHAEL, 1889 (figure 6) leads to drying out and thickening of the skin, heavy itching and severe loss of hair and spines (GERSON and BOEVER 1983, KUTZER 1992). *C. tripilis* is regularly found on hedgehogs from New Zealand (SWEATMAN 1962) and, in combination with the fungus *Trichophyton mentagrophytes* var. *erinacei*, the mange mite kills a large number of hedgehogs there (BROCKIE 1975).

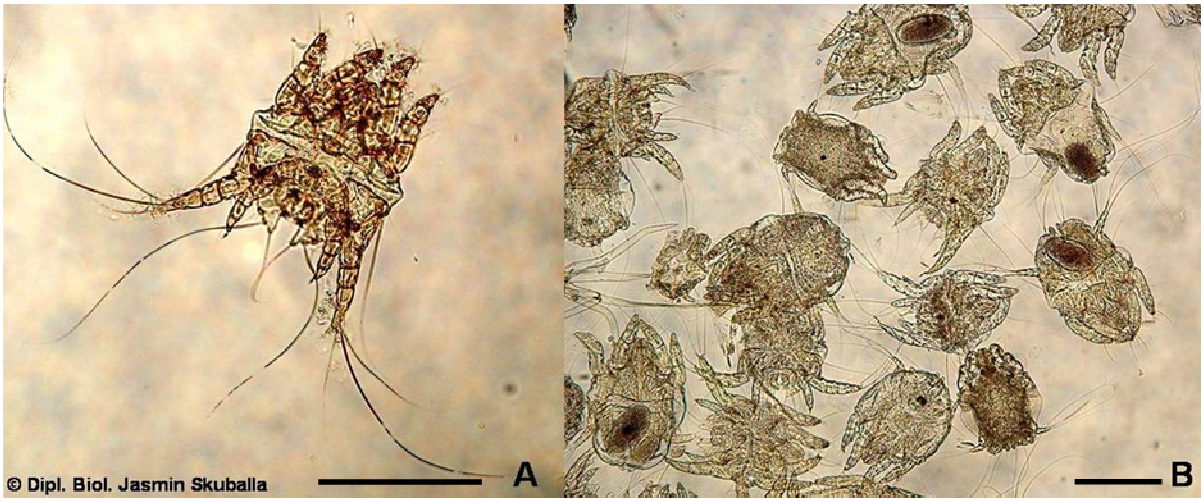

Figure 6: *Caparinia tripilis* from skin samples of a European hedgehog. (A) A single male mite, (B) multiple mites with females with brownish eggs. Scale bars represent 0.5 mm.

The agent of the sarcoptic mange, *Sarcoptes scabiei* DE GEER, 1778, also occurs on hedgehogs. Infestations lead to heavy itching, alterations of the skin and cachexia (TADMOR and RAUCHBACH 1972, KUTTIN et al. 1977). TADMOR and RAUCHBACH (1972) associated the heavy infestation of a hedgehog with *S. scabiei* to the death of the animal. KUTTIN et al. (1977) mentioned *Sarcoptes* infections together with multiple fungal infections (*Alternaria* spp., *Helminthosporium* spp. and *T. mentagrophytes* var. *erinacei*).

Occasionally *Notoedres cati* HERING, 1836, a cat mite, occurs on hedgehogs. This can lead to similar pathology of the head and the ear as observed in cats, causing mange with crusty thickenings of the skin (CARLSON 1980, 1990, SAUPE 1988, KUTZER 1992, RÜMPLER 1995). Other mite species found on hedgehogs are for example the larvae of the harvest mite *Trombicula autumnalis* SHAW (figure 7), *Chorioptes* spp. and *Rodentopus* spp. (SCHÜTZE 1980, SAUPE 1988, CARLSON 1990, BECK et al. 2005).

Figure 7: Larvae of *Trombicula autumnalis* (reddish spots) on the upper hind leg of a European hedgehog.

Ticks (Acari):

There are basically two tick species (Acari: Ixodidae) found on the European hedgehog, the hedgehog tick *Ixodes* (*Pholeoixodes*) *hexagonus* LEACH, 1815 and the sheep tick *I. (I.) ricinus* LINNAEUS, 1758 (figure 8). Both species have four developmental stages, the eggs, the larvae, the nymphs and the adults. Once the larvae hatch, each stage feeds on blood in order to develop to the next life stage, or in case of females to lay eggs. The males of *Ixodes* normally do not feed on blood, but depend on their fat reserves (ARTHUR 1962).

I. hexagonus is a monotropic and triphasic nest-dwelling species, (TOUTOUNGI et al. 1995). It is highly specific to *E. erinaceus* (PFÄFFLE et al. 2009) with some records coming from mustelid species (*Mustela nivalis*, *Martes foina*), badgers (*Meles meles*) and foxes (*Vulpes vulpes*) (AUBERT 1975, LIEBISCH and WALTER 1986). Larvae feed 3-4 days before detaching from the host and the premoult time is temperature dependent and varies between 23-60 days (ARTHUR 1963). Nymphs feed for an average of 5-7 days. After detaching it takes between 32-77 days to moult, which, as with the larvae, is also temperature dependent (ARTHUR 1963). Emerging females have a translucent greyish hue, but darken after about five days with a dark brown scutum and a greyish-blue alloscutum (ARTHUR 1963). The legs have a banded appearance due to paler colouration at the bases of the appendages and the scutum is typically shaped as a hexagon (ARTHUR 1963). After finding a host, females feed for about eight days before detaching. An average female lays about 1,000-1,500 eggs within a period of 19-25 days (about 100-130 eggs per day). Emerging males have a slate-grey tint and are translucent, but they darken within a week to ten days (ARTHUR 1963).

I. ricinus is a generalist with over 300 different host species including mammals, birds and reptiles (BENINATI et al. 2002, GERN and HUMAIR 2002, GERN 2005). Larvae feed for about 3-5 days before dropping off the host and moulting into nymphs. After finding a new host these feed for about 5-7 days. It appears that blood alone is not essential for the development of the immature stages, since ticks which feed on tissue fluid only (white body appearance) usual moult to the next stage (ARTHUR 1963). Females show a brown-black capitulum, scutum and legs and a dark red-brown body. An average female *I. ricinus* feeds for 7-13 days on its host, drops off and lays up to 2,500 eggs (ARTHUR 1963, BALASHOV 1968). Males are coloured dark red-brown to black.

On-host habitat preferences of both species cover the whole body, but especially the hairy body parts, the areas around the eyes, the ears and the region around the anus (ISENBÜGEL 1976, CARLSON 1980). The effect of ticks on hedgehogs and other animals will be discussed later. Other tick species which can occasionally be found on hedgehogs are *I. trianguliceps* (WALTER 1981), *Dermacentor reticulatus*, *D. sinicus*, *Haemaphysalis concinna*, *H. punctata*, *H. numidiana*, *Rhipicephalus bursa* and *R. sanguineus* (SMITH 1968a).

Figure 8: Tick species infecting *Erinaceus europaeus*. Upper row shows unengorged *Ixodes hexagonus* of different life history stages (from left to right: larvae, nymph, female, male). Lower row shows unengorged *I. ricinus* of different life history stages (from left to right: larvae, nymph, female, male). Scale bar represents 3 mm.

2.4.2 Endoparasites

Nematodes:

The hedgehog lungworm *Crenosoma striatum* ZEDER, 1800 is specific to the hedgehog and is the most important parasite of the lung (BARUTZKI et al. 1984, BECK 2007). The whitish adult worms are 15-20 mm (females) or 10-15 mm (males) long (CARLSON 1980). *C. striatum* has a heteroxenous life cycle. The ovo-viviparous females lay eggs with a transparent, elastic integument, which consist the L1-stage (BECK 2007). The egg integument gets lost very early, so one can find the 300 µm long L1-stages in the bronchial tubes. The L1-stages are coughed up, swallowed and shed with the faeces (BECK 2007). The larvae penetrate the feet of their intermediate hosts, predominantly land snails, and develop to the infectious L3-stage in three to four weeks (SCHÜTZE 1980). BARUŠ and BLAŽEK (1971) could not find intermediate host preferences, while LÄMMLER and SAUPE (1968) described the snails *Cepaea nemoralis*, *C. hortensis* and *Arianta arbustorum* as being especially capable hosts for the lungworm. Hedgehogs become infected by ingesting infected snails. After a prepatent period of 21 days the worms become sexually mature and the first larvae can be found in the faeces (BECK 2007). Figure 9 shows the developmental cycle of *C. striatum*.

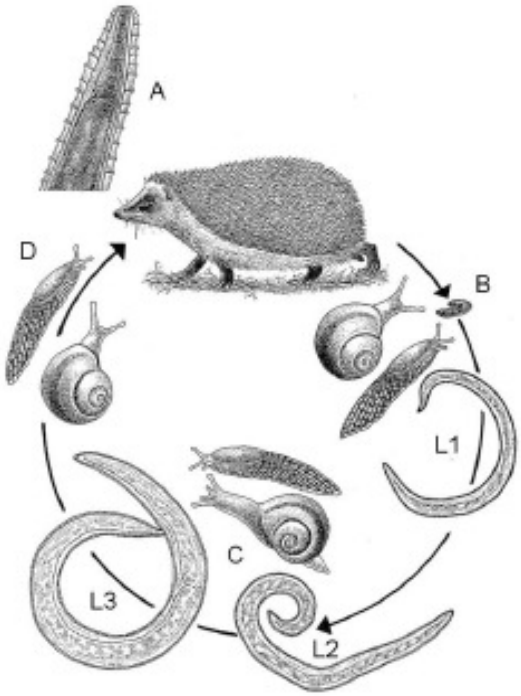

Figure 9: Developmental cycle of *Crenosoma striatum*. (A) Adult female in the lungs of a hedgehog. (B) L1-larvae from the faeces actively penetrate the snail intermediate hosts. (C) Development to the infectious L3-larvae within the intermediate host. (D) Ingestion of infectious snails by a hedgehog (after REEVE 1994).

An infection with *C. striatum* can cause loss of weight, dry cough, bronchitis with ulcerous reactions based on secondary bacterial infections, pulmonary damage, thickening of the tracheal wall and pulmonary emphysema up to cardiovascular failure (CARLSON 1980, TIMME 1980, SAUPE 1988, MAJEED et al. 1989). The prevalences of infection in hedgehogs vary depending on different habitats and biotopes (BARUTZKI et al. 1984). Prevalences in wild populations range between 45% (PANTCHEV et al. 2005), 52% (MAJEED et al. 1989), 62.4% (FELIU et al. 2001), 72.3% (BARUTZKI et al. 1987) and 77.5% (LIESEGANG and LEHMANN 2003). Figure 10 shows a section of a *C. striatum* infected lung from a European hedgehog.

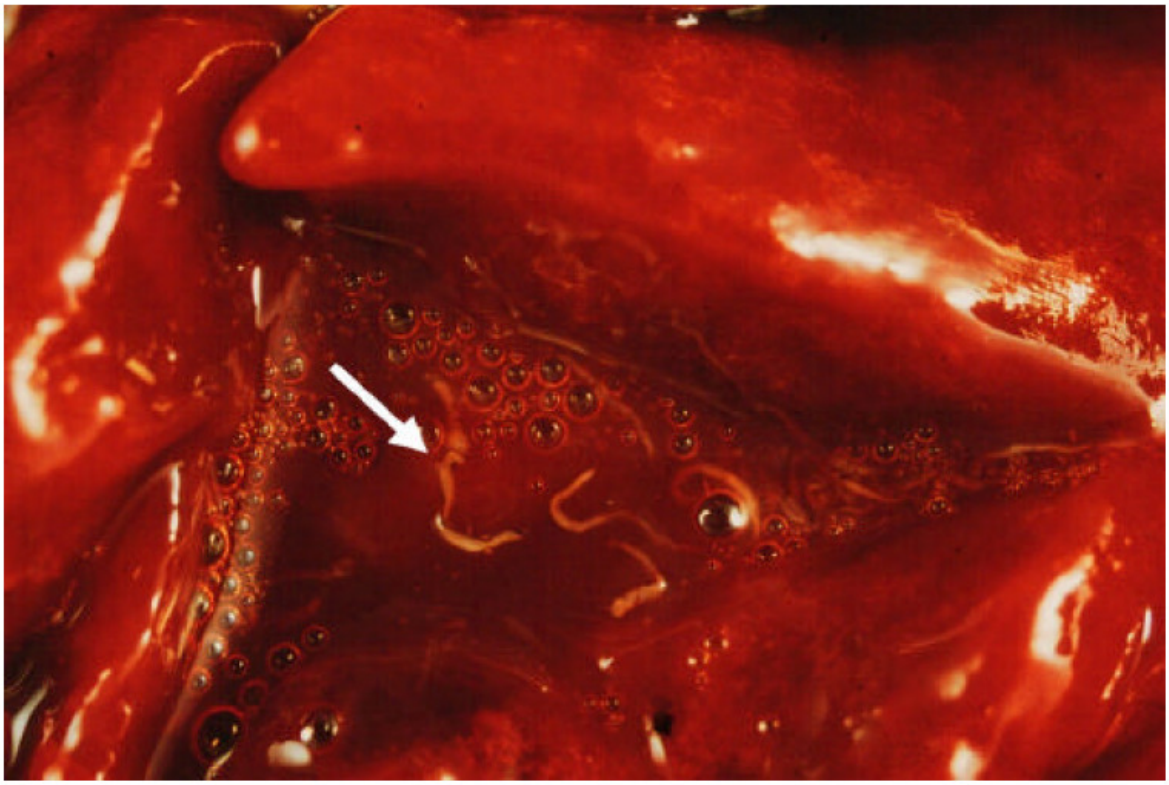

Figure 10: Section of an opened lung from a European hedgehog. Arrow indicates adult lungworms inside the lung surrounded by mucosa (from DÖPKE 2002).

Several *Capillaria* species can be found in the lung and intestine. There are possibly two species infecting the smaller bronchi, *Capillaria aerophila* CREPLIN, 1839 (syn. *Thominx aerophilus*) and *C. tenuis* (syn. *Eucoleus tenuis*) (SCHÜTZE 1980, SAUPE 1988), but most authors mention only *C. aerophila*. *C. aerophila* often occurs in mixed infections with *C. striatum* (SAUPE 1988, BECK 2007). Both sexes are 10-13 mm long and hair thin. In contrast to *C. striatum*, the life cycle is monoxenous or facultative heteroxenous with earthworms as paratenic hosts (SAUPE 1988, BECK 2007). Excretion of the eggs occurs in batches (SAUPE 1988), and like *C. striatum* the eggs are coughed up, swallowed and shed with the faeces.

They have a size of 60-80 µm, are dark brown with a meshed surface, the sidewalls are convex and they have clearly emergent opercular plugs (CARLSON 1980, SAUPE 1988). The very stable, sticky lipid envelopes of the eggs lead to high persistence (BECK 2007). Because of their morphology, the eggs of *Capillaria* species are often confounded with "whip worm" infections of the genus *Trichuris*, but infection of hedgehogs with *Trichuris* spp. has never been detected (SCHÜTZE 1980, SAUPE 1988). An infection with *C. aerophila* occurs exclusively peroral when the hedgehog eats embryonated eggs or infested earthworms. The prepatent period is about three to four weeks (SAUPE 1988, BECK 2007). *C. aerophila* infections cause less breathing handicaps than those of *C. striatum* (CARLSON 1980), but clinical symptoms such as loss of weight, bronchitis or pulmonary damage can occur (SAUPE 1988, MAJEED et al. 1989).

At least two different *Capillaria* species parasitizing the intestinal tract of *E. erinaceus* are known, *C. erinacei* RUDOLPHI, 1819 and *C. ovoreticulata* LAUBMEIER, 1985. Since both species are very hard to distinguish, most authors refer to them as *Capillaria* spp.. Adult male worms reach a length of about 10 mm while females grow to 15 mm (ROMASHOV 1981). Similarly to *C. aerophila*, the life cycle can be either direct or indirect with earthworms such as *Lumbricus terrestris* and *Eisenia rosea* as paratenic hosts (ROMASHOV 1981). The eggs differ from the *Capillaria* found in the lung. One egg type is 55-65 µm long having a dark brown, meshed surface with parallel sidewalls and countersunk opercular plugs (SAUPE 1988). The other type is smaller (50-60 µm), with lightly convex sidewalls and flat plugs. The surface seems to be even or fine grained resulting in a light brown colour (CARLSON 1980, SAUPE 1988). The prepatent period after infection is three to four weeks (ROMASHOV 1981, SAUPE 1988, BECK 2007). Adult worms parasitize the intestinal mucosa which can lead to infectious lesions, chronically enteritis, and strong diarrhoea leading to exsiccosis with lowered turgor of the spines, excessive loss of weight, faintness, anaemia and even death (TIMME 1980, ISENBÜGEL 1976, SAUPE 1988, BECK 2007). Prevalences of 74% has been recorded by BARUTZKI et al. (1987) and LIESEGANG and LEHMANN (2003).

Less common nematodes occurring in hedgehogs are spiruids like the stomach worm *Physaloptera clausa* and oesophageal worms of the genus *Gongylonema* (KUTZER 1992, BECK 2007). Individuals of *P. clausa* reach 17-25 mm length and 2 mm thickness (BECK 2007). They parasitize in the stomach and high intensities of infection can lead to weakness, dyspepsia, cachexia or light diarrhoea (BECK 2007). Intermediate hosts are different insect species. *Gongylonema* spp. occur in the oesophagus and develop in insects as intermediate hosts (KUTZER 1992).

Trematodes:

The most important trematode infecting hedgehogs is the digenean *Brachylaemus erinacei* BLANCHARD, 1847 which has different synonyms, amongst others *Distomum caudatum*, *D. leptostomum*, *Heterolope leptostomum*, *Harmostomum helicis* and *Brachylaemus helicis* (KREHMER 1967). The lanceolate worms are 0.5 to 1 cm long, about 1 mm wide (SAUPE 1988, CARLSON 1990, BECK 2007) and are host specific (SCHÜTZE 1980). The adults live in the distal intestinal tracts of the hedgehogs, but they can move into the bile ducts if mass infection occurs (CARLSON 1980). The eggs are about 30 to 35 µm long, capped, with a thick integument, light reddish colour and containing a miracidium (SAUPE 1988, CARLSON 1990, BECK 2007). The eggs are shed with the faeces and are ingested by different gastropod species such as *Helix* spp., *Arion* spp. or *Succinea* spp. (KREHMER 1967). The integument of the egg is digested in the stomach of the snails and the free miracidium penetrates the stomach wall to reach the other organs (KREHMER 1967). The miracidium develops over different larval stages to the infectious cercariae which are ingested by the hedgehogs. They adhere to the intestinal wall via their oral sucker where they develop into adult worms (KREHMER 1967). The prepatent period is about 17 days (KREHMER 1967).

An infection with *B. erinacei* can lead to restlessness, strong appetite with an excessive loss of weight at the same time, diarrhoea with blood in the stool, haemorrhagic enteritis, and inflammation of the bile ducts with secondary bacterial infections, anaemia and even death (CARLSON 1980, SCHÜTZE 1980, SAUPE 1988, BECK 2007). KREHMER (1967) described a case of a juvenile hedgehog infected with a total of 2,516 trematodes which obviously lead to its death.

There seem to be regional differences in prevalences. SCHÜTZE (1980) reports prevalences of 80% around Berlin, 20% in Bremen and only 1% in Central Hesse around the area of Gießen. BARUTZKI et al. (1984) also report only small prevalences of 0-4.8% around Munich.

Other trematodes which are occasionally found in *E. erinaceus* are *Dicrocoelium dendriticum*, *Brachylecitum aetechini*, *B. mackoi* and *Zonorchis guevarai* which all parasitize the liver or bile ducts (CASANOVA and RIBAS 2004).

Cestodes:

Infections with cestodes are not very common, but when they occur it normally involves *Hymenolepis erinaceus* GMELIN, 1790 (syn. *Vampirolepis erinacei*, *Rodentolepis erinacei*) (CARLSON 1980, 1990, SCHÜTZE 1980, TIMME 1980). The adult tapeworms can reach lengths from 34-84 mm (VERSLUYS 1975) and shed 2-8 mm long proglottides with the faeces. The

proglottides contain the eggs, which are ingested by coprophagous insects of the families Scarabaeidae and Silphidae (VALKOUNOVÁ and PROKOPIČ 1980, BECK 2007). The eggs contain the oncosphere with its hooks (CARLSON 1980, 1990, SAUPE 1988). These penetrate the intestinal wall of the intermediate host and reach the body cavity where they develop to the cysticercoid (BECK 2007). The ingestion of beetles which contain the cysticercoids leads to an infection of the hedgehog. Occasional symptoms are diarrhoea and sometimes reduced weight gain (SAUPE 1988, BECK 2007). Prevalences are normally very low. TIMME (1980) describes prevalences of 3.2% for Germany, BARUTZKI et al. (1984, 1987) found prevalences from 0-3.7% in Bavaria, BOAG and FOWLER (1988) 8% in north-east Scotland and in Cumbria in northern England.

Acanthocephalans:

The European hedgehog is a paratenic host for *Plagiorhynchus cylindraceus* GOEZE, 1782, which is an intestinal parasite of passerine birds but also occurs parenterally or in the intestinal tract of carnivorous mammals, small marsupials and rodents (RICHARDS et al. 1995, SMALES 2003, SKUBALLA et al. 2010). Woodlice such as *Armadillidium vulgare*, but also other isopods, function as intermediate hosts (SCHMIDT and OLSEN 1964, NICKOL and DAPPEN 1982, MOORE 1983, LEVRI and COPPOLA 2004, DIMITROVA 2009). *P. cylindraceus* is not able to reproduce in the hedgehog. By ulcerating through the intestinal wall, causing infection and inflammation, and then encystating in the body cavity they can cause diarrhoea, weakness, abdominal swelling and even lead to death in young hedgehogs (SKUBALLA et al. 2010).

Another acanthocephalan parasite ocurring in hedgehogs is *Nephridiorhynchus major* BREMSER, 1811 (syn. *Nephridiacanthus major*, *Echinorhynchus major*, *Gigantorhynchus major*) which can reach a length of up to 15 cm. The hosts become infected by feeding on insects containing infectious cystacanths. Unlike *P. cylindraceus*, *N. major* reproduces in the hedgehog. While *N. major* does not occur in German hedgehogs (personal observations), it is a common parasite of *E. roumanicus* (reports from Poland, Czech Republic), *E. concolor* (reports from Lebanon, Turkey, Israel) but also of *E. europaeus* from the Iberian Peninsula and Italy (FURMAGA 1961, SCHMIDT 1972, GIANNETTO et al. 1993, FELIU et al. 2001, POGLAYEN et al. 2003, personal observations). There is also a record about *N. major* from *E. europaeus* in Jerusalem/Israel (SCHMIDT 1975), although it is not clear whether the host was *E. concolor* rather than *E. europaeus*, which is not native to this country.

Pathogens:

Different viruses, bacteria, protozoans and fungi found in *E. europaeus* are listed in table 1 and 2.

Table 1: Bacteria occurring in the European hedgehog (*Erinaceus europaeus*).

Genus/Species	Symptoms	References
Salmonella spp.		TIMME 1980, LIESEGANG and LEHMANN 2003
Salmonella enteritidis	anorexia, diarrhoea, weight loss	SMITH 1968a, BURGISSER 1983, KEYMER et al. 1991
Salmonella typhimurium		KEYMER et al. 1991, HANDELAND et al. 2002
Yersinia pseudotuberculosis	gastroenteritis, weight loss	TIMME 1980, KEYMER et al. 1991
Escherichia coli	not known	SMITH 1968a, TIMME 1980, LIESEGANG and LEHMANN 2003
Bordetella bronchiseptica	tracheitis, catarrhal rhinitis, nasal discharge, broncho-pneumonia	SMITH 1968a, KEYMER et al. 1991, REEVE 1994
Pasteurella multocida	secondary infections	SMITH 1968a, TIMME 1980, REEVE 1994
Leptospira spp.	seldom appearance of clinical signs of infection	BROOM and COGHLAN 1960, TURNER 1969, FENNESTAD and BORG-PETERSEN 1972, REEVE 1994, COLLARES-PEREIRA et al. 1997
Anaplasma phagocytophilum	not known	SKUBALLA et al. in press
Borrelia spp.	not known	GERN et al. 1997, SKUBALLA et al. 2007
Coxiella burnetti	not known	SIXL et al.1989

Table 2: Viruses, protozoans and fungi occurring in the European hedgehog (*Erinaceus europaeus*).

Genus/Species	Symptoms	References
Viruses		
TBE (tick-borne encephalitis)-Virus	not known	SKUBALLA et al. unpublished
Mouth-and-Foot Disease	vesicular lesions, day-activeness	MCLAUCHLAN and HENDERSON 1947, VIZOSO and THOMAS 1981, REEVE 1994
Herpes virus	not known	SIXL 1989, STACK et al. 1990, WIDEN et al. 1996
Fungi		
Trichophyton mentagrophytes var. *erinacei*	loss of spines and hair, crusty malformations of ear margins, lesions	LA TOUCHE and FORSTER 1963, MORRIS and ENGLISH 1969
Protozoans		
Isospora spp.	poor appetite, emaciation, lethargy, haemorrhagic diarrhoea	CARLSON 1980, REEVE 1994, SAUPE 1988, EPE et al. 2004
Toxoplasma spp.	not known	SIXL 1989
Cryptosporidia spp.	not known	STURDEE et al. 1999, ENEMARK et al. 2002, PANTCHEV et al. 2005, WARD et al. 2006

3. Study aims

As described in the chapters above, knowledge of the factors which influence the population dynamics of the European hedgehog is scarce. For a better understanding of the ecology of hedgehogs and the improvement of conservation of these animals, it is important to investigate these factors, including the role of parasites in the morbidity and mortality of hedgehog individuals, i.e. their influence on health and possible survival, as well as for populations.

The aim of this study is to clarify the possible role of parasites for individual hedgehogs and to extrapolate this information to hedgehog populations by investigating the impact of parasites on various fitness-related parameters.

I tried to approach this goal from two different perspectives: (i) on a specific level, by measuring the influence of a certain parasite group (ticks) on the physiological parameters of hedgehogs, and (ii) on a general, more natural level, by determining the influence of the whole macroparasite community on the morbidity of hedgehogs.

In the first part I intended to examine the effect of tick infestation on host morbidity at a blood physiological level by measuring stress-levels, reproductive ability and haematological values of individual hedgehogs in an experimental hedgehog population over the period of three years. Here I mainly concentrated on:

- Hedgehog cortisol levels subject to the individual tick infestation
- Male hedgehogs testosterone levels subject to the individual tick infestation
- Hedgehog differential blood count parameters subject to the individual tick infestation.

I have chosen ticks as the specific parasite group for this experimental setup for various reasons. Ticks are important ectoparasites of different animal species and vectors of various diseases in Europe; in comparison to endoparasites it is relatively easy to determine and manipulate infestation rates in a semi-natural host population, and to measure the direct influence on host morbidity.

In order to be able to exclude confounding effects such as abiotic climatic factors, I tested for correlations between the biological parameters and the environmental factors (temperature, relative humidity and rainfall).

An additional component of this work was to investigate the population dynamics of the two tick species, *I. ricinus* and *I. hexagonus.* My main interest here was to determine the differences in seasonal dynamics between the generalist tick, *I. ricinus*, and the specialist *I. hexagonus*, a focusing on potentially density-dependent mechanisms regulating the tick populations and their role in epidemiological cycles of hedgehogs and tick-borne diseases.

In the second part of my study I examined the impact of the whole parasite community on morbidity as well as on reproductive fitness in dissected hedgehogs. I used dissected hedgehogs because it is not possible to do this in a living animal population under controlled conditions. Additionally, the real level of infestation is hard to determine. Nevertheless, it is important to look at the whole parasite community because this is more natural than focusing on only one parasite species.
I investigated hedgehogs from two areas with high parasite infestation rates (Germany and the UK) and one with low infestation rates (New Zealand). In this part of the study I mainly focused on:

- The impact of single parasite species and the parasite community on the condition of hedgehogs.
- The impact of single parasite species and the parasite community on the weight of different organs
- The impact of single parasite species and the parasite community on size and weight of gonads

II. Materials, animals and methods

1. The experimental hedgehog population

1.1 Hedgehogs

This project was complied under national and European Union regulations (Tierschutzgesetz §8 Abs.1 and §11; Bundesnaturschutzgesetz §43 Abs.8) with respect to the use of animals for scientific purposes. It was accepted by the ethics committee of the Karlsruhe Institute of Technology (KIT) and the Regierungspräsidium Karlsruhe (project number 35-9185.81/G-30/05).

The study was conducted in the years 2006-2008 on a captive hedgehog population consisting of 46 animals in 2006 (19 females, 27 males), 36 animals in 2007 (16 females, 20 males) and 27 animals in 2008 (14 females, 13 males). The population was located in a natural grass and bush garden habitat (1100 m² next to the Zoological Institute, Kornblumenstrasse 13, 76131 Karlsruhe, Germany, figure 11A) with enough opportunities to hide and build nests, including the addition of 40 nest boxes (60 x 42 x 30 cm, figure 11B, 11C). The nest boxes were filled with a bottom layer of newspaper covered by straw. Nests were cleaned when they became unhygienic (damp or contaminated with faeces). This was done at irregular intervals (2006: 0.09 houses/month, 2007: 0.11 houses/month, 2008: 0.06 houses/month).

Figure 11: (A) View on the eastern part of the hedgehog garden with a nesting box placed under a tree. (B) Closed wooden nest boxes. (C) Open nest box, divided into a sleeping area (30 x 42 x 30 cm) filled with hay and a feeding area (30 x 42 x 30 cm) laid out with newspaper.

The animals of this experimental population came from hedgehog care stations from Hamburg, Mühlheim (Hesse), Stocksberg and Forst (Baden-Württemberg), Germany, where they were treated for injuries, diseases and parasite infections prior to the transport to Karlsruhe. All hedgehogs were fully cured, were of normal weight and parasite-free before they were released in their new habitat. They were marked with an electronic chip (Trovan® ID-100, Euro ID Identifikationssysteme GmbH & Co. KG, Weilerswist 53919, Germany) injected under the skin of the back to facilitate the recognition of the individual animals. All experiments were carried out in the period between the end of hibernation in March and the next hibernation period in October. From November to March the hedgehogs hibernated naturally without disturbances.

Cat food (provided by Masterfoods GmbH, Verden 27281, Germany) and fresh water were supplied every evening in each nest box. The animals were weighed and checked for wounds and injuries daily. To minimize the confounding effect of other parasites, faecal samples from each hedgehog were examined once a month for endoparasite infections. Highly infected animals were treated with anti-parasitic drugs according to the nature of infection. In addition, fleas were removed at regular intervals with Bolfo®, and visible mite infections were treated with a bath of Ivamerol® and Hexocil® (active ingredients and manufacturers of all anti-parasitic drugs are listed in appendix I).

The hedgehogs were naturally infested with ticks (*I. ricinus* and *I. hexagonus*). Both tick populations occurred in the habitat prior to the experimental setup and where not manipulated. Once a month every hedgehog was moved into a tick collecting box (60 x 38.5 x 29 cm) for five days. The boxes had a grid of holes 1 cm in diameter and separated from one another by 1 cm in the base, through which ticks detaching from the hedgehogs fell into a shallow, water-filled box. The holding boxes were filled with a layer of scrunched up newspaper. During the five days, the ticks detaching from the hedgehogs were collected daily and blood samples were taken once during this time. Sampling of ticks and blood was made at intervals of four weeks for each hedgehog. After the five days, the hedgehogs were returned to the hedgehog enclosure.

1.2 Ticks

Engorged ticks naturally detaching from the hedgehogs were collected and dried on tissue paper. All ticks remaining on the hedgehogs after five days were removed with fine forceps. The life-history stages of the ticks were determined and they were identified to species after ARTHUR (1963). Then they were counted and each life-history stage and species weighed separately in milligrams using an analytical balance (AB204, Mettler-Toledo GmbH, Gießen, 35353, Germany). To obtain a measure correlated to the total blood loss induced by ticks I pooled the weight of engorged and partial or fully unengorged ticks of both species and all life stages.

1.3 Blood sampling

The method I describe here was developed in our department under the supervision of Dr. med. vet. Thomas Bücher. It is superior to more commonly used methods in being quick, relatively painless for the hedgehog, and requiring no anaesthesia. The hedgehog is held under the rump and head by one person wearing leather gloves for protection from the spines. This person then unrolls the hedgehog gently and secures it, so that it cannot move too much while a hind leg is pulled carefully downwards by a second person (figure 12). This second person also places a tourniquet for small animals (Sarstedt, Lower Saxony, 31157, Germany) as high up the leg as possible to make the veins visible and to accumulate blood (figure 13). The surface of the skin is then cleansed and disinfected with a swab soaked in 70% ethyl alcohol by a third person.

Figure 12: Person securing an unrolled hedgehog under the chin and the rump. The hind leg is pulled gently by second person who also places a tourniquet for small animals around the hind leg.

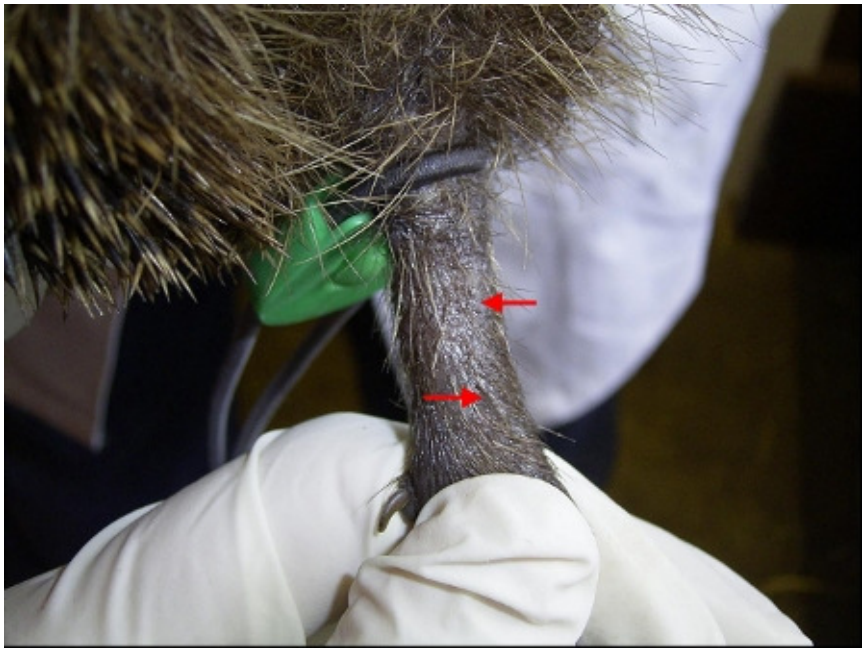

Figure 13: Hind leg of a hedgehog with a placed tourniquet. Red arrows indicate visible veins.

Prior to puncture, the needle (21 G x 5/8", Terumo Europe, Leuven, 3001, Belgium) and the potassium-EDTA-coated multivette tube for blood counts or the multivette tubes for serum collection (1000 µl, Sarstedt, Lower Saxony, 31157, Germany) are connected to each other. The needle is then inserted, as obliquely as possible, into the lateral saphenous vein. Thereafter, the tourniquet is loosened. Although blood can now be seen at the end of the

needle, it does not always flow immediately into the collecting tube. In this case, the position of the needle must be corrected so that it is centred in the lumen of the vein. Blood will now move into the tube under capillary action (figure 14). This step must be carried out patiently. If the blood flows too slowly it will coagulate and clog the needle or tube. If this happens the procedure must be stopped immediately.

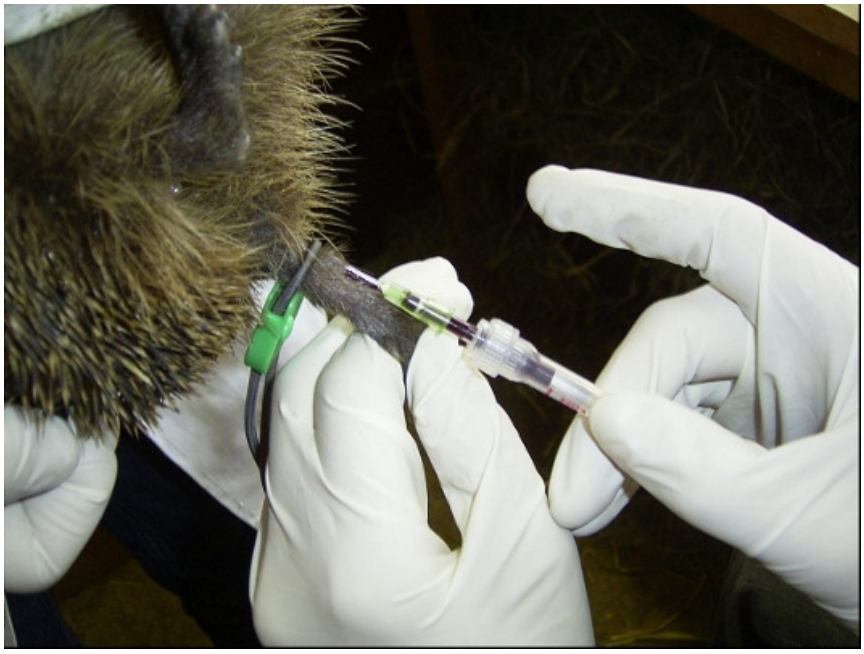

Figure 14: Needle and connected multivette tube inserted in the lateral saphenous vein of a hedgehog. Notice: the tourniquet is loosened and the blood flows under capillary action into the tube.

The sampling is complete once the multivette tube is full. At this stage, the tourniquet should be completely removed and the site dabbed with Lotagen® concentrate (active ingredient policresulen, Essex Tierarznei, Munich, 81737, Germany) after removing the needle until the bleeding stops. The cessation of blood flow should be observed, after which the hedgehog can be released back into its natural environment.

1.4 Blood parameters

Blood samples were examined during 2006 (June-October), 2007 and 2008 (March-October). March is the month that the hedgehogs awake from hibernation and November the month when hibernation begins.

A sample of 1000 µl of blood was collected from the lateral saphenous vein of each hedgehog in 2006 for serum analysis. In 2007 and 2008 two blood samples with 1000 µl each were taken for (i) serum collection and (ii) for blood counts. For each hedgehog blood samples

were taken at intervals of four weeks. The collected volume is small in relation to that taken by the ticks. Within one hour after collection of the samples, the blood was taken to the Institute for Medical Laboratory Diagnostics of the Städtische Klinikum Karlsruhe and tested using a haematology automated analyzer, the Sysmex XE-2100 (Sysmex Deutschland GmbH, Norderstedt, 22848, Germany) instrument that is usually used in human medicine. Among other features this instrument allows the measurement of platelets with two different methods: (i) radio-frequency resistance (impedance method) and (ii) flow cytometry (optical fluorescence method). Since microcytic or fragmented erythrocytes may be mistaken for platelets if measured by the impedance method, the hedgehog thrombocytes were determined flow cytometrically. The flow cytometry on the Sysmex instrument series has already been successfully evaluated and established for the measurement of thrombocytes in various vertebrate species (XT-2000iV – Fluoreszenz-Durchflusszytometrie in der Tierblutanalytik, Sysmex Xtra 2/2007; www.sysmex.de/files/articles/Xtra_XT-VET_FFC.pdf, 15.12.2009). Furthermore, the XE-instrument counts nucleated red blood cells (NRBC) and subtracts their number from the white cell count. On other automated analyzers these NRBCs may be misclassified as leucocytes, thus falsely elevating the white blood cell count. Due to the large variability in both white and red cell morphology the automated differential blood count was not included in the analyses. Instead, conventional thin blood smears were prepared and dyed with May-Grünwald-Giemsa stain. Dyes and phosphate buffer tablets (pH 7.2) were purchased from Merck (Darmstadt, 64293, Germany). Blood films were microscopically investigated using an oil-immersion lens at 1000-fold magnification, and a differential blood cell count was done on 100 leucocytes per smear.

The following parameters were measured: leucocytes (/nl) [monocytes (%), lymphocytes (%), neutrophils (%), eosinophils (%), basophils (%)], erythrocytes (/pl), haemoglobin (g/dl), haematocrit (%), MCV (mean corpuscular volume in fl), MCH (mean corpuscular haemoglobin in pg), MCHC (mean corpuscular haemoglobin concentration in g/dl), thrombocytes (/nl) and relative (‰) and absolute reticulocytes (/nl).

The blood samples for the serum were treated as follows: multivette tubes were centrifuged for 10 min at a speed of 13,200 rpm (Eppendorf Centrifuge 5415D, Eppendorf AG, Hamburg, 22339, Germany). The blood sample was then separated in the blood clot at the bottom of the tube and the serum at the top of the clot. The serum was pipetted of and transferred to a reaction tube (Eppendorf tubes, 1.5 ml, Eppendorf Vertrieb Deutschland GmbH, Wesseling/Berzdorf, 50389, Germany) which was frozen at -20°C until further use.

From 2006 to 2008 the serum was examined to determine the cortisol concentrations (µg/dl) of both sexes and testosterone concentrations of the males (ng/dl). No blood counts were made in 2006. Correlations were sought between the blood parameters and the total weight of ticks (both species, all life stages) which infested the individual hedgehogs. All analyses involving the blood sera were conducted with the Architect device series (Architect I1000, CI8200, CI16200; Abbot Diagnostics Deutschland, Abbott GmbH & Co. KG, Wiesbaden, 65205, Germany). Hormone concentrations were tested using enzyme immunoassays.

1.5 Regeneration

To test whether changes in blood parameters were influenced by ticks, I carried out a regeneration experiment in 2009. Five hedgehogs (two females, three males; R-group) which hibernated in the hedgehog garden and were naturally infested with ticks were taken out of the garden. The ticks were collected as described previously (chapter II.1.2), and blood samples for a blood count were taken (14.4.2009). Additionally, I looked at a control group (C-group) of five male hedgehogs which hibernated in a tick-free enclosure and were tick-free for at least half a year. Blood samples from these were taken at the same time as for the R-group. After blood sampling and tick collection all animals were transferred to a tick-free enclosure. After four (12.5.2009) and six weeks (26.5.2009) blood counts were conducted again for each animal. Blood parameters of the different sampling dates and the two sample groups were then compared with each other.

1.6 Climate parameters

To test for correlations between climate parameters (mean temperature in °C, relative humidity in %, rainfall in mm) and blood parameters, hormones and tick densities respectively I used climatic data from a meteorological station in Karlsruhe (station ID 10727, Hertzstrasse 137, 76187, Karlsruhe, Germany), provided by the Deutscher Wetterdienst DWD (http://www.dwd.de/bvbw/appmanager/bvbw/dwdwwwDesktop?_nfpb=true&_pageLabel=_dwdwww_klima_umwelt_klimadaten_deutschland&T82002gsbDocumentPath=Navigation%2FOeffentlichkeit%2FKlima__Umwelt%2FKlimadaten%2Fkldaten__kostenfrei%2Fausgabe__tageswerte__node.html__nnn%3Dtrue, 18.12.2009). For the correlations I chose the mean daily values of the climate data both from two weeks and four weeks before the blood sampling and tick collection in order to determine potential short term and long term effects

of climate on physiological parameters. All climate data are shown in the appendix II tables I-III.

2. Hedgehog dissections

2.1 Hedgehog samples

The hedgehog samples from Germany and the UK comprised animals which had died naturally and were provided by cooperating wildlife rescue stations or from road kills collected by members of the working group and students of the Karlsruhe Institute of Technology. Only those hedgehogs were included in the analyses which were not treated with anthelmintica, for which date of death and origin were known, and in which all internal organs were fully existent (no signs of decomposition). In addition, pregnant females were excluded from the analyses. Hedgehogs from New Zealand were provided by predator/pest-control programs organized by the government (e.g. Department of Conservation), caught with live traps and killed afterwards or were collected as road kills. All hedgehogs were either examined immediately after death or the bodies were frozen at –20 °C until they were used for dissection. The hedgehogs from the experimental population which died during the experiment were not used for the statistical analyses, since they were regularly treated with anti-parasitic drugs, so confounding effect cannot be excluded.

2.2 Biometrical data

Frozen hedgehogs were thawed at room temperature and then weighed accurate to the gram. Hedgehogs were classified either as hoglets (< 100 g), juveniles (< 500 g) or adults (> 500 g). The sex of hedgehogs was identified by the position of the primary sexual organs. The vulva of the females is positioned directly anterior to the anus, while the penis sheath is about in the middle of the body (figure 15). The body length in cm (nose tip to tail) of the unrolled hedgehog was taken with a measuring tape attached closely to the body.

The body length and weight of the hedgehogs were used to calculate an index for condition. Therefore I used the method described in KREBS and SINGLETON (1993) in the cases where I found a significant correlation between body weight and body length. This involves three steps: (i) to calculate the regression between the body length (x) and the body mass (y), (ii) to predict the body mass from the observed body length using the estimated regression and (iii)

to estimate the condition for each individual by using the ratio of observed body weight to predicted body weight.

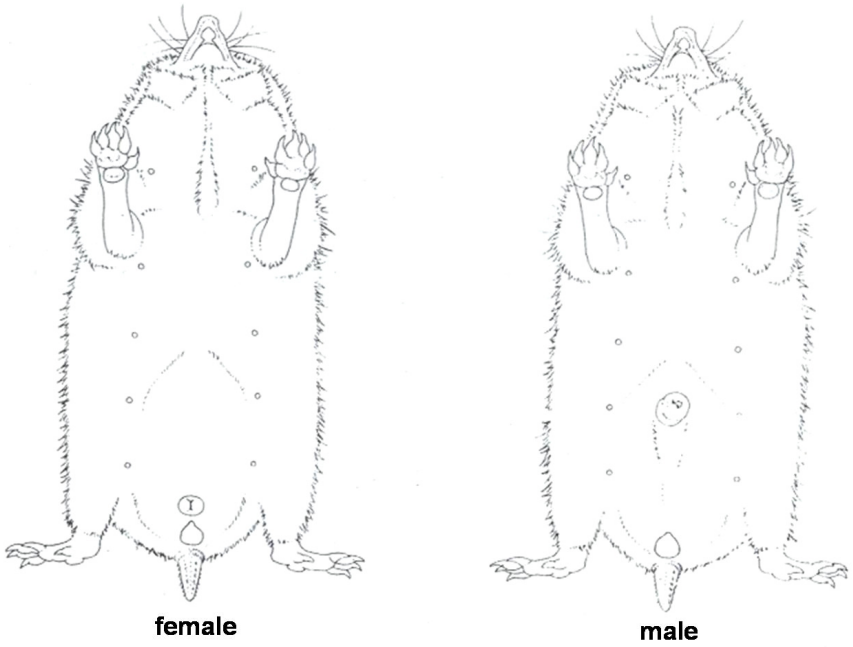

Figure 15: Primary sex characteristics of hedgehogs. The female's vulva is positioned directly above the anus, the penis sheath of the male lays in the middle of the body (modified after REEVE 1994).

2.3 Organs

Organ weight was measured in grams, accurate to two decimal places, with an analytical balance (AB204, Mettler-Toledo GmbH, Gießen, 35353, Germany). The following organs were weighed: liver (including the gall bladder), spleen, kidneys (including the suprarenal glands), heart, and lungs. In addition measurements of the sexual organs for both sexes were made. For males I weighed the prostate, seminal vesicles, testes (including epididymis) and the penis. Additionally, I measured the length of the penis and the length and width of both testes. For females, I weighed the uterus, including the uterine horns and ovaries, and measured the length of the uterine horns and the length and width of the uterus. Figure 16 illustrates the reproductive organs of male and female hedgehogs.

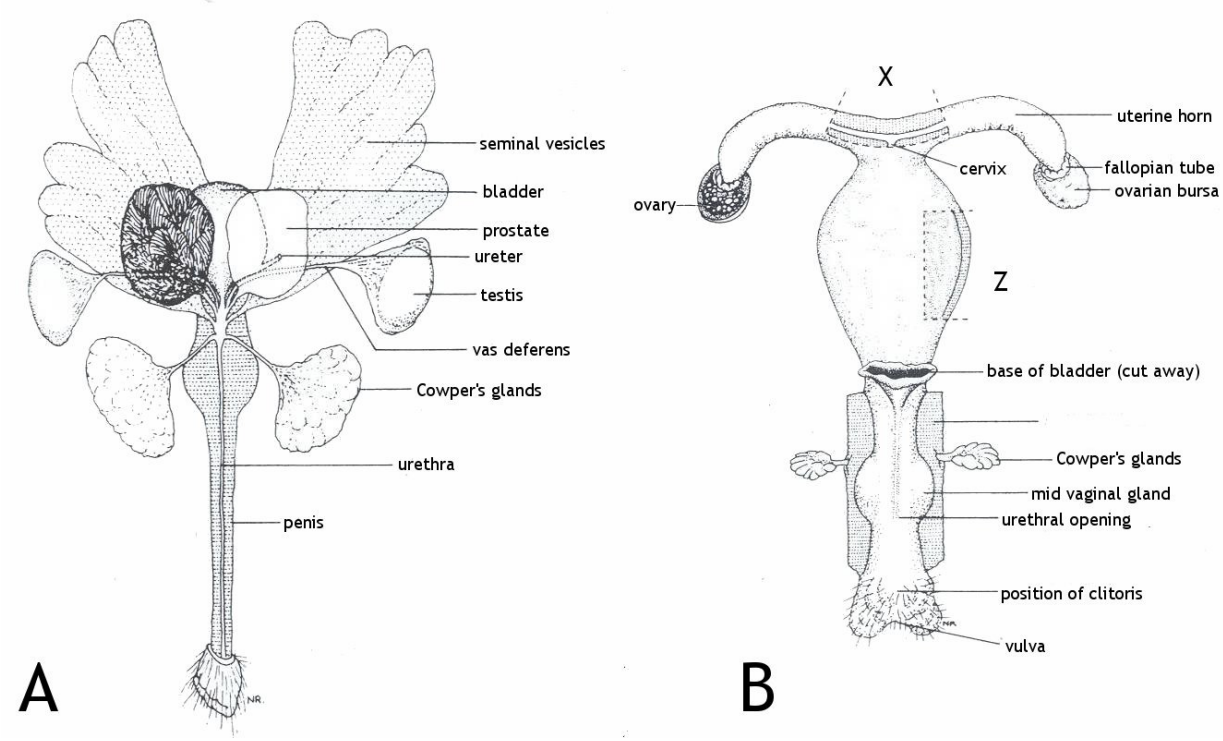

Figure 16: Illustration of the reproductive organs of male (A) and female (B) hedgehogs in breeding condition. X shows a cut away of the uterus showing the lumen between the uterine horns. Z shows a cut away of the upper vagina to show the relatively thin wall (modified after Reeve 1994).

2.4 Parasites

Fleas and ticks were collected, identified to species, quantified and stored in 70% alcohol. Due to the difficulty of quantifying infestation rates, mites were not included in the investigation.

The body cavity (peritoneum), connective tissue and the surface of the organs were examined for encysted acanthocephalans (*Plagiorhynchus cylindraceus*). Encysted acanthocephalans were relaxed over night in tap water and then stored in 4% formalin.

The lung was examined under a binocular microscope (Stemi 2000, Carl Zeiss Mikroskopie, Jena, 07740, Germany) for nematode infections. *Crenosoma striatum* and *Capillaria aerophila* from the bronchi and bronchioles were quantified and stored in 70% ethanol. The intestine was divided into eight sections of the same length (not including the stomach). The stomach and the single sections were stored over night in tap water in the refrigerator at 4 °C to allow the intestinal parasites from the intestinal wall to move into the water. The next day, the water and the intestinal sections were examined under a binocular microscope (water with transmitted light, intestinal sections with direct light). All parasites found were identified,

quantified and stored. *Capillaria* spp. were stored in 70% ethanol, *Brachylaemus erinacei* and *P. cylindraceus* were stored in 4% formalin.

3. Statistics

All statistical analyses were carried out using the statistical program SPSS for Windows version 11.5 or 17 respectively (SPSS Inc®). Prior to all tests, an exploratory data analysis was performed to check whether data was normally distributed or not. Normally distributed data sets were analyzed with parametric tests, while non-parametric tests were used for data with non-normal distributions. To test for differences between means I have chosen a t-test (parametric) or a Mann-Whitney U-test (non-parametric) for unpaired two-sample data sets and an analysis of variance (one-way ANOVA, parametric) or a Kruskal-Wallis analysis of variance (Kruskal-Wallis test, non-parametric) for multi-sample data sets. In the regeneration experiment I used a two-way ANOVA (repeated measures) to test for differences in means. A Pearson correlation was used to determine the association between two parameters. Chi-square and Fisher's exact tests were used to test for differences in parasite prevalence in the hedgehog dissections. I used multiple regressions with a stepwise method to analyze the relationship between several predictor variables (parasites) and a criterion variable (weight/length ratio, condition factor, organ weights). For all tests performed a critical p-value of $\alpha = 0.05$ was used to define significance. The result chapters III.1 and IV.1 provide exact information about which test was used to analyze the different data sets.

III. The experimental hedgehog population

1. Results

1.1 Tick population

Ticks were collected from March to October in every year (2006-2008). In 2006 I collected ticks from 46 hedgehogs (19 females, 27 males), in 2007 from 36 (16 females, 20 males) and in 2008 from 27 (14 females, 13 males). Figures 17-20 show the annual distribution of ticks, separated by species and life stage, for the whole investigation period.

No differences were found between male and female hedgehogs at any time of the year, except for larvae (*I. ricinus* October 2006, $p = 0.044$; *I. hexagonus* May 2007, $p = 0.032$), nymphs (*I. hexagonus* September 2006, $p = 0.021$, July 2008, $p = 0.031$), females (*I. ricinus* April 2006, $p = 0.038$, September 2006, $p = 0.011$; *I. hexagonus* June 2007, $p = 0.049$) and males (*I. ricinus* September 2006, $p = 0.038$, September 2007, $p = 0.027$; *I. hexagonus* September 2006, $p = 0.031$). Given an α-value of 0.05 and the total number of tests carried out, these results can be considered as a type 1 error and I therefore pooled both sexes for the statistical analyses. Table 3 shows the number of hedgehogs from which I collected ticks for each month and year. Each year was analyzed separately as there were differences in temperature, hedgehog population density and vegetation (data not shown).

Table 3: Number of hedgehogs used for the tick counts during the investigation period (2006-2008, March-October). Total represents the cumulative sum of hedgehogs used during a year and not the number of individual hedgehogs in the experimental population.

Month	2006	2007	2008
March	3	22	10
April	32	28	21
May	37	31	20
June	33	32	23
July	31	30	21
August	29	26	13
September	33	22	10
October	23	18	9
Total	221	209	127

Table 4: Mean numbers of *I. ricinus* ticks counted for each life stage during the investigation period (2006-2008, March-October). Standard deviation is shown in brackets. P shows differences between the years and was evaluated with an ANOVA [tick numbers were logged ($log_{10}x+1$) prior to the analysis]. Significant values are in bold.

I. ricinus		March	April	May	June	July	August	September	October
Larvae	2006	0 (0)	8.25 (10.28)	23.73 (19.66)	31.09 (51.4)	470.01 (377.11)	228.93 (153.56)	97.82 (175.05)	16.48 (16.21)
	2007	11.09 (24.79)	12.63 (15.86)	35.03 (40.24)	101.44 (113.72)	195.33 (171.96)	213.62 (168.61)	66.55 (51.15)	19.44 (17.49)
	2008	14.6 (15.48)	42.57 (48.39)	90.9 (81.12)	83.3 (108.5)	575.05 (513.74)	308.23 (291.9)	41.4 (49.24)	39.89 (45.82)
	p	**0.023**	**0.001**	**0.01**	**0.001**	0.428	0.685	0.109	0.277
Nymphs	2006	3.33 (4.93)	103.81 (106.38)	40.27 (27.43)	4.55 (4.62)	6.19 (7.94)	33.45 (71.26)	145.45 (120.23)	128.91 (128.52)
	2007	54.05 (61.17)	46.3 (46.56)	24 (22.57)	4.39 (9.23)	10.47 (10.22)	22.19 (26.24)	50.05 (42.64)	79.61 (87.73)
	2008	127.8 (114.81)	234.52 (248.27)	130.65 (105.98)	25.91 (29.01)	17.9 (22.66)	45.85 (45.34)	43.2 (42.11)	131 (151.04)
	p	**0.001**	**0.001**	**0.001**	**0.001**	**0.039**	0.201	**0.001**	0.708
Females	2006	0 (0)	7.63 (7.28)	7.38 (6.22)	0.94 (1.56)	0.13 (0.34)	4.41 (6.75)	18.58 (14.78)	9.7 (8.41)
	2007	7.36 (5.44)	12.58 (14.73)	13.35 (12.12)	2.16 (2.46)	0.3 (0.65)	6.54 (6.28)	8.91 (6.73)	4.61 (4.86)
	2008	18.4 (19.59)	22.05 (18.97)	19 (14.31)	6.3 (8.07)	0.94 (2.1)	15.23 (13.68)	11.9 (7.68)	13.67 (12.9)
	p	**0.003**	**0.031**	**0.009**	**0.001**	0.061	**0.001**	**0.018**	**0.048**
Males	2006	0 (0)	1.84 (2.4)	2.11 (2.13)	0.15 (0.36)	0 (0)	1.31 (1.97)	6.03 (5.44)	3.04 (3.78)
	2007	1.59 (1.4)	2.29 (3.43)	1.65 (1.76)	0.25 (0.62)	0.03 (0.18)	2.46 (2.58)	2.59 (2.16)	1.28 (1.84)
	2008	6.8 (7.71)	7.95 (7.91)	0.05 (0.22)	3.75 (5.05)	0.29 (0.78)	6.54 (7.22)	5.6 (4.74)	4.67 (4.18)
	p	**0.017**	**0.001**	0.182	**0.001**	**0.036**	**0.001**	**0.011**	**0.039**

Table 5: Mean numbers of *I. hexagonus* ticks counted for each life stage during the investigation period (2006-2008, March-October). Standard deviation is shown in brackets. P shows differences between the years and was evaluated with an ANOVA [tick numbers were logged ($log_{10}x+1$) prior to the analysis]. Significant values are in bold.

I. hexagonus		March	April	May	June	July	August	September	October
Larvae	2006	4.33 (5.13)	26.91 (34.74)	38.49 (51.25)	22.27 (15.03)	9.03 (17.86)	3.83 (4.33)	99 (103.14)	90.7 (159.17)
	2007	15.05 (39.38)	6.39 (9.84)	16.58 (24.62)	24.22 (34.05)	22.33 (49.32)	4.58 (7.09)	4.5 (8.17)	9.22 (13.31)
	2008	0.4 (0.84)	4.43 (11.21)	11 (31.65)	7.91 (9.36)	25 (64.33)	40.08 (95.5)	3.3 (7.42)	4 (5.5)
	p	**0.001**	**0.001**	**0.001**	**0.001**	0.66	**0.011**	**0.001**	**0.001**
Nymphs	2006	6.67 (4.93)	11.66 (20.78)	14.57 (25.52)	31.09 (46.41)	11.77 (12.5)	7.07 (11.35)	14.52 (22.5)	29.7 (37.14)
	2007	5.41 (9.9)	2.36 (3.72)	13.58 (14.21)	15.56 (23.82)	26.33 (34.09)	6.23 (5.57)	2.59 (3.62)	3.56 (5.09)
	2008	3.6 (6.19)	1.95 (3.77)	7.55 (11.84)	7.52 (12.96)	7.14 (11.34)	12.69 (15.27)	6.3 (11.54)	3.89 (4.73)
	p	0.330	**0.001**	**0.017**	**0.001**	**0.001**	0.750	**0.002**	**0.001**
Females	2006	0.33 (0.58)	2.75 (4.23)	1.24 (1.23)	12.42 (10.10)	15.71 (19.12)	11.03 (12.7)	8 (7.73)	3.78 (5.96)
	2007	4.95 (12.75)	0.79 (1.29)	2.65 (3.46)	4.75 (6.37)	4 (3.01)	6.96 (6.49)	2.36 (2.66)	1.72 (2.44)
	2008	1.1 (1.73)	0.52 (0.93)	4.5 (6.44)	5 (4.9)	6.05 (8.71)	6.38 (7.41)	3.3 (4.95)	1.67 (2.29)
	p	0.242	**0.002**	**0.012**	**0.001**	**0.001**	0.138	**0.001**	0.233
Males	2006	0 (0)	0.03 (0.18)	0.05 (0.23)	0.55 (1.06)	0.16 (0.45)	0.1 (0.31)	0.21 (0.55)	0.35 (0.49)
	2007	0.14 (0.35)	0.07 (0.38)	0.03 (1.8)	2.16 (2.46)	0 (0)	0.15 (0.37)	0.18 (0.5)	0 (0)
	2008	0.2 (0.42)	0 (0)	0.05 (0.22)	0.13 (0.46)	0.52 (1.78)	0.08 (0.28)	0 (0)	0.11 (0.33)
	p	0.699	0.644	0.909	**0.023**	0.114	0.753	0.460	**0.012**

1.1.1 Larvae

I. ricinus larvae peaked in summer (2006 July-August, 2007 June-September, 2008 May-August) reaching very high densities in July 2006 and 2008 (figure 17). There were differences in the larval counts between the years for March, April, May and June (table 4). In April and May the larval numbers were highest in 2008 and lowest in March and June in 2006.

I. hexagonus showed a conspicuously different pattern, with comparatively little seasonal shift in abundance and considerably lower overall density compared to *I. ricinus*. During *I. ricinus* peak periods the densities of *I. hexagonus* reached their lowest values (figure 17). There were differences in the tick counts over the years from March-June and August-October (table 5). For April, May, September and October I found the highest larval numbers in 2006, for August in 2008 and for March in 2007. June had the lowest tick numbers in 2008.

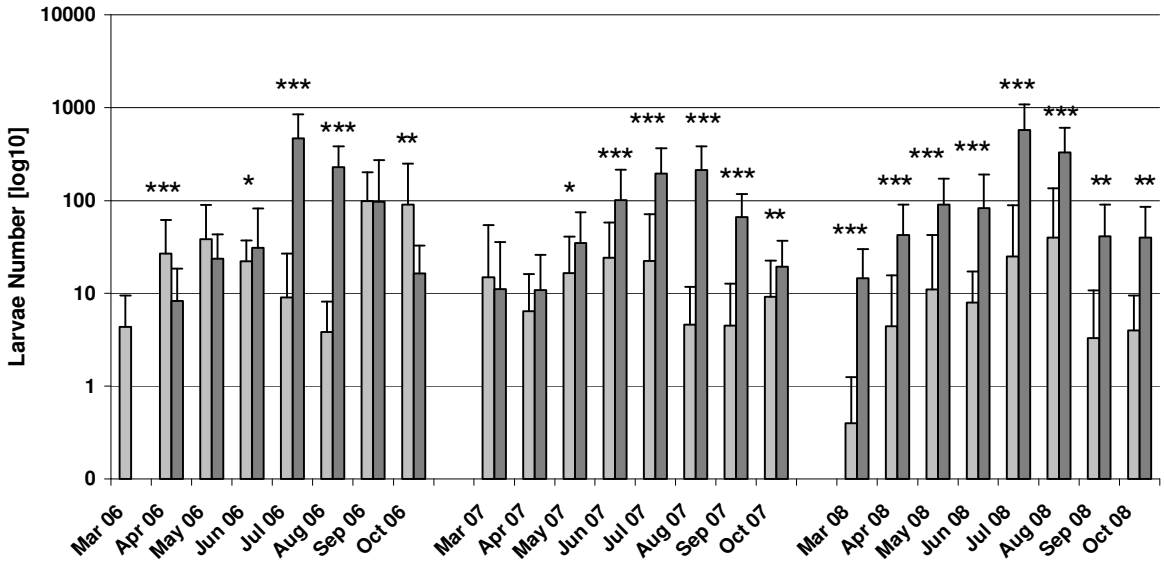

Figure 17: Seasonal distribution of mean larval numbers ($\log_{10}x+1$) of *Ixodes ricinus* ■ and *I. hexagonus* □ during the investigation period (2006-2008, March-October). Error bars indicate standard deviation of mean tick numbers. Hedgehog sexes are pooled. Asterisks show significance between both tick species (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$). P was estimated with a Mann-Whitney U-Test.

1.1.2 Nymphs

I. ricinus nymphs revealed a bimodal seasonal distribution peaking in spring (2006 April-May, 2007 March-May, 2008 March-May) and autumn (2006 September-October, 2007 September-October, 2008 August-October) of each year. This is in contrast to the larvae of this species with only one population peak in summer. During these peaks the densities were always higher than that of *I. hexagonus* (figure 18). The abundance of *I. ricinus* nymphs displayed no yearly differences in August and October (table 4). From March to July the highest nymphal counts were observed in 2008. In September most nymphs were found in 2006.

The population density of *I. hexagonus* nymphs, like larvae, changed only little in 2006 and 2008. Again, the amplitude of variation was comparatively stable and lower in abundance than that for nymphs of *I. ricinus* (figure 18). In 2007 I found a slight peak in May-July (figure 18). Yearly differences were observed from April-July and September-October with the highest nymph counts in 2006. In 2007 the highest nymph numbers appeared in July (table 5).

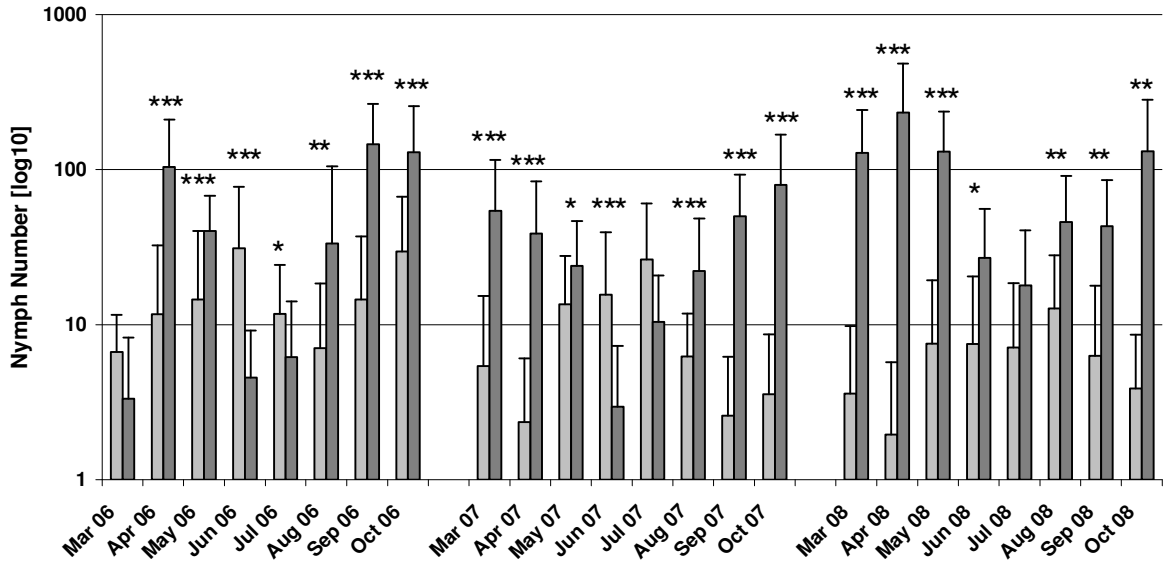

Figure 18: Seasonal distribution of mean nymph numbers ($log_{10}x+1$) of *Ixodes ricinus* ■ and *I. hexagonus* □ during the investigation period (2006-2008, March-October). Error bars indicate standard deviation of mean tick numbers. Hedgehog sexes are pooled. Asterisks show significance between both tick species (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$). P was estimated with a Mann-Whitney U-Test.

1.1.3 Females

Female adult *I. ricinus* had consistent peaks in spring (2006 April-May, 2007 March-May, 2008 March-May) and autumn (2006 August-October, 2007 August-October, 2008 August-October) comparable with the nymphs of that species. At these periods their density considerably exceeded that of *I. hexagonus* (figure 19). Female numbers differed monthly in all years except for July. In all cases tick counts were highest in 2008 (table 4). The only exception was September 2006 with the highest tick numbers.

Female *I. hexagonus* were seasonally distributed with summer peaks in 2006 (June-September) and 2007 (June-August) (figure 19). In 2008 the tick density changed little, with the lowest values in March and April. Yearly variation in abundance occurred from April-July and in September (table 5). April, June, July and September had the highest tick numbers in 2006, May in 2008.

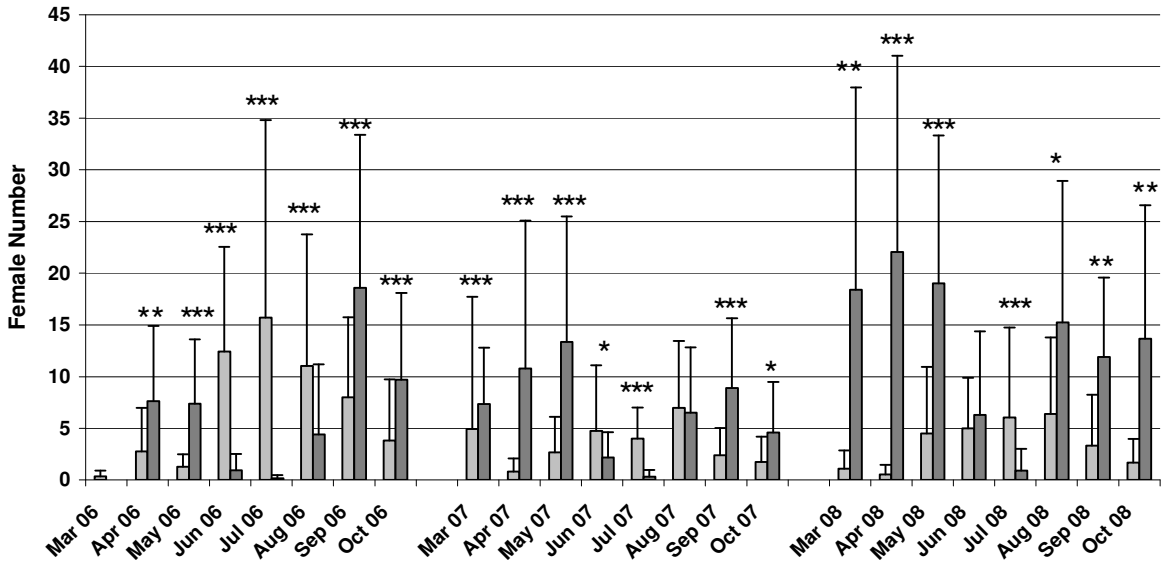

Figure 19: Seasonal distribution of mean female numbers of *Ixodes ricinus* ■ and *I. hexagonus* □ during the investigation period (2006-2008, March-October). Error bars indicate standard deviation of mean tick numbers. Hedgehog sexes are pooled. Asterisks show significance between both tick species (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$). P was estimated with a Mann-Whitney U-Test.

1.1.4 Males

Males of *I. ricinus* showed a similar yearly pattern compared to females and nymphs. In 2006 I detected only one peak in September and October. In 2007 and 2008 there were two peaks from March-May and August-October. As with the other life history stages, male *I. ricinus* were usually much more common than *I. hexagonus* and the amplitude of variation was considerably higher (figure 20). In 2008 I counted the highest male numbers of *I. ricinus* from March-May and August-October (table 4). *I. ricinus* counts differed yearly for every month, except for May. Most males were found in 2008, except for September. Here the counts from 2006 and 2008 did not differ from each other, but I detected the lowest counts in 2007.
Male *I. hexagonus* showed no clear seasonal distribution pattern (figure 20). Tick counts were low at all times of the year. Yearly differences were found in June and October, with the highest (June) and lowest (October) tick counts in 2007 (table 5).

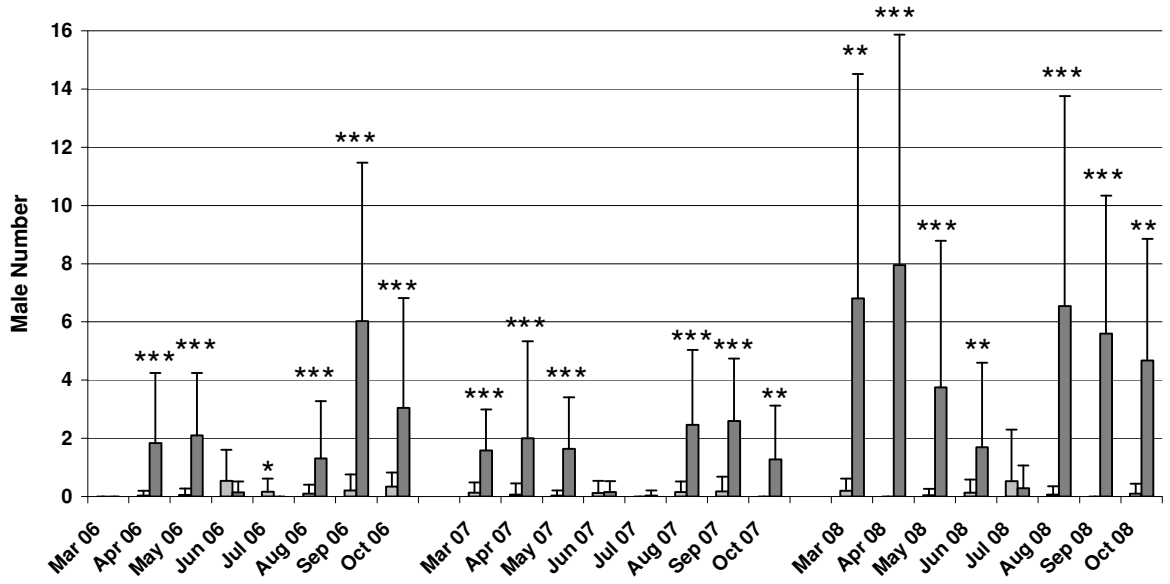

Figure 20: Seasonal distribution of mean male numbers of *Ixodes ricinus* ■ and *I. hexagonus* □ during the investigation period (2006-2008, March-October). Error bars indicate standard deviation of mean tick numbers. Hedgehog sexes are pooled. Asterisks show significance between both tick species (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$). P was estimated with a Mann-Whitney U-Test.

1.1.5 Ticks and climate parameters

To test for correlations between temperature, relative humidity, rainfall and tick density I used a Pearson correlation. Years were treated separately. Tables 6-8 present the results of these correlations.

Larvae of *I. ricinus* correlated significantly positively with temperature in all years. Negative significant correlations with humidity were found in 2006 and 2008, positive significant correlations in 2007. Rainfall correlated significantly positively two weeks before sampling in 2006 and 2008 and four weeks before sampling in 2006 and 2007.

Nymphs of *I. ricinus* correlated significantly negatively with temperature in all years. Positive significant correlations with humidity were only found in 2006. Rainfall correlated significantly negatively in 2006 two weeks before sampling and in 2007 four weeks before sampling.

I. ricinus females showed a similar pattern in their relation to temperature as nymphs. I found positive significant correlations with humidity in 2006 and negative significant correlations in 2007. Rainfall correlated significantly negatively with tick numbers in 2007 four weeks before sampling and 2008 two weeks before sampling and significantly positively in 2007 two weeks before sampling.

Males of *I. ricinus* correlated significantly negatively with temperature in 2006 and 2008 two weeks before sampling and in 2008 four weeks before sampling. Significant positive correlations with humidity were found in 2006 and 2008, significant negative correlations in 2007. The only significant negative correlation with rainfall was found in 2007 four weeks before sampling.

For larvae of *I. hexagonus* I found positive significant correlations with temperature in 2008 but not in the other years. Larval numbers correlated significantly positively with humidity two weeks before blood sampling in 2006 and 2007 and four weeks before sampling date in 2006 but no significant correlations were found in 2008. For rainfall I found both positive and negative significant correlations but no clear trend.

Nymphs of *I. hexagonus* correlated significantly positively with temperature in 2007 and 2008 two weeks and four weeks before sampling, but no significant correlations were found in 2006. For humidity I only found a significant positive correlation in 2007 two weeks before sampling date. No significant correlations were found for rainfall.

I. hexagonus female abundance correlated significantly positively with temperature two weeks before sampling in 2006 and 2008 and four weeks before sampling in all years. For

humidity no clear trends were found. For rainfall significant positive correlations were found in 2006 and in 2007, but here only four weeks before blood sampling.

Male *I. hexagonus* correlated significantly positively with temperature in 2006 two weeks before blood sampling. No relationship was found for humidity. For rainfall I found significant positive correlations for 2006 and 2008 two weeks before blood sampling.

Table 6: Pearson correlation between temperature (°C) and tick density. Hedgehog sexes and months are pooled, years are treated separately. N = number of samples, r = correlation coefficient, p = probability, *Ir* = *I. ricinus*, *Ih* = *Ixodes hexagonus*. Significant p-values are in bold.

Tick species and life history stage	Year	Mean temperature two weeks before sample date			Mean temperature four weeks before sample date		
		N	r	p	N	r	p
Larvae *Ir*	2006	220	0.525	**0.001**	220	0.535	**0.001**
	2007	208	0.429	**0.001**	208	0.482	**0.001**
	2008	124	0.413	**0.001**	124	0.432	**0.001**
Nymphs *Ir*	2006	220	-0.286	**0.001**	220	-0.202	**0.001**
	2007	208	-0.327	**0.001**	208	-0.297	**0.001**
	2008	124	-0.453	**0.001**	124	-0.490	**0.001**
Females *Ir*	2006	220	-0.203	**0.002**	220	-0.202	**0.003**
	2007	208	-0.132	0.058	208	-0.167	**0.016**
	2008	124	-0.316	**0.001**	124	-0.388	**0.001**
Males *Ir*	2006	220	-0.140	**0.038**	220	-0.117	0.083
	2007	208	-0.099	0.157	208	-0.095	0.174
	2008	124	-0.341	**0.001**	124	-0.346	**0.001**
Larvae *Ih*	2006	220	-0.092	0.175	220	-0.045	0.504
	2007	208	0.074	0.285	208	0.095	0.172
	2008	124	0.194	**0.031**	124	0.204	**0.023**
Nymphs *Ih*	2006	220	-0.063	0.350	220	-0.025	0.707
	2007	208	0.224	**0.001**	208	0.246	**0.001**
	2008	124	0.248	**0.005**	124	0.239	**0.008**
Females *Ih*	2006	220	0.362	**0.001**	220	0.332	**0.001**
	2007	208	0.122	0.079	208	0.141	**0.042**
	2008	124	0.274	**0.002**	124	0.300	**0.001**
Males *Ih*	2006	220	0.140	**0.038**	220	0.094	0.163
	2007	208	-0.048	0.495	208	-0.016	0.823
	2008	124	0.076	0.399	124	0.099	0.274

Table 7: Pearson correlation between relative humidity (%) and tick density. Hedgehog sexes and months are pooled, years are treated separately. N = number of samples, r = correlation coefficient, p = probability, *Ir* = *I. ricinus*, *Ih* = *Ixodes hexagonus*. Significant p-values are in

Tick species and life history stage	Year	Mean humidity two weeks before sample date			Mean humidity four weeks before sample date		
		N	r	p	N	r	p
Larvae *Ir*	2006	220	-0.220	**0.001**	220	-0.245	**0.001**
	2007	208	0.138	**0.047**	208	0.165	**0.017**
	2008	124	-0.265	**0.003**	124	-0.305	**0.001**
Nymphs *Ir*	2006	220	0.378	**0.001**	220	0.357	**0.001**
	2007	208	-0.029	0.678	208	0.033	0.641
	2008	124	0.062	0.493	124	0.141	0.118
Females *Ir*	2006	220	0.345	**0.001**	220	0.357	**0.001**
	2007	208	-0.399	**0.001**	208	-0.452	**0.001**
	2008	124	0.039	0.667	124	0.108	0.232
Males *Ir*	2006	220	0.318	**0.001**	220	0.295	**0.001**
	2007	208	-0.212	**0.002**	208	-0.200	**0.004**
	2008	124	0.180	**0.046**	124	0.192	**0.032**
Larvae *Ih*	2006	220	0.244	**0.001**	220	0.179	**0.008**
	2007	208	0.141	**0.042**	208	0.071	0.305
	2008	124	-0.050	0.581	124	-0.105	0.245
Nymphs *Ih*	2006	220	0.083	-0.131	220	0.091	0.177
	2007	208	0.148	**0.033**	208	0.073	0.295
	2008	124	-0.117	0.197	124	-0.237	0.008
Females *Ih*	2006	220	-0.131	0.052	220	-0.155	**0.022**
	2007	208	0.149	**0.031**	208	0.126	0.070
	2008	124	-0.165	0.067	124	-0.159	0.077
Males *Ih*	2006	220	-0.022	0.741	220	0.043	0.528
	2007	208	0.025	0.717	208	0.030	0.664
	2008	124	-0.061	0.500	124	-0.063	0.490

Table 8: Pearson correlation between rainfall (mm) and tick density. Hedgehog sexes and months are pooled, years are treated separately. N =number of samples, r = correlation coefficient, p = probability, *Ir* = *I. ricinus*, *Ih* = *Ixodes hexagonus*. Significant p-values are in bold.

Tick species and life history stage	Year	Mean rainfall two weeks before sample date			Mean rainfall four weeks before sample date		
		N	r	p	N	r	p
Larvae *Ir*	2006	220	0.227	**0.001**	220	0.068	**0.318**
	2007	208	-0.099	0.153	208	0.241	**0.001**
	2008	124	0.281	**0.002**	124	-0.073	0.418
Nymphs *Ir*	2006	220	-0.151	**0.025**	220	-0.052	0.446
	2007	208	0.007	0.919	208	-0.281	**0.001**
	2008	124	-0.154	0.088	124	-0.016	0.862
Females *Ir*	2006	220	-0.131	0.052	220	-0.056	0.048
	2007	208	0.289	**0.001**	208	-0.393	**0.001**
	2008	124	-0.185	**0.040**	124	-0.072	0.428
Males *Ir*	2006	220	-0.114	0.092	220	-0.034	0.617
	2007	208	0.061	0.386	208	-0.255	**0.001**
	2008	124	-0.173	0.055	124	-0.074	0.414
Larvae *Ih*	2006	220	-0.168	**0.012**	220	-0.063	0.353
	2007	208	0.043	0.533	208	0.195	**0.005**
	2008	124	0.187	**0.038**	124	-0.037	0.680
Nymphs *Ih*	2006	220	-0.007	0.918	220	-0.053	0.437
	2007	208	-0.014	0.837	208	0.223	0.001
	2008	124	0.110	0.222	124	-0.047	0.605
Females *Ih*	2006	220	0.261	**0.001**	220	0.189	**0.005**
	2007	208	-0.084	0.228	208	0.229	**0.001**
	2008	124	0.151	0.093	124	-0.086	0.342
Males *Ih*	2006	220	0.142	**0.035**	220	-0.022	0.742
	2007	208	-0.075	0.281	208	0.053	0.450
	2008	124	0.204	**0.023**	124	-0.031	0.737

1.2 The hedgehog population

The size of my hedgehog population in 2006 was 46 animals, in 2007 36 animals and 27 animals in 2008 (see chapter III.1.1). The population density was 4.2 hedgehogs/ha in 2006, 3.3/ha in 2007 and 2.5/ha in 2008. In wild hedgehog populations density varies for different landscapes and regions. BERGERS and NIEUWENHUIZEN (1999) assume population densities of 0.02-0.05 animals/ha in forests, 0.3 animals/ha in rural landscapes, 0.8 animals/ha in suburban areas and 0.007-0.046 animals/ha in large scale agriculture and urban centres. BERTHOUD (1982, citation from HOECK 1987) reports population densities in Switzerland of 0.53-0.6 animals/ha in areas around villages and 0.27-0.34 animals/ha in more rural and forest landscapes. The density of the experimental hedgehog population was thus about 5-10 times higher than wild populations in rural and suburban areas respectively.

During the experiment hedgehogs died naturally. Mortality rates were measured from the arousal from hibernation in one year to the arousal from the next hibernation period in the

next year. In 2006 22 hedgehogs died which accounts for 47.83 % of the population (9 females, 13 males). In April 2007, 12 new hedgehogs (6 females, 6 males) were added to the population. In 2007 the mortality rate was 41.67 % (7 females, 7 males). In April 2008, 6 hedgehogs were added to the population (4 females, 2 males). In 2008 the mortality rate was 81.48 % (11 females, 11 males). Mortality rates from 2006 and 2007 match with the annual mortality rates from wild populations in Sweden with 47 % (KRISTIANSSON 1990) and 40 % in the UK (ESSER 1984). The extremely high mortality rates in 2008 can be explained by the age of the animals. From the 27 animals in 2008, eleven hedgehogs were involved in the experiment from the beginning in 2006. At this time, these animals were at least two years old. The animals added in 2007 were also already mature when they were put in the hedgehog garden, with an average age of about two years. So the majority of the hedgehogs in 2008 had an age of 3-4 years which is the average life span of a hedgehog in the wild (LIENHARDT 1979). As it is impossible to accurately determine the age of a living adult hedgehog, the hedgehogs in the experimental population could be even older than four years. In table 9 the causes of mortality during the years are listed.

Table 9: Mortality in the experimental hedgehog population during the investigation period (2006-2008, March-October), divided into winter mortality (during hibernation), disease (lethargy, apathy, diarrhoea, anorexia, severe weight loss), death after pregnancy or parturition and unknown reasons (NK). Percentage of whole population is shown in brackets. 2006: N = 46, 2007: N = 36, 2008: N = 27.

	2006			2007			2008		
	male	female	total	male	female	total	male	female	total
Winter	3 (6.52)	3 (6.52)	6 (13.04)	4 (11.1)	2 (5.56)	6 (16.67)	2 (7.41)	1 (3.7)	3 (11.11)
Disease	9 (19.57)	4 (8.7)	13 (28.26)	2 (5.56)	4 (11.11)	6 (16.67)	5 (18.52)	2 (7.41)	7 (25.93)
Pregnancy		1 (2.17)	1 (2.17)					3 (11.11)	3 (11.11)
NK	1 (2.17)	1 (2.17)	2 (4.35)	2 (5.56)	1 (2.78)	3 (8.33)	4 (14.81)	5 (18.52)	9 (33.33)
Total	13 (28.26)	9 (19.57)	22 (47.83)	8 (22.22)	7 (19.44)	15 (41.67)	11 (40.74)	11 (40.74)	22 (81.48)

1.3 Hedgehog weight

1.3.1 Annual weight distribution

I tested for differences in total body weight (mean weight one week before blood sampling) and weight gain in % between both sexes with a t-test. I found no significant differences for total body weight except for April ($p = 0.009$), September ($p = 0.012$) and October ($p = 0.05$) 2006 and May 2008 ($p = 0.005$) with females being lighter than males, and I also found no differences in weight gain except for August 2008 ($p = 0.024$) with females loosing weight and males gaining weight in comparison to the previous month. Given an α-value of 0.05 and the total number of tests carried out these results can be considered as a type 1 error and I therefore pooled the data of both sexes and tested with a one-way unpaired ANOVA and a Tukey multiple comparison test for monthly differences between the years. I was not able to use a paired ANOVA because this requires paired data for each hedgehog during the whole investigation period. This was not possible as some hedgehogs died during the experiment, became sick or were not able to be found during several months.

There were no yearly differences for individual months, so I pooled the monthly data for all years. The seasonal weight distribution is shown in figure 21. The lowest weights are found in March, directly after hibernation. The weight peaks are in June and October. The lowest weight occurs in spring and summer. The year can be divided in four weight subgroups presented in table 10. The mean weight of the hedgehogs in the experimental population was 952 g over all years (2006: 913.22 g, 2007: 997.22 g, 2008: 939.78 g).

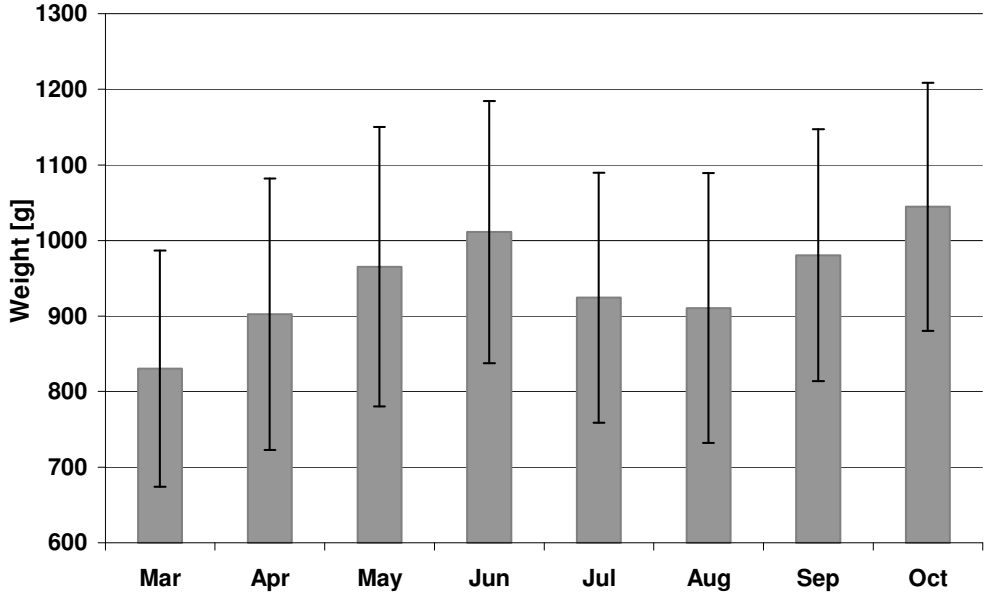

Figure 21: Seasonal distribution of the mean body weight of hedgehogs for the investigation period (2006-2008, March-October). Sexes and years are pooled. Error bars indicate standard deviation for mean body weight.

Table 10: Homogenous subgroups for mean body weight (g) of hedgehogs from the experimental population measured with an ANOVA and a Tukey test. Years and hedgehogs sexes are pooled. N = number of samples, p = probability.

Month	N	Subgroups for α = 0.05			
		Mean subgroup 1	Mean subgroup 2	Mean subgroup 3	Mean subgroup 4
March	38	830.41			
April	82	902.46	902.46		
August	77	910.53	910.53		
July	89		924.28	924.28	
May	96		965.35	965.35	965.35
September	75		980.51	980.51	980.51
June	91			1011.18	1011.18
October	60				1044.35
p		0.112	0.133	0.060	0.123

I also pooled the data for weight gain (or loss) of all years. The distribution and the homogenous subgroups are shown in figure 22 and table 11. During the years there are two periods of high weight gain, one during spring and one in autumn. Between these two periods I observed substantial weight loss in July and August and a very low weight gain in June.

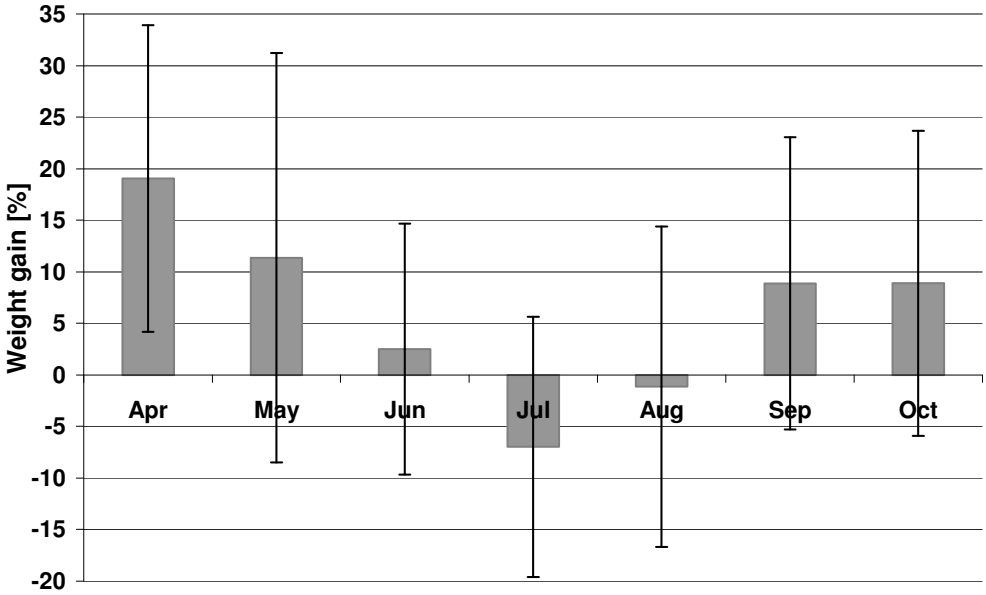

Figure 22: Seasonal distribution of mean weight gain (or loss) in % for the experimental hedgehog population during the investigation period (2006-2008, March-October). Sexes and years are pooled. Error bars indicate standard deviation for mean weight gain.

Table 11: Homogenous subgroups for mean weight gain (or loss) in % of hedgehogs from the experimental population measured with an ANOVA and a Tukey test. Years and hedgehogs sexes are pooled. N = number of samples, p = probability.

Month	N	Subgroups for α = 0.05				
		Mean subgroup 1	Mean subgroup 2	Mean subgroup 3	Mean subgroup 4	Mean subgroup 5
July	80	-6.9747				
August	75	-1.1433	-1.1433			
June	86		2.4950	2.4950		
September	67			8.8766	8.8766	
October	55			8.8956	8.8956	
May	75				11.3673	11.3673
April	34					19.0379
p		0.319	0.828	0.213	0.969	0.069

1.3.2 Hedgehog weight and ticks

I tested for correlations between total tick weight and hedgehog weight and hedgehog weight change with a Pearson correlation. Results are shown in table 12. The mean tick load on the hedgehogs for the whole investigation period was 1.74 g (2006: 2.23 g, 2007: 1.01 g, 2008: 2.14 g). The maximum weight of ticks on a hedgehog was 12.81 g in 2006 (214 *I. hexagonus*- 178 larvae, 25 nymphs, 11 females; 473 *I. ricinus*- 29 larvae, 379 nymphs, 58 females, 7 males), 5 g in 2007 (246 *I. hexagonus*- 187 larvae, 45 nymphs, 14 females; 415 *I. ricinus*- 120 larvae, 279 nymphs, 16 females) and 9.31 g in 2008 (1 *I. hexagonus* female; 1118 *I. ricinus*- 169 larvae, 861 nymphs, 63 females, 25 males) (mean monthly tick weights are shown in appendix III tables IV-VI). Except for weight change in the period June/September/October no correlations were found between the weight of the tick infrapopulation and hedgehog body weight or hedgehog body weight change. Therefore I suggest that ticks do not have a direct influence on body weight of hedgehogs.

Table 12: Pearson correlation between tick weight and hedgehog weight or weight change of hedgehogs for the investigation period (2006-2008, March-October). Years and hedgehog sexes are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: different homogenous groups (calculated with an ANOVA and a Tukey test) were treated separately.

Period	Total body weight in gram		
	N	r	p
March-April, August	183	0.048	0.515
April-May, July-September	386	0.076	0.137
May-July, September	327	0.062	0.262
May, June, September, October	296	0.082	0.158
	Weight change in %		
	N	r	p
July, August	143	0.097	0.251
June, August	151	0.147	0.070
June, September, October	191	0.169	**0.019**
May, September, October	181	0.095	0.204
April, May	109	0.121	0.211

1.4 Cortisol

1.4.1 Annual cortisol levels

Blood samples were taken from 41 hedgehogs in 2006 (17 females, 24 males), 35 in 2007 (15 females, 20 males) and 25 in 2008 (12 females, 13 males). To examine the annual cortisol levels a t-test was used to check for differences between female and male hedgehogs for the investigation period 2006-2008 (months and years separated). I found no significant differences except for June 2006 ($p = 0.016$), and May 2007 ($p = 0.005$) and 2008 ($p = 0.005$) with females having significantly higher cortisol levels in each case. Figure 23 shows the annual distribution for cortisol, separated for both sexes for the whole investigation period.

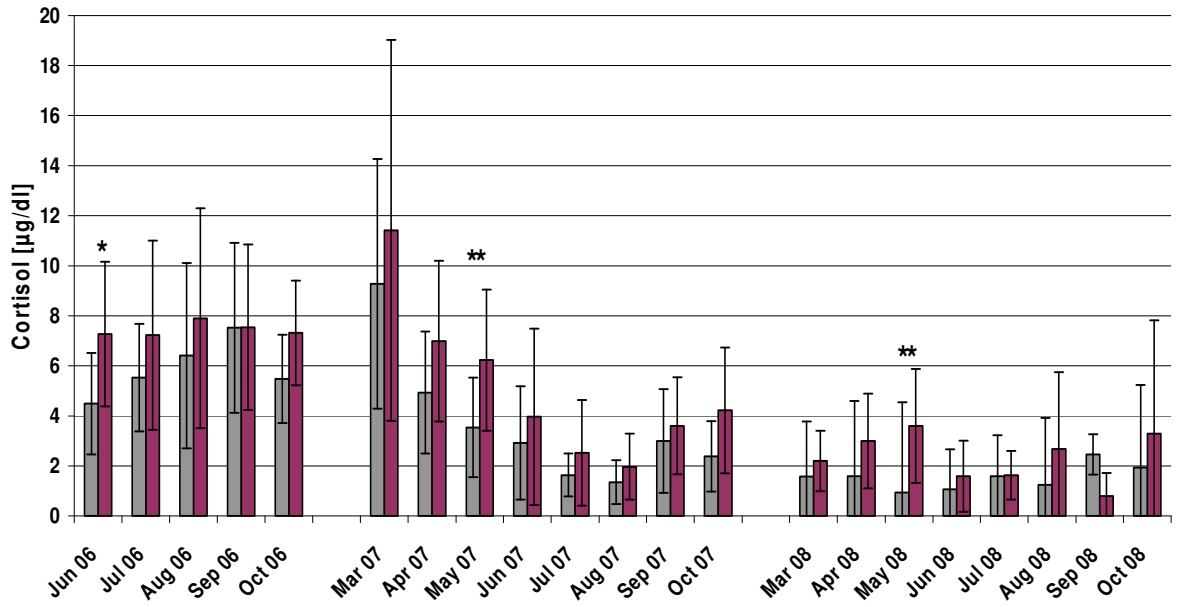

Figure 23: Annual distribution for mean cortisol levels (µg/dl) during the investigation period 2006-2008. ▒ Male hedgehogs, ▒ female hedgehogs. Error bars indicate standard deviation, asterisks show significant differences between male and female hedgehogs (* $p \leq 0.05$, ** $p \leq 0.001$).

Figure 23 displays that, although not significant, the mean cortisol levels of females are constantly higher than those of male hedgehogs, except for September 2008, when males had higher levels. Therefore, I counted the total number of months over all years in which females had higher mean cortisol concentrations than males and conversely, and tested for differences in distribution with a Chi-square test. I measured cortisol levels during 21 months (sum of all three years) and females had higher cortisol levels than males in 20 months ($\chi^2_1 = 34.381$, $p = 0.001$). Although I only found three months in which sexes differed significantly with the

t-test, the results from the Chi-square makes it obvious that females have higher cortisol levels throughout the year.

Figure 23 indicates the same distribution for males and females. This is supported by results of an ANOVA with a Tukey test done separately for both sexes. While in 2006 and 2008 there are no significant monthly differences for cortisol levels for the individual sexes (two homogenous subgroups for males in 2006), in 2007 I found three homogeneous groups (tables 13-14) for both sexes, with very high cortisol levels in spring and lowest levels in summer and early autumn.

Table 13: Homogenous subgroups for annual cortisol levels (µg/dl) of female hedgehogs during the investigation period (2006-2008, March-October) calculated with an ANOVA and a Tukey test. N = number of samples, p = probability.

		Subgroups for α =0.05		
Month 2006	N	Mean subgroup 1		
July	14	7.23		
June	10	7.27		
October	8	7.31		
September	12	7.54		
August	14	7.9		
p		0.992		
Month 2007		Mean subgroup 1	Mean subgroup 2	Mean subgroup 3
August	10	1.97		
July	12	2.53	2.53	
September	8	3.6	3.6	
June	12	3.97	3.97	
October	8	4.23	4.23	
May	12	6.23	6.23	
April	8		6.99	6.99
March	5			11.42
p		0.107	0.078	0.082
Month 2008		Mean subgroup 1		
September	3	0.8		
June	10	1.59		
July	8	1.63		
March	4	2.2		
August	4	2.68		
April	7	3.0		
October	2	3.3		
May	10	3.6		
p		0.391		

Table 14: Homogenous subgroups for annual cortisol levels (µg/dl) of male hedgehogs during the investigation period (2006-2008, March-October) calculated with an ANOVA and a Tukey test. N = number of samples, p = probability.

		Subgroups for α =0.05		
Month 2006	N	Mean subgroup 1	Mean subgroup 2	
June	12	4.49		
October	11	5.48	5.48	
July	18	5.53	5.53	
August	14	6.41	6.41	
September	20		7.53	
p		0.371	0.306	
Month 2007		Mean subgroup 1	Mean subgroup 2	Mean subgroup 3
August	17	1.35		
July	16	1.64		
October	10	2.38	2.38	
June	18	2.92	2.92	
September	16	3.0	3.0	
May	18	3.54	3.54	
April	12		4.93	
March	11			9.28
p		0.191	0.07	1.00
Month 2008		Mean subgroup 1		
May	12	0.94		
June	11	1.07		
August	9	1.24		
March	5	1.58		
April	11	1.6		
July	8	1.6		
October	6	1.93		
September	7	2.45		
p		0.250		

To compare the years (separated sexes) I used an ANOVA with a Tukey test for the period June-October and, since in 2006 blood samples were not taken during the period March-May, a t-test for these months. For females I found the highest cortisol levels in 2006 compared to 2007 (June $p = 0.027$, July-August $p = 0.001$, September $p = 0.013$) and 2008 (June-July $p = 0.001$, August $p = 0.033$, September $p = 0.003$). No differences could be detected for October. In April and May the mean cortisol levels were higher in 2007 than in 2008 (April $p = 0.013$, May $p = 0.028$). March did not differ significantly, but a trend to higher levels in 2007 ($p = 0.053$) occurred.

For males I found a similar pattern. From July-October the cortisol levels were higher in 2006 compared to 2007 (July-October $p = 0.001$) and to 2008 (July-October $p = 0.001$). In June I found no differences between 2006 and 2007, but 2008 had significantly lower cortisol

concentrations (2006 p = 0.001, 2007 p = 0.042). From March-May the cortisol values for males were significantly higher in 2007 than in 2008 (March p = 0.005, April-May p = 0.001).

1.4.2 Cortisol and tick infestation

I tested for correlations between total tick weight and cortisol levels. As mentioned above there were no monthly differences in cortisol levels for 2006 and 2008, while I found three homogenous subgroups in 2007 for both sexes. Those homogenous groups were treated separately as presented in tables 15-16.

Table 15: Pearson correlation between tick weight and cortisol levels (µg/dl) of female hedgehogs for the investigation period (2006-2008, March-October). Months are pooled, years are examined separately. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups in 2007 (calculated with an ANOVA and a Tukey test) these groups were treated separately.

Year (period)	N	r	p
2006	53	-0.117	0.406
2007 (May-October)	56	0.092	0.501
2007 (March, April)	13	0.737	**0.004**
2007 (April-July, September-October)	57	0.195	0.146
2008	45	0.246	0.103

Table 16: Pearson correlation between tick weight and cortisol levels (µg/dl) of male hedgehogs for the investigation period (2006-2008, March-October). Months are pooled, years are examined separately. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups in 2006 and 2007 (calculated with an ANOVA and a Tukey test) these groups were treated separately.

Year (period)	N	r	p
2006 (July-October)	55	0.368	**0.006**
2006 (June-August, October)	47	0.155	0.297
2007 (May-October)	90	0.284	**0.007**
2007 (April-June, September-October)	67	0.245	**0.045**
2007 (March)	10	0.334	0.346
2008	68	0.013	0.913

Male hedgehogs showed a different pattern compared to females. I found significant positive correlations in 2006 (July-October) and 2007 (May-October, April-June and September-October).

1.4.3 Cortisol and climate parameters

To check whether cortisol levels are associated with weather parameters I tested for correlations between cortisol and temperature in °C, relative humidity in % and rainfall in mm with a Pearson correlation. The climate values I used where either means of all values two weeks or four weeks before blood sampling. Hedgehog sexes were treated separately. The results are presented in tables 17-19.

For females temperature did not correlate with cortisol levels in 2006, 2007 (March, April) and 2008. Significant negative correlations were found for the period of May-October 2007 and the period April-July, September-October 2007 both for temperature two weeks and four weeks before sampling date. There seems to be no clear trend suggesting that cortisol levels are not associated with temperature.

In males no significant correlations between temperature and cortisol in 2006, March 2007 and 2008 both for temperature two weeks and four weeks before sampling date could be detected. I found negative significant correlations for May-October 2007 both for temperature two and four weeks before blood sampling, and for the period April-June, September-October 2007, but only for mean temperature four weeks before blood sampling. For males as for females it was not possible to detect a clear correlation trend between cortisol and temperature, indicating that there is no natural association between these parameters.

Table 17: Pearson correlation between temperature (°C) and cortisol levels (µg/dl) during the investigation period (2006-2008, March-October). Years and hedgehog sexes are treated separately. Months are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups in 2007 (calculated with an ANOVA and a Tukey test) these groups were treated separately.

Year (period)	Mean temperature two weeks before sample date			Mean temperature four weeks before sample date		
	N	r	p	N	r	p
Females						
2006	58	0.071	0.599	58	0.057	0.672
2007 (May-October)	62	-0.257	**0.043**	62	-0.347	**0.006**
2007 (March, April)	13	-0.102	0.740	13	-0.240	0.429
2007 (April-July, September-October)	60	-0.311	**0.016**	60	-0.384	**0.002**
2008	48	-0.155	0.294	48	-0.235	0.108
Males						
2006 (July-October)	63	-0.197	0.123	63	-0.206	0.105
2006 (June-August, October)	55	-0.162	0.236	55	-0.094	0.494
2007 (May-October)	95	-0.233	**0.023**	95	-0.281	**0.006**
2007 (April-June, September-October)	73	-0.199	0.091	73	-0.277	**0.018**
2007 (March)	11	0.118	0.730	11	-0.132	0.689
2008	69	-0.131	0.285	69	-0.064	0.603

Females showed no correlations between cortisol and relative humidity in 2006, 2008 and March-April 2007 (mean humidity two weeks before blood sampling). Significant negative correlations were found in May-October 2007 and April-July and September-October 2007, both for mean humidity two and four weeks before blood sampling and 2008 four weeks before blood sampling. As for temperature there is no clear trend, indicating that humidity is not associated with cortisol levels of female hedgehogs.

In males I measured significant positive correlations between relative humidity two weeks and four weeks before blood sampling and cortisol levels in 2008 and significant negative correlations for May-October 2007 four weeks before blood sampling. Again there seems to be no association between cortisol and humidity.

Table 18: Pearson correlation between relative humidity (%) and cortisol levels (µg/dl) during the investigation period (2006-2008, March-October). Years and hedgehog sexes are treated separately. Months are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups in 2007 (calculated with an ANOVA and a Tukey test) these groups were treated separately.

Year (period)	Mean humidity two weeks before sample date			Mean humidity four weeks before sample date		
	N	r	p	N	r	p
Females						
2006	58	-0.026	0.846	58	0.054	0.687
2007 (May-October)	62	-0.262	**0.040**	62	-0.388	**0.002**
2007 (March, April)	13	0.221	0.468	13	0.391	0.187
2007 (April-July, September-October)	60	-0.340	**0.008**	60	-0.370	**0.004**
2008	48	-0.154	0.297	48	-0.361	**0.012**
Males						
2006 (July-October)	63	0.169	0.185	63	0.168	0.188
2006 (June-August, October)	55	0.204	0.136	55	0.181	0.185
2007 (May-October)	95	-0.165	0.110	95	-0.280	**0.006**
2007 (April-June, September-October)	73	-0.208	0.077	73	-0.163	0.169
2007 (March)	11	0.044	0.898	11	-0.084	0.807
2008	69	0.267	**0.027**	69	0.250	**0.038**

For rainfall I found no significant correlations for males and only two significant negative correlations for females in 2007 (May-October; April-July, September-October). As well as for temperature and humidity there is no direct association between rainfall and stress levels in hedgehogs.

Table 19: Pearson correlation between rainfall (mm) and cortisol levels (µg/dl) during the investigation period (2006-2008, March-October). Years and hedgehog sexes are treated separately. Months are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups in 2007 (calculated with an ANOVA and a Tukey test) these groups were treated separately.

Year (period)	Mean rainfall two weeks before sample date			Mean rainfall four weeks before sample date		
	N	r	p	N	r	p
Females						
2006	58	-0.216	0.103	58	0.036	0.790
2007 (May-October)	62	0.188	0.144	62	-0.284	**0.025**
2007 (March, April)	13	0.432	0.141	13	0.148	0.629
2007 (April-July, September-October)	60	0.101	0.444	60	-0.264	**0.041**
2008	48	0.038	0.798	48	-0.195	0.184
Males						
2006 (July-October)	63	-0.021	0.869	63	0.245	0.053
2006 (June-August, October)	55	0.065	0.638	55	-0.103	0.453
2007 (May-October)	95	0.056	0.592	95	-0.194	0.060
2007 (April-June, September-October)	73	-0.067	0.573	73	-0.181	0.126
2007 (March)	11	0.145	0.671	11	-0.205	0.545
2008	69	-0.118	0.333	69	0.028	0.822

1.5 Testosterone

1.5.1 Annual testosterone levels

Testosterone measurements were made from June-October 2006 (24 males) and from March-October in 2007 (20 males) and 2008 (13 males). Figure 24 shows the annual distribution of testosterone levels during the investigation period.

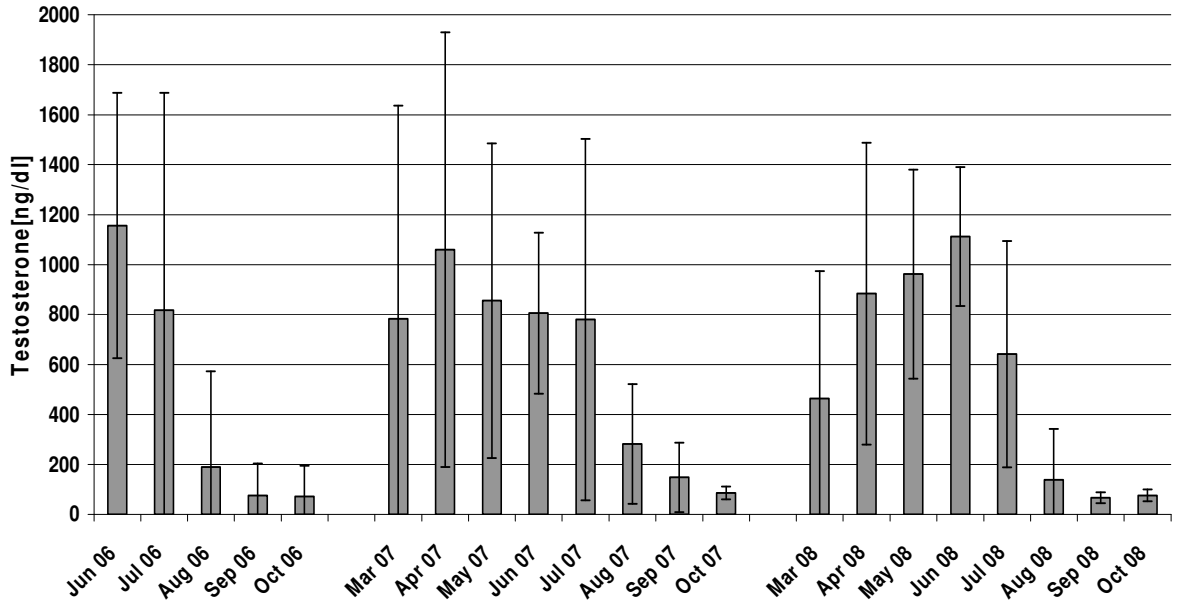

Figure 24: Annual distribution for mean testosterone levels (ng/dl) of male hedgehogs during the investigation period (2006-2008, March-October). Error bars indicate standard deviation for mean testosterone values.

At the beginning of the year, directly following hibernation in March, the testosterone levels were high. They then increased or remained stable until July, after which they decreased rapidly to very low levels in October. I used an ANOVA with a Tukey multiple comparison test to check for differences in monthly testosterone levels. I measured two homogenous groups in 2006 (June-July, August-October) and 2007/2008 (March-July, August-October).

To test whether the monthly distributions of testosterone were reproducible throughout the trial period 2006-2008, I used an ANOVA with a Tukey test and a t-test for March-May since I did not have any data from 2006 for this period. I found no significant differences for any month (table 20 and table 21).

Therefore I pooled the months for the three years and checked again for the annual distribution of testosterone (figure 25).

Table 20: Monthly comparison of mean testosterone levels (ng/dl) for 2007 and 2008 (March-May). N = number of samples SD = standard deviation, p = probability was estimated with a t-test.

Month	Year	N	Testosterone	SD	p
March	2007	11	783.24	853.71	0.455
	2008	5	463.80	510.13	
April	2007	11	1059.75	870.26	0.587
	2008	11	883.62	604.25	
May	2007	18	855.56	630.42	0.878
	2008	13	887.96	480.69	

Table 21: Monthly comparison of mean testosterone levels (ng/dl) for 2006-2008 (June-October) with an ANOVA and a Tukey test. N = number of samples, p = probability, significant p-values are in bold. Note: ANOVA was only done for June-October since blood sampling in 2006 started first in June.

Month	(I) Year	(J) Year	N	Testosterone	Mean difference (I-J)	p
June	2006	2007	12	1156.25	350.36	0.052
		2008			43.75	0.963
	2007	2006	18	805.89	-350.36	0.052
		2008			-306.61	0.126
	2008	2006	10	1112.50	-43.75	0.963
		2007			306.61	0.126
July	2006	2007	19	817.96	37.90	0.988
		2008			176.24	0.861
	2007	2006	16	780.06	-37.90	0.988
		2008			138.35	0.916
	2008	2006	7	641.71	-176.24	0.861
		2007			-138.35	0.916
August	2006	2007	18	189.07	-92.92	0.646
		2008			50.07	0.929
	2007	2006	17	281.99	92.92	0.646
		2008			142.99	0.558
	2008	2006	7	139.00	-50.07	0.929
		2007			-142.99	0.558
September	2006	2007	20	75.68	-72.57	0.198
		2008			9.02	0.987
	2007	2006	17	148.25	72.57	0.198
		2008			81.59	0.365
	2008	2006	6	66.67	-9.02	0.987
		2007			-81.59	0.365
October	2006	2007	13	72.07	-13.61	0.927
		2008			-3.93	0.996
	2007	2006	10	85.68	13.61	0.927
		2008			9.68	0.978
	2008	2006	5	76.00	3.93	0.996
		2007			-9.68	0.978

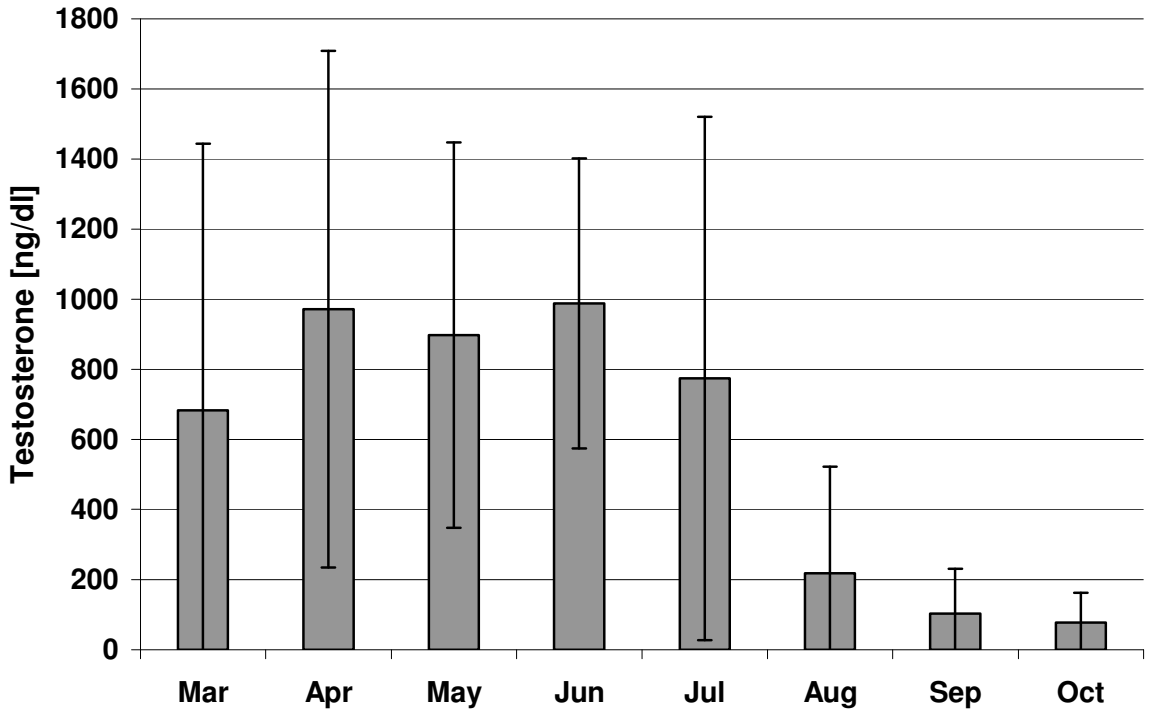

Figure 25: Annual distribution for mean testosterone levels (ng/dl) of male hedgehogs during the investigation period (2006-2008, March-October). Years are pooled; error bars indicate standard deviation.

The annual distribution of testosterone from the pooled data fits the distribution of the individual years, with high levels after hibernation until July. These decrease rapidly in August and remain low until the end of the investigation period. Again there were two homogenous groups (March-July and August-October).

1.5.2 Testosterone and tick infestation

To test for correlations between testosterone levels and total tick weight I used a Pearson correlation. Since it is known that there are seasonal cycles of testosterone levels in male hedgehogs (DUTOURNÉ and SABOUREAU 1983), and my results are consistent with these authors, it is important to correlate the subgroups (see chapter III.1.5.1) with the tick weight. In addition, I correlated the testosterone levels of all months (years separately) with the tick weight. The results for the correlations within the subgroups are shown in table 22.

The subgroups for the single years and the period March-July for the pooled years did not correlate with total tick weight. The only significant negative correlation between testosterone levels and total tick weight could be detected in the period of August-October for the pooled years. After correlating the testosterone levels with the tick weights for the whole year I detected significant negative correlations for 2006 (N = 72, r = -0.342, p = 0.003) and negative, but not significant correlations for 2007 (N = 82, r = -0.136, p = 0.157) and 2008 (N = 62, r = - 0.139, p = 0.280).

Although most measured correlations are not significant, they are all negative and indicate therefore a trend to a negative association between tick weight and testosterone levels.

Table 22: Pearson correlation between tick weight (g) and testosterone levels (ng/dl) for the investigation period (2006-2008, March-October). Months are pooled, years are examined separately. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Based on the different homogenous groups (calculated with an ANOVA and a Tukey test) such groups were treated separately.

Year (period)	N	r	p
2006 (August-October)	43	-0.223	0.150
2006 (June, July)	29	-0.125	0.520
2007 (August-October)	41	-0.093	0.563
2007 (March, July-September)	58	-0.064	0.631
2007 (March, May-August)	77	-0.159	0.166
2007 (March-July)	69	-0.131	0.283
2008 (March-July)	44	-0.089	0.565
2008 (March, July-October)	40	-0.226	0.160
All years (August-October)	102	-0.213	**0.031**
All years (March-July)	142	-0.090	0.289

1.5.3 Testosterone and cortisol

To test for correlations between testosterone and cortisol levels of male hedgehogs I used a Pearson correlation. Every year was treated separately, because of the differences in the cortisol levels between years. For every year I divided the dataset into the periods March-July and August-October (see chapter III.1.5.1). Table 23 shows the correlation for testosterone and cortisol of the subgroups.

Table 23: Pearson correlation between testosterone (ng/dl) and cortisol levels (µg/dl) for the investigation period (2006-2008, March-October). Months are pooled, years are examined separately. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups during the research period (calculated with an ANOVA and a Tukey test) those groups were treated separately.

Year (period)	N	r	p
2006 (June-July)	30	0.304	0.102
2006 (August-October)	45	-0.114	0.457
2007 (March-July)	74	0.136	0.249
2007 (August-October)	43	-0.379	**0.012**
2008 (March-July)	45	-0.273	0.069
2008 (August-October)	18	-0.161	0.524

A significant negative correlation between testosterone and cortisol was found in 2007 in the period from August-October. In 2008 I detected a negative correlation approaching significance from March-July. In all other periods no trends or significant correlations occurred. As for the correlations with tick weight I also correlated cortisol levels and testosterone levels of all months (years separately). No significant correlations could be found in 2006 (N = 75, r = - 0.095, p = 0.418), significant positive correlations were measured in 2007 (N = 117, r = 0.299, p = 0.013), significant negative correlations in 2008 (N = 63, r = -0.259, p = 0.04). These results indicate that testosterone has no effect on cortisol concentrations and conversely.

1.5.4 Testosterone and climate parameters

To check whether testosterone levels are influenced by certain climate parameters I tested for correlations between testosterone and temperature in °C, relative humidity in % and rainfall in mm with a Pearson correlation. The climate parameters I used where either means of all data two weeks or four weeks before blood sampling. Correlations were done with the homogenous groups described in chapter III.1.5.1. The results are shown in tables 24-26. I discovered significant positive correlations for temperature in the period August-October 2007 (two and four weeks before blood sampling) and August-October for pooled years (four weeks before blood sampling). All other values did not correlate with temperature (table 24). Since the data show no special trend and according to the number of tests carried out the significant correlations fall in the range of a type 1 error. Therefore there is no clear association between testosterone levels and temperature.

Table 24: Pearson correlation between temperature (°C) and testosterone levels (ng/dl) during the investigation period (2006-2008, March-October). Years are treated separately. Months are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups (calculated with an ANOVA and a Tukey test) these groups were treated separately.

Year (period)	Mean temperature two weeks before sample date			Mean temperature four weeks before sample date		
	N	r	p	N	r	p
2006 (August-October)	51	0.038	0.794	51	0.222	0.118
2006 (June, July)	31	-0.208	0.262	31	-0.289	0.115
2007 (August-October)	44	0.352	**0.019**	44	0.335	**0.026**
2007 (March, July-September)	61	-0.224	0.082	61	-0.242	0.061
2007 (March, May-August)	80	-0.155	0.171	80	-0.147	0.192
2007 (March-July)	73	-0.107	0.367	73	-0.102	0.389
2008 (March-July)	46	0.191	0203	46	0.154	0.306
2008 (March, July-October)	30	-0.005	0.978	30	-0.010	0.958
All years (August-October)	113	0.136	0.152	113	0.209	**0.026**
All years (March-July)	150	0.019	0.816	150	-0.065	0.432

Relative humidity and testosterone correlated significantly positively in 2007 (March, July-September) both two and four weeks before sample date. Additionally, I found significant negative correlations for 2008 (March, July-October) and August-October of the pooled years. All other values did not correlate significantly (table 25). This indicates no real trend for correlations with humidity and there seems to be no observable link between testosterone and humidity.

Table 25: Pearson correlation between relative humidity (%) and testosterone levels (ng/dl) during the investigation period (2006-2008, March-October). Years are treated separately. Months are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups (calculated with an ANOVA and a Tukey test) these groups were treated separately.

Year (period)	Mean humidity two weeks before sample date			Mean humidity four weeks before sample date		
	N	r	p	N	r	p
2006 (August-October)	51	-0.058	0.551	51	-0.150	0.292
2006 (June, July)	31	0.302	0099	31	0.267	0.146
2007 (August-October)	44	0.113	0.464	44	-0.267	0.079
2007 (March, July-September)	61	0.264	**0.039**	61	0.421	**0.001**
2007 (March, May-August)	80	-0.030	0.790	80	-0.083	0.462
2007 (March-July)	73	-0.069	0.562	73	-0.060	0.616
2008 (March-July)	46	0.058	0703	46	-0.120	0.425
2008 (March, July-October)	30	-0.408	**0.025**	30	-0.358	0.052
All years (August-October)	113	-0.148	0.118	113	-0.185	**0.05**
All years (March-July)	150	0.001	0.988	150	0.020	0.809

Significant positive correlations with rainfall were found in 2007 (March, May-August - two weeks before blood sampling and March, July-September - four weeks before blood sampling). All other values did not show any significant correlations (table 26). As for temperature and humidity, there is no clear trend for the relationship between testosterone and rainfall. To summarize it appears that, although significant correlations occurred, these were only individual cases and no constant trend could be detected. Therefore testosterone levels in males do not seem to depend on the abiotic factors temperature, rainfall and humidity.

Table 26: Pearson correlation between rainfall (mm) and testosterone levels (ng/dl) during the investigation period (2006-2008, March-October). Years are treated separately. Months are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups (calculated with an ANOVA and a Tukey test) these groups were treated separately.

Year (period)	Mean rainfall two weeks before sample date			Mean rainfall four weeks before sample date		
	N	r	p	N	r	p
2006 (August-October)	51	-0.035	0.808	51	-.008	0.955
2006 (June, July)	31	-0.245	0.183	31	-0.277	0.132
2007 (August-October)	44	0.183	0.235	44	0.078	0.615
2007 (March, July-September)	61	0.090	0.491	61	0.298	**0.020**
2007 (March, May-August)	80	0.236	**0.035**	80	0.026	0.820
2007 (March-July)	73	0.146	0.219	73	-0.044	0.711
2008 (March-July)	46	-0.022	0.887	46	0.016	0.916
2008 (March, July-October)	30	0.131	0.490	30	0.012	0.948
All years (August-October)	113	0.013	0.894	113	-0.022	0.822
All years (March-July)	150	0.002	0.981	150	-0.104	0.205

1.6 Haematological values

A summarized version of this section has been published as Pfäffle M., Petney T., Elgas M., Skuballa J. and Taraschewski H. (2009), Tick-induced blood loss leads to regenerative anaemia in the European hedgehog (*Erinaceus europaeus*), Parasitology 136: 443-452.

There were no significant differences in haematological parameters between female and male hedgehogs except for: MCV (October 2007, t-test p = 0.027), MCH (October 2007, p = 0.014), MCHC (July 2007, p = 0.044), thrombocytes (August, 2008 p = 0.049), neutrophils (October 2007, p = 0.043), eosinophils (August 2008, p = 0.047), basophils (April 2008, p = 0.047; May 2008, p = 0.012), monocytes (June 2007, p = 0.021; October 2007, p = 0.005; March 2008, p = 0.006), lymphocytes (October 2007, p = 0.049) and absolute reticulocytes (June 2007, p = 0.048; September 2008, p = 0.006). Given an α-value of 5% and the total number of tests carried out these results are lying within the range of a type 1 error. Thus I decided to pool the parameters for female and male hedgehogs.

I measured differences within months between years in the haematological values throughout 2007 and 2008, but given the total number of tests carried out these results are also within the

range of a type 1 error. In addition, assuming that months are only notional units and that they should have no affect on haematological values I also considered all months in a year to be independent of one another. The descriptive statistics for the haematological parameters for the years 2007 and 2008 are presented in table 27.

Table 27: Descriptive statistics of the haematological values for 2007 and 2008 (March-October). Hedgehog sexes and months are pooled. N = number of samples, SD = standard deviation.

Parameter	Year	N	Mean	SD	Minimum	Maximum
Leucocytes (/nl)	2007	178	10.13	4.85	3.95	46.15
	2008	115	9.50	3.48	4.57	22.36
Erythrocytes (/pl)	2007	178	8.00	1.65	2.32	12.16
	2008	115	6.71	1.89	1.92	11.27
Haemoglobin (g/dl)	2007	178	12.07	2.27	3.90	16.90
	2008	115	10.81	2.74	2.40	17.20
Haematocrit (%)	2007	178	39.32	6.44	14.40	56.40
	2008	115	36.69	7.57	9.70	52.60
MCV (fl)	2007	178	50.02	6.53	38.70	71.20
	2008	115	56.79	11.05	41.10	100.40
MCH (pg)	2007	178	15.21	1.18	13.00	18.50
	2008	115	16.35	2.11	10.20	30.00
MCHC (g/dl)	2007	178	30.60	2.17	24.20	35.10
	2008	115	29.22	3.02	19.20	35.40
Thrombocytes (/nl)	2007	178	317.17	131.92	16.00	840.00
	2008	115	338.04	154.81	39.00	1066.00
Neutrophils (%)	2007	173	34.93	13.89	5.00	83.00
	2008	111	39.32	13.63	5.00	76.00
Eosinophils (%)	2007	166	7.73	5.08	1.00	27.00
	2008	107	8.18	6.01	1.00	30.00
Basophils (%)	2007	137	2.80	2.08	1.00	14.00
	2008	91	3.86	3.01	1.00	18.00
Monocytes (%)	2007	170	5.96	5.91	1.00	65.00
	2008	107	5.28	3.13	1.00	14.00
Lymphocytes (%)	2007	174	48.12	14.01	1.00	88.00
	2008	112	42.80	14.85	8.00	83.00
Reticulocytes (‰)	2007	178	91.88	53.56	8.50	345.70
	2008	114	99.19	82.84	13.20	581.20
Reticulocyte conc. (/nl)	2007	162	634.81	295.08	65.00	1727.00
	2008	110	553.82	308.44	98.80	1787.00

A comparison of the means and the ranges of my haematological parameters with values for wild hedgehogs presented by other authors (QUILLIAM et al. 1971, WENZEL et al. 1977, LEWIS et al. 2002, see table 28) proved to be of little value. The reported ranges in these references differ substantially from each other and assuming, a broad range, covering all of those previously reported, I found very few outlying results.

Table 28: Means of haematological values from the experimental hedgehog population (data from 2007 and 2008 pooled, N = 293), QUILLIAM et al. (1971, N = 3), WENZEL et al. (1977, N = 14) and LEWIS et al. (2002, N = 50). Ranges are shown in brackets.

Parameter	Experimental population	QUILLIAM et al. (1971)	WENZEL et al. (1977)	LEWIS et al. (2002)
Leucocytes (/nl)	9.89 (3.95-46.15)	3.27 (1.4-4.7)	7.58	7.4 (1.7-11.4)
Erythrocytes (/pl)	7.5 (1.92-12.16)	4.93 (4.7-5.1)	6.93	8.1 (6.2-10.0)
Haemoglobin (g/dl)	11.58 (2.4-17.2)	11.17 (10.9-11.5)	13.93	12.5 (9.6-16.6)
Haematocrit (%)	38.29 (9.7-56.4)	33.67 (32.0-36.0)	47.0	33.0 (25.0-46.0)
MCV (fl)	52.68 (38.7-100.4)	68.33 (64.0-71.0)	71.34	40.6 (35.4-46.4)
MCH (pg)	15.66 (10.2-30.0)	22.82 (22.5-23.0)	21.85	15.4 (13.7-17.5)
MCHC (g/dl)	30.06 (19.2-35.4)	33.33 (32.0-35.0)	30.14	38.1 (34.8-42.2)
Thrombocytes (/nl)	325-37 (16.0-1066.0)	141.0 (100.0-197.0)	399.29	134.0 (29.0-338.0)
Neutrophils (%)	36.64 (5.0-83.0)	69.33 (65.0-74.0)	44.4 (13.0-66.0)	40.14 (5.68-86.22)
Eosinophils (%)	7.9 (1.0-30.0)	3.0 (2.0-3.0)	5.0 (0.0-16.0)	5.95 (0.0-18.24)
Basophils (%)	3.22 (1.0-18.0)		0.4 (0.0-6.0)	1.08 (0.0-3.78)
Monocytes (%)	5.7 (1.0-65.0)	3.67 (3.0-4.0)	2.9 (0.0-23.5)	2.16 (0.0-6.49)
Lymphocytes (%)	46.03 (1.0-88.0)	24.0 (19.0-29.0)	43.8 (20.0-68.0)	50.68 (11.49-68.16)
Reticulocytes (‰)	94.73 (8.5-581.2)	0.4 (0.32-0.38)		
Reticulocyte conc. (/nl)	602.06 (65.0-1787.0)			

1.6.1 Haematological values and tick infestation

Tables 29 and 30 show the correlation between measured haematological values and tick infestation for 2007 and 2008 evaluated with a Pearson correlation. Except for thrombocytes, for which I found no significant correlation in 2008 all other parameters indicate the same trend. Figures 26-36 present significant correlations between haematological parameters and total tick weight pooled for both years.

Table 29: Pearson correlation between tick weight (g) and haematological values for 2007 (March-October). Hedgehog sexes and months are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold.

2007	N	r	p
Leucocytes (/nl)	166	-0.098	0.211
Erythrocytes (/pl)	166	-0.423	**0.001**
Haemoglobin (g/dl)	166	-0.370	**0.001**
Haematocrit (%)	166	-0.252	**0.001**
MCV (fl)	166	0.433	**0.001**
MCH (pg)	166	0.246	**0.001**
MCHC (g/dl)	166	-0.449	**0.001**
Thrombocytes (/nl)	166	0.200	**0.01**
Neutrophils (%)	162	0.226	**0.004**
Eosinophils (%)	157	-0.121	0.132
Basophils (%)	131	0.041	0.644
Monocytes (%)	161	-0.024	0.759
Lymphocytes (%)	163	-0.206	**0.008**
Reticulocytes (‰)	166	0.445	**0.001**
Reticulocyte conc. (/nl)	150	0.248	**0.002**

Table 30: Pearson correlation between tick weight (g) and haematological values for 2008 (March-October). Hedgehog sexes and months are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold.

2008	N	r	p
Leucocytes (/nl)	109	0.072	0.456
Erythrocytes (/pl)	109	-0.499	**0.001**
Haemoglobin (g/dl)	109	-0.406	**0.001**
Haematocrit (%)	109	-0.336	**0.001**
MCV (fl)	109	0.470	**0.001**
MCH (pg)	109	0.363	**0.001**
MCHC (g/dl)	109	-0.371	**0.001**
Thrombocytes (/nl)	109	0.064	0.510
Neutrophils (%)	106	0.238	**0.014**
Eosinophils (%)	102	0.038	0.703
Basophils (%)	89	-0.009	0.934
Monocytes (%)	103	-0.086	0.390
Lymphocytes (%)	107	-0.256	**0.008**
Reticulocytes (‰)	108	0.443	**0.001**
Reticulocyte conc. (/nl)	104	0.216	**0.028**

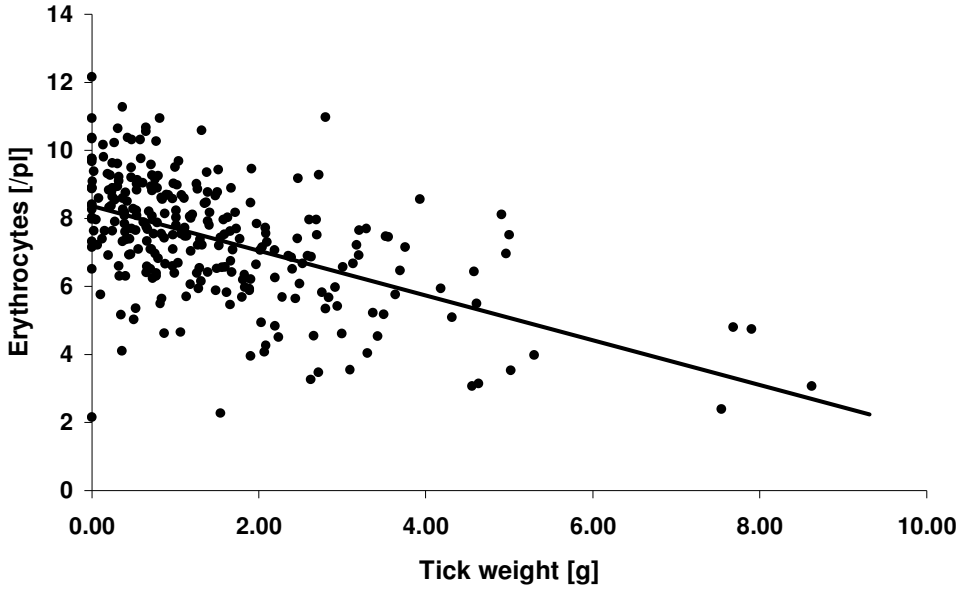

Figure 26: Relationship between the erythrocyte concentration (/pl) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years, months and hedgehog sexes are pooled (N = 275). A Pearson correlation coefficient r was calculated (r = -0.526, p = 0.001).

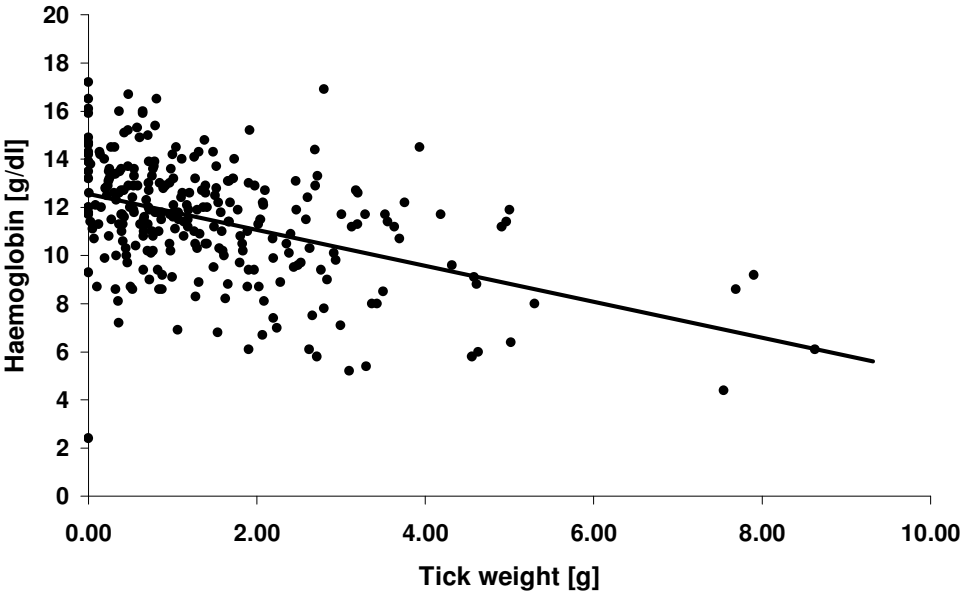

Figure 27: Relationship between the haemoglobin concentration (g/dl) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years, months and hedgehog sexes are pooled (N = 275). A Pearson correlation coefficient r was calculated (r = -0.437, p = 0.001).

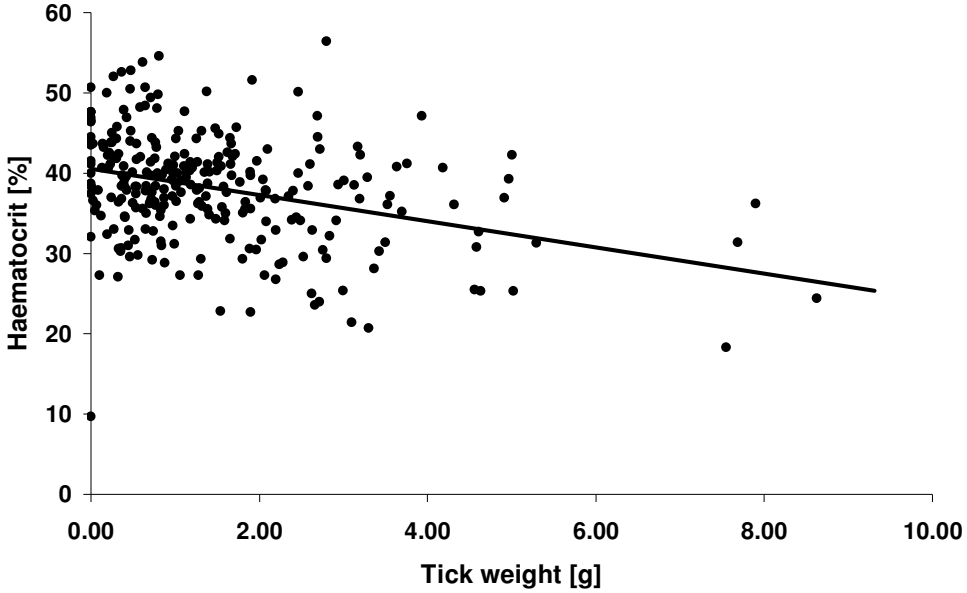

Figure 28: Relationship between the haematocrit (%) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years, months and hedgehog sexes are pooled (N = 275). A Pearson correlation coefficient r was calculated (r = -0.337, p = 0.001).

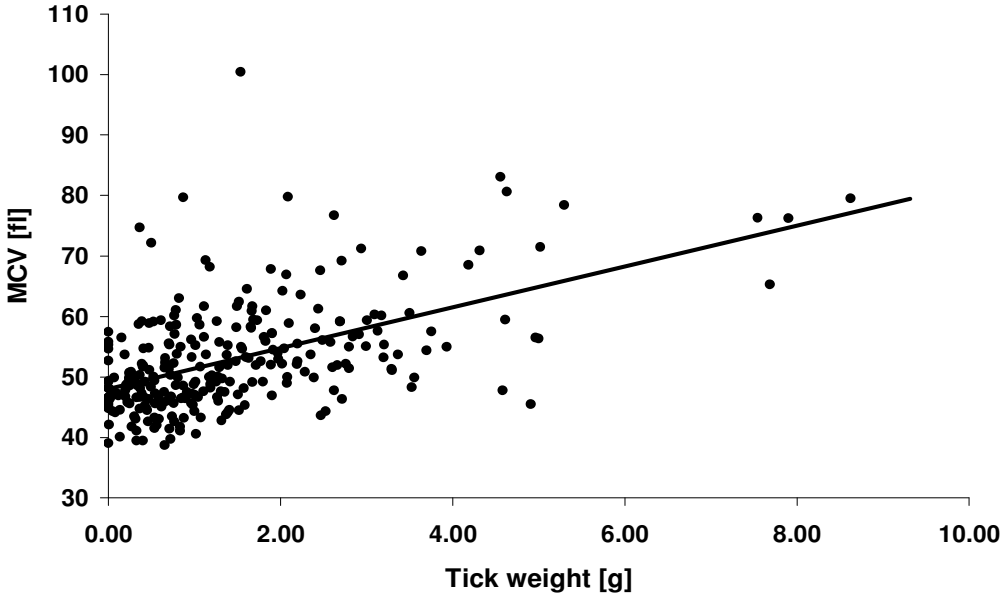

Figure 29: Relationship between the mean corpuscular volume MCV (fl) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years, months and hedgehog sexes are pooled (N = 275). A Pearson correlation coefficient r was calculated (r = 0.533, p = 0.001).

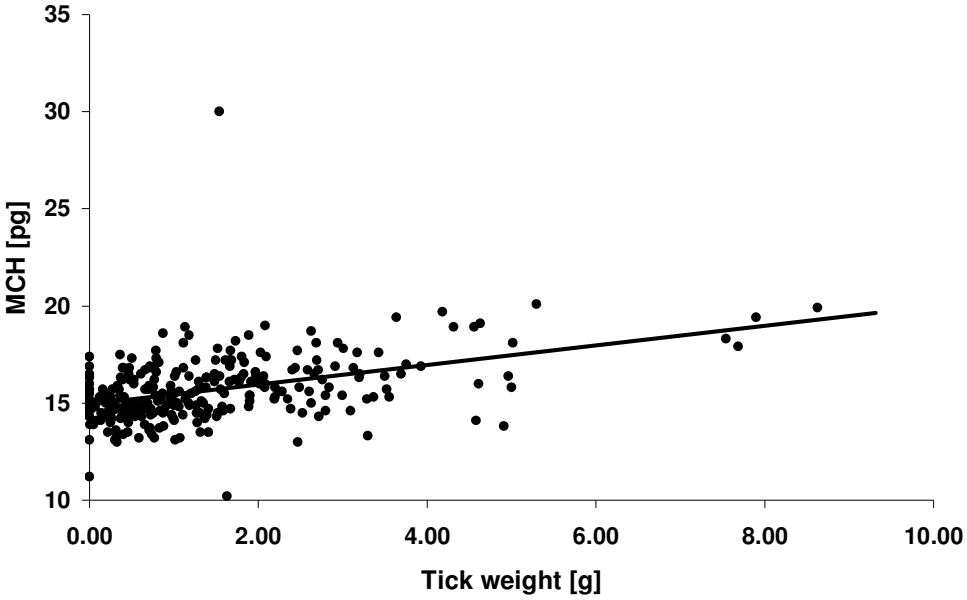

Figure 30: Relationship between the mean corpuscular haemoglobin MCH (pg) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years, months and hedgehog sexes are pooled (N = 275). A Pearson correlation coefficient r was calculated (r = 0.416, p = 0.001).

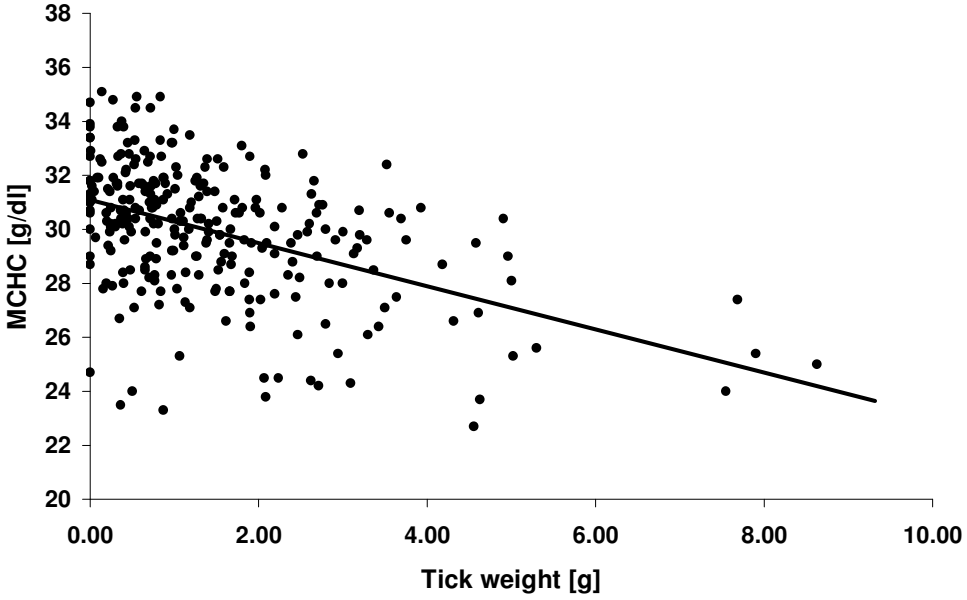

Figure 31: Relationship between the mean corpuscular haemoglobin concentration MCHC (g/dl) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years, months and hedgehog sexes are pooled (N = 275). A Pearson correlation coefficient r was calculated (r = -0.454, p = 0.001).

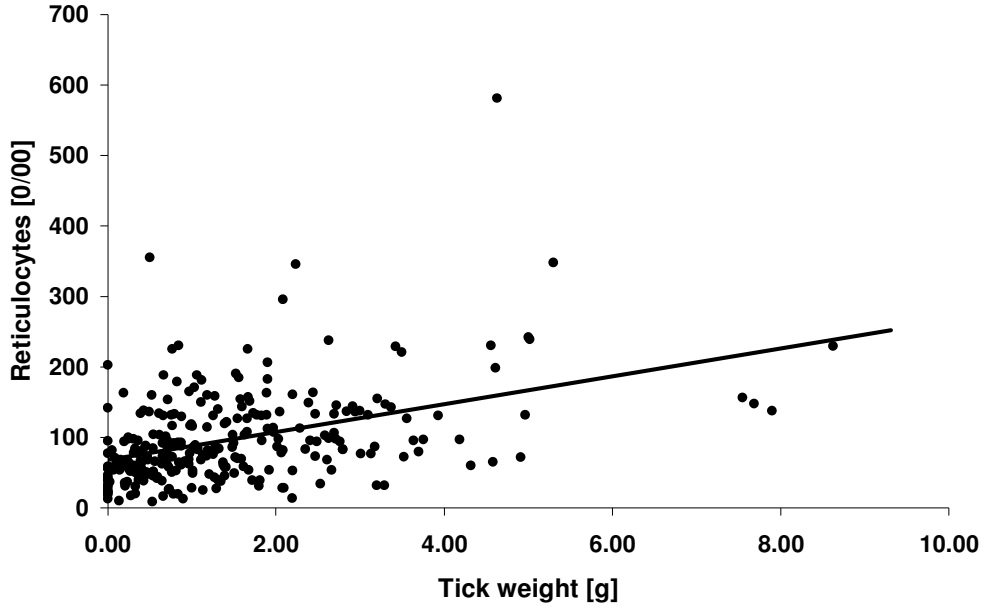

Figure 32: Relationship between the relative reticulocyte concentration (‰) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years, months and hedgehog sexes are pooled (N = 274). A Pearson correlation coefficient r was calculated (r = 0.425, p = 0.001).

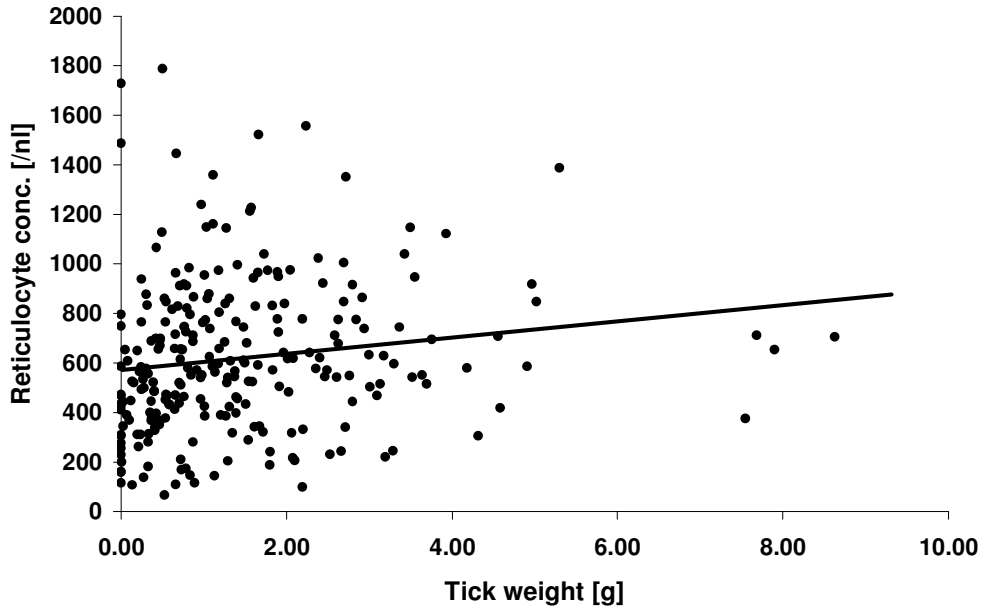

Figure 33: Relationship between the absolute reticulocyte concentration (/nl) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years, months and hedgehog sexes are pooled (N = 254). A Pearson correlation coefficient r was calculated (r = 0.153, p = 0.015).

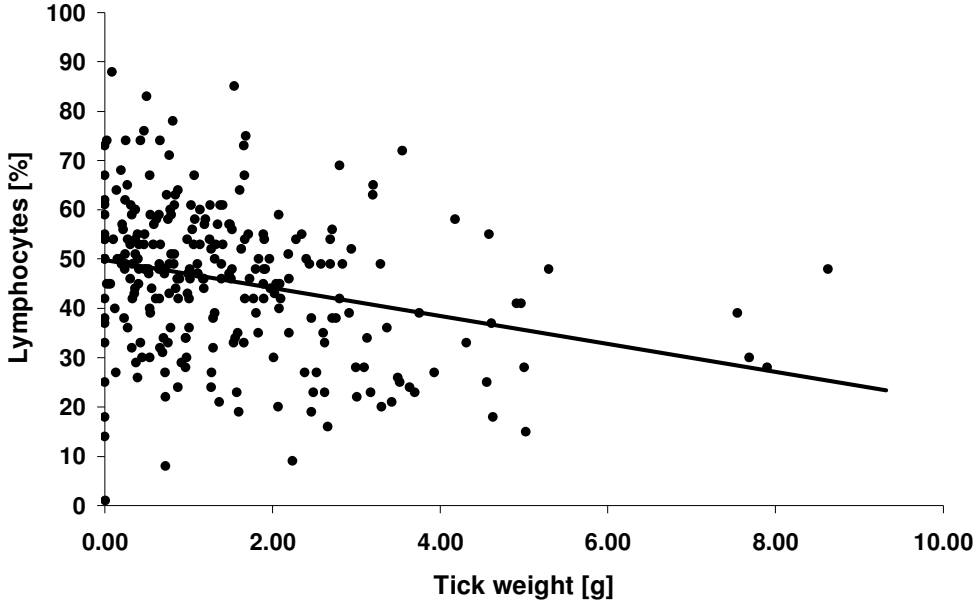

Figure 34: Relationship between lymphocytes (%) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years, months and hedgehog sexes are pooled (N = 270). A Pearson correlation coefficient r was calculated (r = -0.276, p = 0.001).

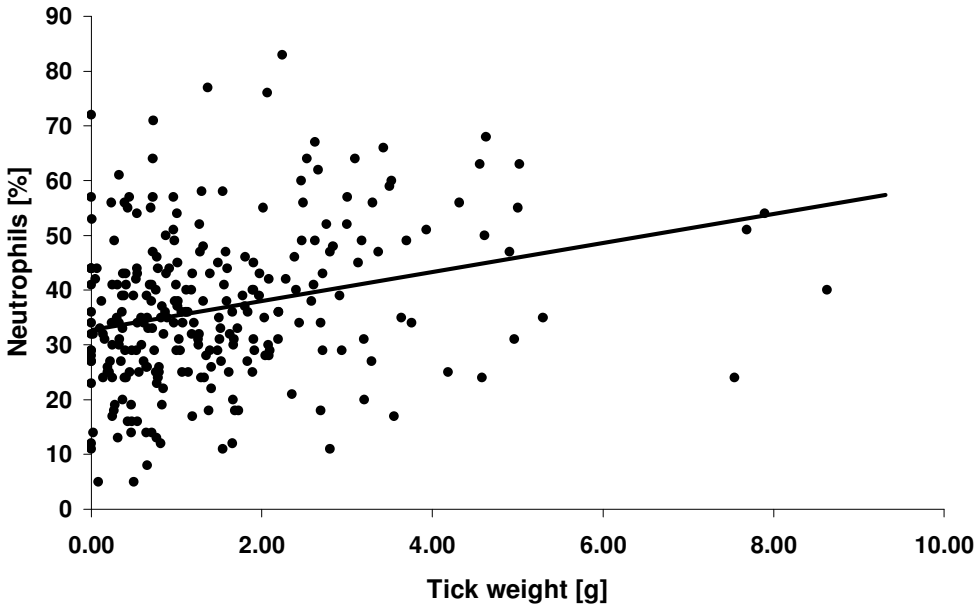

Figure 35: Relationship between neutrophils (%) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years, months and hedgehog sexes are pooled (N = 268). A Pearson correlation coefficient r was calculated (r = 0.267, p = 0.001).

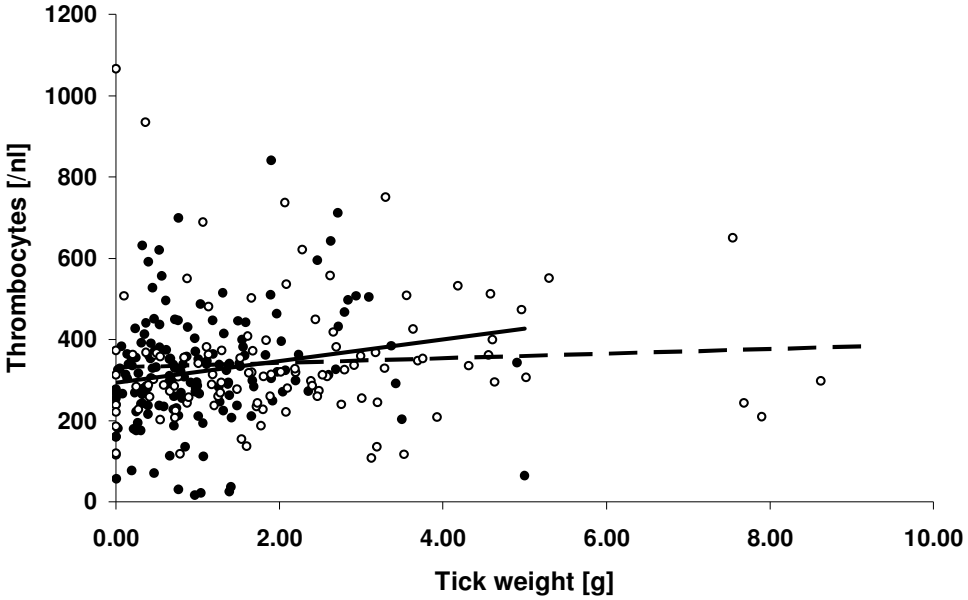

Figure 36: Relationship between the thrombocytes concentration (/nl) and the total tick weight (g) for the whole experimental population during the investigation period (2007-2008, March-October). Years are treated separately, months and hedgehog sexes are pooled (2007 N = 166,●; 2008 N = 109, ○). A Pearson correlation coefficient r was calculated (2007 r = 0.200, p = 0.01,——; 2008 r = 0.064, p = 0.510, – –).

I detected significant negative correlations between the total tick weight and erythrocyte count (figure 26), haemoglobin (figure 27), haematocrit (figure 28), MCHC (figure 31) and lymphocytes (figure 34). Significant positive correlations were found for relative and absolute reticulocytes (figure 32 and 33), MCV (figure 29), MCH (figure 30) and neutrophils (figure 35). Thrombocytes correlated significantly only in 2007 (figure 36). No significant correlations were found for leucocytes (r = -0.034, p = 0.579, N = 275), eosinophils (r = -0.007, p = 0.910, N = 259), basophils (r = 0.084, p = 0.217, N = 220) and monocytes (r = -0.07, p = 0.255, N = 264).

1.6.2 Haematological values and climate parameters

The tests for correlations between haematological values and climate parameters were carried out in the same manner as described for cortisol and testosterone levels (see chapter III.1.4.3 and III.1.5.4). Significant correlations between temperature and the haematological values are shown in table 31. Temperature did not correlate significantly with leucocytes, erythrocytes, basophils, monocytes, lymphocytes and relative and absolute reticulocytes in 2007. In 2008 there were no significant correlations between temperature and leucocytes, erythrocytes,

haemoglobin, haematocrit, MCV, MCH, MCHC, thrombocytes, neutrophils, eosinophils, monocytes, lymphocytes and reticulocytes (‰). This shows that the correlations between haematological values and temperature are not reproducible for the years. In 2007 correlations occurred which were not existent in 2008 and conversely. This strongly suggests that the significant correlations are only random effects.

Table 31: Pearson correlation between haematological values and mean temperature (°C) for 2007 and 2008 (March-October). Months and hedgehog sexes are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. (Note: only haematological values which correlated significantly are shown in the table).

	Mean temperature two weeks before sample date			Mean temperature four weeks before sample date		
2007	N	r	p	N	r	p
Haemoglobin (g/dl)	178	-0.191	**0.01**	178	-0.240	**0.001**
Haematocrit (%)	178	-0.295	**0.001**	178	-0.370	**0.001**
MCV (fl)	178	-0.205	**0.006**	178	-0.212	**0.004**
MCH (pg)	178	-0.193	**0.01**	178	-0.182	**0.015**
MCHC (g/dl)	178	0.149	**0.047**	178	0.186	**0.013**
Thrombocytes (/nl)	178	0.113	0.134	178	0.151	**0.044**
Neutrophils (%)	173	0.153	0.045	173	0.196	**0.01**
Eosinophils (%)	166	-0.213	**0.006**	166	-0.251	**0.001**
2008						
Basophils (%)	91	0.232	**0.027**	91	0.223	**0.034**
Reticulocyte conc. (/nl)	110	-0.197	**0.039**	110	-0.216	**0.023**

In table 32 the significant correlations for haematological values and humidity in % are presented. In 2007 no significant correlations between humidity and the haematological values occurred at all and in 2008 no correlations between humidity and leucocytes, haematocrit, MCH, thrombocytes, neutrophils, eosinophils, basophils, monocytes, lymphocytes and absolute reticulocyte concentration could be detected. Similar to the results of the correlations between temperature and haematological parameters I found no reproducible results for humidity. This implies that humidity has no effect on haematological values.

Table 32: Pearson correlation between haematological values and relative humidity (%) for 2008 (March-October). Months and hedgehog sexes are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. (Note: only haematological values which correlated significantly are shown in the table).

	Mean humidity two weeks before sample date			Mean humidity four weeks before sample date		
2008	N	r	p	N	r	p
Erythrocytes (/pl)	115	-0.248	**0.008**	115	-0.180	0.054
Haemoglobin (g/dl)	115	-0.255	**0.006**	115	-0.196	**0.035**
MCV (fl)	115	0.228	**0.014**	115	0.120	0.202
MCHC (g/dl)	115	-0.311	**0.001**	115	-0.148	0.115
Reticulocytes (‰)	114	0.219	**0.020**	114	0.179	0.057

The significant correlations between rainfall in mm and haematological values are shown in table 33. In 2007 there were no significant correlations for erythrocytes, haemoglobin, haematocrit, MCV, MCH, MCHC, neutrophils, eosinophils, basophils, monocytes and lymphocytes. In 2008 I found no significant correlations between rainfall and leucocytes, erythrocytes, haemoglobin, haematocrit, thrombocytes, eosinophils, basophils and monocytes. Again the results are not reproducible between years. The most striking evidence that rainfall is unlikely to have any influence on haematological values is that reticulocytes (‰ and /nl) correlate negatively with rainfall in 2007 while I measured a positive correlation in 2008. Therefore, I suggest that rainfall has no major effect on haematological values.

Table 33: Pearson correlation between haematological values and mean rainfall (mm) for 2007 and 2008 (March-October). Months and hedgehog sexes are pooled. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. (Note: only haematological values which correlated significantly are shown in the table).

	Mean rainfall 2 weeks before sample date			Mean rainfall 4 weeks before sample date		
2007	N	r	p	N	r	p
Leucocytes (/nl)	178	-0.06	0.428	178	0.229	**0.002**
Thrombocytes (/nl)	178	-0.213	**0.004**	178	0.086	0.254
Reticulocytes (‰)	178	-0.171	**0.023**	178	0.063	0.404
Reticulocytes (/nl)	162	-0.167	**0.033**	162	0.139	0.077
2008						
MCV (fl)	115	0.003	0.972	115	0.245	**0.008**
MCH (pg)	115	-0.024	0.796	115	0.105	0.264
MCHC (g/dl)	115	-0.044	0.640	115	-0.264	**0.004**
Neutrophils (%)	111	-0.058	0.546	111	-0.221	**0.020**
Lymphocytes (%)	112	0.105	0.270	112	0.257	**0.006**
Reticulocytes (‰)	114	-0.013	0.891	114	0.194	**0.038**
Reticulocytes (/nl)	110	-0.02	0.838	110	0.228	**0.017**

1.7 Regeneration

1.7.1 Comparison of the R- and C-groups

In contrast to the C-group, which consisted of males (N = 5) only, the R-group consisted of three males and two females. Since I could not measure any significant sex-biased differences in blood parameters in the experimental population, I decided to pool male and female animals for this experiment. The haematological values between the two groups for each sampling date were compared with each other using a t-test. Table 34 shows the results for the first sampling date (14.4.2009). No significant differences were found for hedgehog weight, leucocytes, haematocrit, thrombocytes, neutrophils, basophils, monocytes, lymphocytes and absolute reticulocytes. I could measure lower erythrocytes ($p = 0.002$), haemoglobin ($p = 0.03$) and MCHC ($p = 0.001$) in the R-group compared to the C-group. Additionally there were higher tick weights ($p = 0.027$), MCV ($p = 0.001$) and MCH ($p = 0.036$) in the R-group.

Table 34: Comparison of haematological values, total tick weight (g) and hedgehog weight (g) of the regeneration group (R) and the control group (C) at the first sampling date (14.4.2009). N = number of samples, SD = standard deviation, probability p was estimated with a t-test, significant p-values are in bold. (Note: the R-group was naturally infested with ticks; the C-group was always kept tick free).

Parameter	Investigation group	N	Mean	SD	p
Tick weight (g)	R	5	5.38	3.54	**0.027**
	C	5	0.00	0.00	
Hedgehog weight (g)	R	5	851.47	84.86	0.262
	C	5	949.84	156.61	
Leucocytes (/nl)	R	5	7.92	3.48	0.522
	C	5	9.50	3.96	
Erythrocytes (/pl)	R	5	4.60	1.87	**0.002**
	C	5	9.58	0.90	
Haemoglobin (g/dl)	R	5	8.12	3.98	**0.03**
	C	5	13.76	1.58	
Haematocrit (%)	R	5	31.66	14.18	0.108
	C	5	44.80	4.48	
MCV /fl)	R	5	68.04	4.36	**0.001**
	C	5	46.72	2.07	
MCH (pg)	R	5	17.14	2.08	**0.036**
	C	5	14.34	0.87	
MCHC (g/dl)	R	5	25.18	1.75	**0.001**
	C	5	30.70	1.04	
Thrombocytes (/nl)	R	5	326.60	133.76	0.139
	C	5	218.00	63.11	
Neutrophils (%)	R	5	44.40	26.35	0.275
	C	5	29.40	4.93	
Eosinophils (%)	R	5	7.40	3.65	0.563
	C	5	9.20	5.59	
Basophils (%)	R	4	2.25	0.96	0.398
	C	3	1.67	0.58	
Monocytes (%)	R	5	5.20	1.79	0.419
	C	5	6.20	1.92	
Lymphocytes (%)	R	5	40.00	24.86	299
	C	5	53.80	10.06	.
Reticulocytes (‰)	R	5	115.44	55.46	**0.019**
	C	5	42.42	5.32	
Reticulocyte conc. (/nl)	R	5	568.08	469.19	0.463
	C	5	405.40	53.60	

After both investigation groups were kept tick-free for four weeks the haematological values did not show any significant differences, except for the monocytes being just significantly higher in the C-group (p = 0.048) (see table 35).

Table 35: Comparison of haematological values and hedgehog weight (g) of the regeneration group (R) and the control group (C) at the second sampling date (12.5.2009). N = number of samples, SD = standard deviation, probability p was estimated with a t-test, significant p-values are in bold. (Note: the R-group was tick free for four weeks on the sample date).

Parameter	Investigation group	N	Mean	SD	p
Hedgehog weight (g)	R	5	1085.63	141.35	0.793
	C	5	1058.60	171.67	
Leucocytes (/nl)	R	5	7.28	1.20	0.573
	C	5	7.80	1.58	
Erythrocytes (/pl)	R	5	9.94	1.07	0.515
	C	5	10.38	0.97	
Haemoglobin (g/dl)	R	5	16.36	2.58	0.493
	C	5	15.42	1.39	
Haematocrit (%)	R	5	52.98	6.54	0.414
	C	5	49.98	4.23	
MCV /fl)	R	5	53.34	3.96	0.08
	C	5	48.36	3.89	
MCH (pg)	R	5	16.40	1.52	0.107
	C	5	14.90	1.05	
MCHC (g/dl)	R	5	30.78	1.28	0.937
	C	5	30.84	1.05	
Thrombocytes (/nl)	R	5	197.40	64.45	0.741
	C	5	187.00	21.47	
Neutrophils (%)	R	4	30.75	12.39	0.887
	C	5	31.60	3.78	
Eosinophils (%)	R	4	8.00	2.94	0.71
	C	5	8.60	1.67	
Basophils (%)	R	4	2.25	1.89	0.363
	C	5	3.80	2.68	
Monocytes (%)	R	4	2.25	0.96	**0.048**
	C	5	6.20	3.19	
Lymphocytes (%)	R	4	55.75	11.50	0.368
	C	5	49.60	7.73	
Reticulocytes (‰)	R	5	27.22	15.03	0.874
	C	5	25.98	7.66	
Reticulocyte conc. (/nl)	R	5	258.80	114.79	0.89
	C	5	267.60	76.08	

On the last sampling date, where both groups were kept tick-free for six weeks no differences in haematological values between the R- and C-group could be detected anymore (table 36).

Table 36: Comparison of haematological values and hedgehog weight (g) of the regeneration group (R) and the control group (C) at the third sampling date (26.5.2009). N = number of samples, SD = standard deviation, probability p was estimated with a t-test, significant p-values are in bold. (Note: the R-group was tick free for six weeks on the sample date).

Parameter	Investigation group	N	Mean	SD	p
Hedgehog weight (g)	R	5	1127.30	147.55	0.592
	C	5	1068.20	185.16	
Leucocytes (/nl)	R	5	7.70	0.84	0.89
	C	4	7.90	2.59	
Erythrocytes (/pl)	R	5	10.30	1.03	0.652
	C	4	10.65	1.20	
Haemoglobin (g/dl)	R	5	16.36	2.25	0.432
	C	4	15.35	0.93	
Haematocrit (%)	R	5	52.62	5.56	0.454
	C	4	50.15	3.04	
MCV /fl)	R	5	51.26	3.37	0.167
	C	4	47.43	4.12	
MCH (pg)	R	5	15.92	1.34	0.134
	C	4	14.53	1.05	
MCHC (g/dl)	R	5	31.02	1.21	0.551
	C	4	30.60	0.61	
Thrombocytes (/nl)	R	5	193.00	64.66	0.971
	C	4	191.50	52.26	
Neutrophils (%)	R	5	30.40	13.58	0.669
	C	4	34.00	9.59	
Eosinophils (%)	R	5	9.80	2.59	0.431
	C	4	8.25	2.99	
Basophils (%)	R	3	2.33	2.31	0.423
	C	1	5.00		
Monocytes (%)	R	5	7.80	5.02	0.174
	C	3	14.33	7.09	
Lymphocytes (%)	R	5	50.60	11.55	0.424
	C	4	43.75	12.66	
Reticulocytes (‰)	R	5	26.32	14.35	0.516
	C	4	21.53	4.97	
Reticulocyte conc. (/nl)	R	5	261.40	122.35	0.579
	C	4	226.50	44.74	

1.7.2 Comparison of sampling dates within the R-group and the C-group

To test for regeneration of the blood parameters I conducted a repeated measures ANOVA which compared the haematological parameters of the different sampling dates within each investigation group. As a post-hoc test a Bonferroni correction was used. If the Mauchly's test indicated a violation of the assumption of sphericity for a parameter, the degrees of freedom were corrected either with a Greenhouse Geisser (epsilon < 0.75) or a Huynh-Feldt correction (epsilon > 0.75). For the R-group all animals were used for the analysis, while for the C-group I had continuous blood counts for all sample dates only for four animals, because of technical problems during the during blood collection of one animal.

The results of the R-group reveal that the values for the haematological values from the different sampling dates differ significantly for erythrocytes ($F_{1.05,\ 4.22} = 100.19$, $p = 0.001$), haemoglobin ($F_{1.09,\ 4.37} = 53.42$, $p = 0.001$), haematocrit ($F_{1.07,\ 4.27} = 21.16$, $p = 0.008$), MCV ($F_{1.04,\ 4.15} = 98.37$, $p = 0.001$), MCHC ($F_{1.01,\ 4.04} = 94.52$, $p = 0.001$) and relative reticulocytes ($F_{1.00,\ 4.01} = 10.08$, $p = 0.034$).

No differences occurred for leucocytes ($F_{1.02,\ 4.08} = 0.131$, $p = 0.740$), MCH ($F_{1.02,\ 4.08} = 2.43$, $p = 0.193$), thrombocytes ($F_{1.01,\ 4.03} = 3.6$, $p = 0.130$), neutrophils ($F_{1.02,\ 3.05} = 1.14$, $p = 0.365$), eosinophils ($F_{2.00,\ 6.00} = 0.66$, $p = 0.550$), basophils ($F_{2.00,\ 6.00} = 0.684$, $p = 0.555$), monocytes ($F_{2.00,\ 6.00} = 2.06$, $p = 0.209$), lymphocytes ($F_{2.00,\ 6.00} = 1.03$, $p = 0.411$) and absolute reticulocytes ($F_{1.00,\ 4.01} = 1.54$, $p = 0.282$).

Significant results for the post-hoc test are presented in table 37, non-significant results are listed in appendix IV table VII.

The values for erythrocytes, haemoglobin, haematocrit and MCHC are significantly lower on the first sample date compared to the second and third sample dates. MCV is higher on the first sample date, while for MCH only the second and the third sample date differed from each other with higher values on the second sample date. Since the repeated measures ANOVA showed no significant F-values for the MCH, these differences can be ignored. For relative reticulocytes I found significant F-values in the repeated measures ANOVA but the Bonferroni correction produced no significant differences.

Table 37: Pairwise comparison of haematological values of the R-group (N = 5) for the different sampling dates. Blood samples were taken on 14.4.2009 (1), 12.5.2009 (2) and 26.5.2009 (3). After the first sampling all hedgehogs were kept tick-free for the rest of the experiment. The probability p was estimated with a Bonferroni correction as a post-hoc test. Significant p-values are in bold.

Parameter	(I) sample date	(J) sample date	Mean difference (I-J)	p	95% Confidence interval for difference	
					Lower bound	Upper bound
Erythrocytes (/pl)	1	2	-5.34	**0.001**	-6.97	-3.71
		3	-5.70	**0.002**	-8.16	-3.24
	2	1	5.34	**0.001**	3.71	6.97
		3	-0.36	0.614	-1.30	0.58
	3	1	5.70	**0.002**	3.24	8.16
		2	0.36	0.614	-0.58	1.30
Haemoglobin (g/dl)	1	2	-8.24	**0.003**	-11.98	-4.50
		3	-8.24	**0.008**	-13.08	-3.40
	2	1	8.24	**0.003**	4.50	11.98
		3	0.00	1	-1.57	1.57
	3	1	8.24	**0.008**	3.40	13.08
		2	0.00	1	-1.57	1.57
Haematocrit (%)	1	2	-21.32	**0.02**	-37.57	-5.07
		3	-20.96	**0.038**	-40.30	-1.62
	2	1	21.32	**0.02**	5.07	37.57
		3	0.36	1	-4.59	5.31
	3	1	20.96	**0.038**	1.62	40.30
		2	-0.36	1	-5.31	4.59
MCV (fl)	1	2	14.70	**0.003**	8.17	21.23
		3	16.78	**0.001**	10.77	22.80
	2	1	-14.70	**0.003**	-21.23	-8.17
		3	2.08	**0.005**	0.96	3.20
	3	1	-16.78	**0.001**	-22.80	-10.77
		2	-2.08	**0.005**	-3.20	-0.96
MCH (pg)	1	2	0.74	1	-2.06	3.54
		3	1.22	0.404	-1.36	3.80
	2	1	-0.74	1	-3.54	2.06
		3	0.48	**0.023**	0.10	0.86
	3	1	-1.22	0.404	-3.80	1.36
		2	-0.48	**0.023**	-0.86	-0.10
MCHC (g/dl)	1	2	-5.60	**0.002**	-7.95	-3.25
		3	-5.84	**0.002**	-8.14	-3.54
	2	1	5.60	**0.002**	3.25	7.95
		3	-0.24	**0.028**	-0.44	-0.04
	3	1	5.84	**0.002**	3.54	8.14
		2	0.24	**0.028**	0.04	0.44

The results of the repeated measures ANOVA for the C-group showed significant differences for erythrocytes ($F_{2.00,\ 6.00} = 8.73$, $p = 0.017$), haemoglobin ($F_{2.00,\ 6.00} = 24.71$, $p = 0001$), haematocrit ($F_{2.00,\ 6.00} = 13.88$, $p = 0.006$), lymphocytes ($F_{2.00,\ 6.00} = 7.46$, $p = 0.024$), relative reticulocytes ($F_{2.00,\ 6.00} = 24.01$, $p = 0.001$) and absolute reticulocytes ($F_{2.00,\ 6.00} = 18.09$, $p = 0.003$). No significant differences were found for leucocytes ($F_{2.00,\ 6.00} = 3.32$, $p = 0.107$), MCV ($F_{2.00,\ 6.00} = 0.63$, $p = 0.566$), MCH ($F_{2.00,\ 6.00} = 1.63$, $p = 0.272$), MCHC ($F_{2.00,\ 6.00} = 0.183$, $p = 0.838$), thrombocytes ($F_{2.00,\ 6.00} = 1.08$, $p = 0.397$), neutrophils ($F_{2.00,\ 6.00} = 0.781$, $p = 0.500$), eosinophils ($F_{2.00,\ 6.00} = 0.353$, $p = 0.716$) and monocytes ($F_{2.00,\ 4.00} = 0.284$, $p = 0.171$). Basophils were not included into the calculation, since the sample size was too low. Table 38 presents the significant results of the post-hoc test for the C-group, not significant results are listed in the appendix IV table VIII.

The haemoglobin values on the first sample date were lower compared to the second and third sample date. Erythrocytes and haematocrit were lower on the first sample date, compared to the third. Higher relative and absolute reticulocyte as well as leucocyte concentrations were measured on the first sample date compared to the second and third sample date. The second and third sample date did not differ from each other in any of these cases. Although I found significant differences in the Bonferroni correction for lymphocytes, no significant differences could be detected in the paired measures ANOVA.

Table 38: Pairwise comparison of haematological values of the C-group (N = 4) for the different sampling dates. Blood samples were taken on 14.4.2009 (1), 12.5.2009 (2) and 26.5.2009 (3). Hedgehogs were kept tick-free before and during the whole experiment. The probability p was estimated with Bonferroni correction as a post-hoc test. Significant p-values are in bold.

Parameter	(I) sample date	(J) sample date	Mean difference (I-J)	p	95% Confidence interval of difference	
					Lower bound	Upper bound
Erythrocytes (/pl)	1	2	-0.78	**0.006**	-1.14	-0.41
		3	-1.05	0.165	-2.72	0.62
	2	1	0.78	**0.006**	0.41	1.14
		3	-0.28	1	-1.65	1.10
	3	1	1.05	0.165	-0.62	2.72
		2	0.28	1	-1.10	1.65
Haemoglobin (mg/dl)	1	2	-1.60	**0.026**	-2.87	-0.33
		3	-1.90	**0.039**	-3.64	-0.16
	2	1	1.60	**0.026**	0.33	2.87
		3	-0.30	0.89	-1.46	0.86
	3	1	1.90	**0.039**	0.16	3.64
		2	0.30	0.89	-0.86	1.46
Haematocrit (%)	1	2	-4.88	0.139	-12.10	2.35
		3	-5.90	**0.038**	-11.25	-0.55
	2	1	4.88	0.139	-2.35	12.10
		3	-1.03	1	-5.56	3.51
	3	1	5.90	**0.038**	0.55	11.25
		2	1.03	1	-3.51	5.56
Reticulocytes (‰)	1	2	13.08	0.119	-5.11	31.26
		3	19.48	**0.023**	4.76	34.19
	2	1	-13.08	0.119	-31.26	5.11
		3	6.40	**0.038**	0.61	12.19
	3	1	-19.48	**0.023**	-34.19	-4.76
		2	-6.40	**0.038**	-12.19	-0.61
Reticulocytes (/nl)	1	2	105.50	0.214	-81.43	292.43
		3	166.25	**0.022**	42.95	289.55
	2	1	-105.50	0.214	-292.43	81.43
		3	60.75	0.079	-11.41	132.91
	3	1	-166.25	**0.022**	-289.55	-42.95
		2	-60.75	0.079	-132.91	11.41
Lymphocytes (%)	1	2	2.23	0.558	-4.10	8.55
		3	2.30	**0.34**	-2.74	7.34
	2	1	-2.23	0.558	-8.55	4.10
		3	0.08	1	-2.66	2.81
	3	1	-2.30	**0.34**	-7.34	2.74
		2	-0.08	1	-2.81	2.66

The comparison of the blood parameters of the different sampling dates indicates that regenerative processes are under way in the R-group as well as in the C-group after tick removal.

2. Discussion

2.1 Haematological values, ticks and climate parameters

The environment of an animal is affected by climatic factors that include temperature, humidity and direct or indirect solar radiation which might act as stressors that increase the strain in animals (GWADZAUKAS 1985, SILANIKOVE 2000). Harsh weather can have a devastating effect on both survival and breeding success of wild animals. Additionally corticosteroids, which are released in response to stress caused by austere conditions, may trigger physiological and behavioural changes (ROMERO et al. 2000).

High ambient temperatures and humidity increase plasma cortisol levels in humans, goats, cows and rats (WISE et al. 1988, BHAT et al. 2008). The enhancement of stress hormones act as a short-term response and a non-specific reaction which occurs for a variety of different stressors. CHRISTISON and JOHNSON (1972) investigated the long-term influence of high ambient temperature on stress levels in cows. They found that, in case of prolonged heat exposure, cows make specific adjustments in the turnover rate of cortisol, leading to a decrease in the stress hormone after an initial increase caused by a short-term response. Weather can also act as a co-stressor. ROMERO et al. (2000) discovered that in two species of Arctic birds, corticosteroid levels and climate conditions were correlated through the moulting phase, which is an energetically costly period, while no such relationship was found during other times of the year.

In addition to stress hormones, other parameters are influenced by weather and season, as for blood parameters of e.g. humans. BAZETT et al. (1940) showed that the exposure of an individual to environmental temperatures maintained at certain levels for a period of time resulted in changes in blood volume. In summer, higher leucocyte concentrations, MCHC and MCH and lower haematocrit and MCV can be found (RÖCKER et al. 1980), and mild surface cooling over a period of six hours increases the haematocrit, thrombocyte concentration and mean platelet volume significantly, which involves normal thermoregulatory adjustments in humans (KEATINGE et al. 1984). Similar results were found for cattle and feral house mice (MACLEAN and LEE 1973, LEE et al. 1976).

I tested for correlations between haematological values (differential blood count, testosterone and cortisol levels) and climate parameters (temperature, relative humidity and rainfall). Although a few significant correlations could be detected, no clear trend was noticeable. Temperature, humidity and rainfall are very variable parameters (climate data is listed in appendix II tables I-III), and since no direct manipulation of these factors is possible in field studies, it is difficult to measure their influence on fitness parameters of animals, since the response to, e.g. high ambient temperatures, can be compensated by a rapid change to lower temperatures. In order to distinguish the effect of weather on the fitness of hedgehogs it is necessary to perform an experiment in which climatic factors are manipulated (e.g. in a climate chamber) and animals are exposed to extreme values for a prolonged period, to test for short-term and long-term responses. However, placing a hedgehog under such artificial conditions is likely to increase natural stress levels which would invalidate the experiment. Thus, I can only speculate as to what influence certain climate parameters can have on fitness parameters of the European hedgehog but no clear conclusions can be made. However, I assume that the climate parameters in this study should have no notable effect on the haematological values, stress and sexual hormones.

In contrast to blood parameters and hormones the seasonal tick density in my study was correlated with temperature. These correlations were clearly connected with the dynamics of the single life stages of both species. For example, the densities of all life stages of *I. ricinus*, except for larvae, are negatively correlated with temperature. All these life stages have their peaks in spring and autumn, both seasons with colder temperatures than in summer. In contrast to females and nymphs, the number of larvae of *I. ricinus* correlated positively with temperature, since they have their population peak in summer.

The pattern for *I. hexagonus* is different, since most life stages did not show such high seasonal variations as *I. ricinus* life stages. Females correlated positively with temperature, because they have their peak in summer. The other life history stages also correlated at some times, because there occurred, although not significant, trends for light seasonal variations. The correlations between seasonal dynamics of the different life history stages and tick species and both humidity and rainfall did not show significant trends.

It is well known that environmental factors have an influence on tick abundance, but it is hard to distinguish between causality and potential autocorrelations between an environmental variable, a true regulating factor, and dynamic processes.

For example temperature and humidity are of particular significance for the local occurrence of ticks, but more at the level of the microclimate of the tick's off-host habitat. This depends

both on abiotic and biotic factors, like vegetation height (shady areas and areas with high vegetation lead to lower temperatures and higher humidity than open sunny areas) or the type of ground, offering interstitial retreat possibilities and water storage capacities (MERLER et al. 1996, SCHWARZ et al. 2009). The abundance of *I. ricinus* is limited by climatic factors, but ESTRADA-PEÑA et al. (2006) classified nine different ecologically and climatically heterogeneous habitats in Europe in which this tick occurs and develops, so there seems to be only limited habitat specificity.

I. hexagonus, as a nest-dwelling species, depends strongly on the microclimate of its habitat, the nest of hedgehogs, and not as much on climatic factors outside of the nest. This explains why *I. hexagonus* density does not show any clear relationship to the climate, except for temperature. Apparently this depends, as for *I. ricinus*, mostly on the seasonal dynamics of this species and not on the temperature itself.

For *I. hexagonus* it is important to compare tick numbers with microclimatic factors inside the nest, while for *I. ricinus* one should look not only at ambient climatic factors, but also at other factors such as vegetation.

2.2 Tick population dynamics and regulation

2.2.1 Sex-biased tick infestation

Differences in tick infestation rates between male and female hedgehogs did not occur in the experimental population, although there are a number of studies on sex-biased variation in parasite burden for several animal species. In most cases males are more highly parasitized than females. This was found for helminth infections in birds and mammals (POULIN 1996, ZUK and MCKEAN 1996), and also for ectoparasite infestations (SCHALK and FORBES 1997, SOLIMAN et al. 2001, AMO et al. 2005, PEREZ-ORELLA and SCHULTE-HOSTEDDE 2005). Two theories exist to explain this pattern: (i) sex-specific behaviour might affect the exposure to parasites, therefore making one sex more vulnerable than the other, and (ii) the adrenal hormones, testosterone in particular, have immunosuppressive effects, and therefore facilitate the infection/infestation with parasites and/or pathogens (CHRISTE et al. 2007). The effect of testosterone will be discussed later (see chapter III.2.4.2).

Differences in exposure to parasites due to different behavioural patterns could for example be a result of increased male aggression or decreased grooming by males during the mating period, spatial aggregation within individuals of one sex or one sex having a larger territory or home range, increasing the risk of being infected with parasites or pathogens (MORAND et al.

2004, KRASNOV et al. 2005). Other ecological features, like different dietary preferences between the sexes, as demonstrated in three-spined sticklebacks (*Gasterosteus aculeatus*), should also be taken into account (REIMCHEN and NOSIL 2001). In this case, parasite species infecting their hosts differed between male and female fish, since male preferred to feed in benthic habitats, while females fed in pelagic habitats, with both habitats harbouring different parasite species.

Sex-biased parasitism can also depend on the type of parasite. HILLEGASS et al. (2008) showed that male Cape ground squirrels (*Xerus inauris*) carried three times more ectoparasites than females, while females had a three times higher endoparasite load than males. The authors explained this pattern with increased androgens reducing the ectoparasite resistance in males and with a smaller home range of females increasing their exposure to endoparasites. This disagrees with the hypothesis of MORAND et al. (2004) who describes an increased parasitism of males with an increased home range and therefore with a higher risk of parasite infection.

There are also several studies reporting female-biased parasitism, for example female European kestrels (*Falco tinnunculus*) harbour more haematozoan parasites than males (KORPIMÄKI et al. 1995), and female wood ducks (*Aix sponsa*) show higher prevalences in plathelminth infections (DROBNEY et al. 1983).

The gender differences can vary according to season (VAINIKKA et al. 2004), because, especially in smaller mammals, differences in mobility or home range size changes seasonally (RANDOLPH 1977).

However, I was not able to detect any differences in tick burden between male and female hedgehogs at any time of the year in the experimental hedgehog population indicating no sex-biased parasite infestation patterns, at least within this experimental population. For hedgehogs, it is known that males, especially during the mating season, have larger home ranges than females (REEVE 1981, KRISTIANSSON 1984). In my study the home range was bordered by fences and therefore males did not have the opportunity to increase their range. This means that in the experimental hedgehog population the exposure to ticks was not higher in males than in females, suggesting that potential differences in parasitation of the sexes occurring in wildlife due to behavioural differences could not be detected in this experiment.

To my knowledge there are no data available about hedgehog grooming behaviour, and whether this differs between the sexes. From personal observations, I could not find any differences in grooming behaviour between the sexes during the year which could explain the sex-biased parasitism.

Male aggression during mating (especially with increased testosterone levels) has been demonstrated in several animal species, for example lizards (SALVADOR et al. 1996) and Common hamsters (FRANCESCHINI et al. 2007). This intrasexual aggression can lead to increased parasite loads. In hedgehogs intrasexual aggression is enhanced in males throughout the mating season, but females also behave aggressively towards courting males (REEVE 1994). Thus, both sexes show behavioural changes during the mating season, nevertheless, no changes in tick infestation levels were found suggesting that seasonally dependent intra- and intersexual aggression does not influence ectoparasite infestation rates.

Differences in tick infestation pattern do not seem to occur between sexes in the European hedgehog because of the behavioural features of the animals in general and/or the experimental setup of this study.

2.2.2 Tick population dynamics and regulation

The annual population cycle of *I. ricinus*, the major vector of diseases to humans and animals in Europe (STEERE et al. 2004, PICHON et al. 2006, WIELINGA et al. 2006), has been well studied (e.g. MACLEOD 1936, KORENBERG 2000). My data are consistent with those of numerous studies in Central and Northern Europe with high amplitudes of nymphal and adult peaks occurring in spring and autumn and larvae peaking in summer (GRESIKÓVA et al. 1968, MERMOD et al. 1973, NILSSON 1988, SZÉLL et al. 2006, FÖLDVÁRI et al. 2007). This indicates that my experimental setup mirrors the natural population dynamic situation for this species.

Most studies on the density of *I. ricinus* in natural habitats were conducted using flagging as the method of tick collection (e.g. RANDOLPH et al. 2002, JOUDA et al. 2004a). The density of ticks collected by flagging and the density of ticks collected directly from the host are not comparable, which makes it difficult to make an estimate of the tick density in my experimental area. However, comparisons with studies from Europe, in which ticks were directly collected from different host species (see NILSSON 1988, MATUSCHKA et al. 1990, HUMAIR et al. 1993, L'HOSTIS et al. 1996, TÄLLEKLINT and JAENSON 1997), although not from hedgehogs, indicate that the *I. ricinus* density in my experimental research area is higher than in most natural environments.

This is the first study with a consistent, comparable sampling procedure carried out on the natural population dynamics and densities of *I. hexagonus*. Previous data derive from the scattered, methodically inconsistent collections from host animals (HESSE and VÖLKER 1983, WALTER et al. 1986, PICHOT et al. 1997, CHRISTIAN 2002), but no data on population dynamics are available.

My study reveals that *I. hexagonus* has much lower amplitude of variation, with relatively low population levels throughout the year, compared to *I. ricinus*. The autumn peak of nymph and female *I. ricinus* is of particular significance since an increased blood loss in the period during which the hedgehogs are building up fat reserves prior to hibernation (REEVE 1994) and a reallocation of energy to blood regeneration could influence the hedgehogs chances of survival during this period of high mortality (PFÄFFLE et al. 2009). In contrast, the much lower amplitude variation of *I. hexagonus* with relatively low population levels throughout the year indicate that the burden of parasitism by this specialist parasite is more evenly distributed over the year causing a consistent, but relatively low drain on host resources. In addition, while the peak densities within each *I. ricinus* life history stage were consistent between years, those for *I. hexagonus* were not, suggesting substantially different regulation mechanisms.

The density of my experimental hedgehog population was about 5 to 10 times higher than for wild populations in rural and suburban areas, respectively (see chapter III.1.2). Although I do not have comparable data for natural, seasonal tick infestation rates from wild hedgehog populations, it seems that the generalist *I. ricinus*, which finds its host outside of the nest in order to have access to a broad variety of hosts, is able to benefit from the high hedgehog densities prevailing in the experimental population, and there seems to be no regulation of its populations in a density-dependent manner. In contrast, the specialist *I. hexagonus*, which is closely associated with its host's nest, seems to benefit less from the high hedgehog density. Concerning the pathological effect of ticks on hedgehogs, a massive build up of *I. hexagonus* in a hedgehog's nest would potentially be a serious health hazard for the hedgehog, but since such a build up does not appear to occur I suggest some density-dependent mechanisms regulating *I. hexagonus* but not *I. ricinus* populations.

This can be attributed to the different ecology of these tick species. All life stages of the generalist *I. ricinus* develop in open habitats, preferably in bushy areas with secondary plant growth and mixed forests with ecotones (ESTRADA-PEÑA 2001). These habitats serve a wide variety of different host species such as rodents, birds, deer, but also hedgehogs, as food sources, shelter and protection. The open habitat in which *I. ricinus* lives provides the tick with the opportunity to increase its population density because host resources are abundant and an increased population density increases the chances to find a potential mating partner (KISZWESKI and SPIELMAN 1999, HINGST 2009). Therefore intraspecific density-dependent mechanisms regulating the tick population would be a disadvantage for the reproduction of *I. ricinus*.

In contrast to *I. ricinus*, the whole development of *I. hexagonus* occurs within its host's nest. The nest, as an enclosed habitat, is limited in space and also in available hosts, meaning that high parasite population densities would be likely to diminish the survival and reproductive success of the ticks (ANDERSON and MAY 1978, MAY and ANDERSON 1978). Something similar was shown for larvae of the hen flea, *Ceratophyllus gallinae*, a nest living species and a common parasite of blue tits (*Parus caeruleus*) (TRIPET and RICHNER 1999), as well as for the larvae of the reptile tick *Aponomma hydrosauri* (TYRE et al. 2003). In both cases, interference between the larvae within the hosts nest or on the host influenced the survival and/or the development of these ectoparasites.

Evidence for similar mechanisms potentially occurring in *I. hexagonus* populations is that even the continuous use of nest boxes did not seem to increase *I. hexagonus* population densities, although data from experimental estimates of tick longevity in these nest boxes, and host nest box use, showed that *I. hexagonus* survived considerably longer than *I. ricinus* and should have had an approximately 100% chance of finding a host and therefore of continuing its life cycle to reproductive age (TOMASCHEWSKI 2009). Nevertheless, *I. hexagonus* population levels, although varying between years, showed no sign of a consistent increase in numbers.

Nest cleaning should not have had an effect on the population dynamics of *I. hexagonus* since the nests were cleaned at irregular intervals with laps of several months between cleaning events (see chapter II.1.1). Data from the cleaned nests showed that removal of the nest material did not change tick abundance compared to other nest boxes at the next cleaning period (MAURER 2008). Additionally, the hedgehogs were able to build their own nests in the research area. These were never cleaned or destroyed and should therefore have supported the developmental cycle of *I. hexagonus*.

A mechanism to maximize reproductive success is to choose habitats which offer the best fitness output (KRASNOV et al. 2003). The habitats of *I. hexagonus* are the host it feeds on and the nest it reproduces in. For a specialist like *I. hexagonus* with only limited host choice it is important to protect the host from an extreme fitness loss and death in order to assure its own survival and reproductive success. In contrast, generalists like *I. ricinus* with very broad host finding possibilities do not need to protect a host from high energy loss and potential death. Thus, in order to increase the fitness of *I. hexagonus*, a density-dependent mechanism in either of the two habitats controlling population growth could be the reason for the stable populations of *I. hexagonus* throughout the year.

Defensive reactions of the host should to be considered as a density-dependent mechanism regulating the populations of *I. hexagonus* but not of *I. ricinus*. RANDOLPH (1994) reports that the engorgement and moulting success of larvae of *Ixodes trianguliceps* decreased with increased tick density as a consequence of acquired resistance of its natural rodent host, the bank vole (*Myodes glareolus*, as *Clethrionomys glareolus* which is a junior synonym). Acquired resistance leads to reduced blood-meal volumes, prolonged duration of feeding, diminished production and reduced viability of ova, and inhibition of moulting as well as increased mortality of engorged ticks (WIKEL 1996). Acquired resistance was also shown in other host species, for example resistance of the bank vole *M. glareolus* to *I. ricinus* (DIZIJ and KURTENBACH 1995), of European (*Bos taurus*) and zebu cattle (*B. indicus*) to *Rhipicephalus* (*Boophilus*) *microplus* (RIEK 1962), or of rabbits to *R. appendiculatus* (DOBBELAERE et al. 1987).

The development of acquired resistance to a certain tick species is host dependent. DIZIJ and KURTENBACH (1995) compared the reaction of *Apodemus flavicollis* and *M. glareolus* to repeated infections with *I. ricinus* larvae. While engorgement and moulting success of larvae feeding on *M. glareolus* were significantly reduced, larvae feeding on *A. flavicollis* were not affected at all. There is no study which describes acquired resistance in hedgehogs to either *I. hexagonus* or *I. ricinus*, but it could explain the low variation in *I. hexagonus* densities throughout the year, especially since this resistance is usually only partial and a proportion of the tick population feeds sufficiently to complete its life-cycle successfully (SHAPIRO et al. 1989).

Although both species investigated here belong to the genus *Ixodes*, it is likely that some differences in the repertoire of genes expressed from the salivary gland transcriptome, and therefore differences in the salivary proteins, occur. *I. ricinus* differs significantly, for example, from the closely related *I. scapularis* in various regions of the sialome (CHMELAŘ et al. 2008). It is possible that the European hedgehog reacts differently to salivary gland products from different tick species. In nature, hedgehogs are predominantly infested with *I. hexagonus*. Results from hedgehog dissections (see chapter IV.1.1.1) showed prevalences for *I. hexagonus* of 53.3% and for *I. ricinus* of 23.4%. For the European hedgehog, developing acquired resistance against a tick species reproducing inside its nests, in order to keep tick population densities at low levels, would be an adequate strategy to prevent and/or reduce energy drain caused by tick-induced blood loss.

Antagonistic interactions and interspecific competition between two tick species are well documented. In Africa, the native cattle tick *Rhipicephalus* (*Boophilus*) *decoloratus* is rapidly

being replaced by the introduced Asian tick *R.* (*B.*) *microplus* (TONNESEN et al. 2004). The success of the invasive species is based on its higher reproductive rate, the result of an increased blood feeding ability (ESTRADA-PEÑA 2002). Both species are able to mate with each other leading to sterile hybrid offspring (SPICKETT and MALAN 1978). The invader *R.* (*B.*) *microplus* benefits from this because of its higher reproductive capacity (TARASCHEWSKI 2006b). Such interspecific competition between different tick species does not appear to be common and seems to occur predominantly between species with, e.g., the same habitat requirements. *I. hexagonus* and *I. ricinus* do not share off-host habitats, since *I. hexagonus* is a nest-dwelling species, reproducing and developing in the nests of its hosts (BELOZEROV 1982, PFÄFFLE et al. 2009) - the majority of ticks found in hedgehog nests in this study were *I. hexagonus* (MAURER 2008) - while *I. ricinus* is normally found in open habitats. Additionally, the European hedgehog is just one of more than 300 hosts the generalist *I. ricinus* feeds on, hence it does not benefit from adjusting to the specialist tick. Moreover, as mentioned previously, *I. hexagonus* is the dominate tick species on wild hedgehog populations, also parasitizing *E. europaeus* when *I. ricinus* does not occur (FISCHER 2007) indicating that the specialist also does not have to adjust to the generalist tick. Therefore, competition for habitat and hosts can probably be excluded as a mechanism to regulate *I. hexagonus* via *I. ricinus* populations.

By comparing the population dynamics of *I. ricinus* and *I. hexagonus*, it is clear that *I. hexagonus* may play an important role in maintaining the epidemiological cycle of various animal and human diseases. The agents of diseases such as borreliosis and anaplasmosis have already been detected in hedgehogs and the ticks infesting them (GRAY et al. 1994, SKUBALLA et al. 2007, in press), as has their ability to transmit these diseases (GERN et al. 1991, 1997). In case of *Borrelia* spp., small rodents like *Apodemus* spp., *Microtus* spp. and *Myodes* spp. serve as reservoir hosts, being the most likely source of infection for ticks (GRAY 1998). Medium sized animals like squirrels or hedgehogs, which share habitats with the rodents, although less numerous, may also be important as a source of infection (CRAINE et al. 1995). Since *I. ricinus* and *I. hexagonus* feed at the same time on their hosts, although with different life history stages, pathogens can be ingested via the host or via co-feeding (RANDOLPH et al. 2006). In the case of the hedgehog, co-feeding would be an important source of infection for the larvae of *I. ricinus*. These have their population peak in summer when nymphs and females of *I. hexagonus* are relatively abundant, so the chances for *I. ricinus* larvae to become infected with a certain pathogen are likely to be high. These larvae moult to nymphs, which

feed predominantly on rodents, the most important reservoir hosts, for example for *Borrelia* species, but which are also the life stages mostly found on humans (JOUDA et al. 2004b).

2.3 Cortisol

In birds and mammals the frontline hormones to overcome stressful periods and situations are the glucocorticoids cortisol and corticosterone, and the catecholamines adrenaline and noradrenaline (PALME et al. 2005). A stressor can be physical, physiological or both and is a disruption to homeostasis. It activates the hypothalamo-pituitary-adrenal axis (HPA-axis) and the sympathroadrenal system (TILBROOK et al. 2000). The stimulation of the HPA-axis leads to a cascade of activations and the release of several factors and hormones including the corticotrophin-releasing factor (CRF), arginine vasopressin (AVP), the adrenocorticotrophic hormone (ACTH), β-endorphine and the α-melanocyte-stimulating hormone. ACTH stimulates the synthesis and secretion of the glucocorticoids. These glucocorticoids again have a negative impact on the HPA-axis and reduce the secretion of CRF, AVP and ACTH (PLOTSKY et al. 1989).

In most animals the secretion of the glucocorticoids underlies a day-night rhythm, with maximum hormone levels prior to the start of the active period. In diurnal animals glucocorticoids raise to high levels during the early morning hours and the day, but stay at low levels during night (OKI and ATKINSON 2004, MOHAWK and LEE 2005, KUDIELKA et al. 2006). In nocturnal animals like the hedgehog this pattern is inverted. This is related to the energy mobilising effect of these hormones, which is important prior to the active period.

The predominant corticosteroid in the hedgehog is cortisol (WERNER and WÜNNENBERG 1980). To prevent false effects from day-night rhythms blood samples were taken during the "normal" resting phase of the hedgehogs between 12:00 and 15:00 o'clock.

In the experimental population neither females nor males showed marked variations in the cortisol cycle throughout the year. The same was observed by FOWLER (1988) on captive adult hedgehogs, although the cortisol levels in 2006 in my study were up to two times higher than in his study.

Female hedgehogs had, although only significant in June 2006 and May 2007/2008, higher cortisol levels than males throughout the year. FOWLER (1988) also reports sex-biased differences in hedgehogs, although his study does not clarify which sex showed higher stress hormone levels.

A sex-biased difference in stress hormone concentrations is described for various mammal species (dogs, cattle, ground squirrels, yellow-pine chipmunks) and is often related to

pregnancy and lactation (SMITH et al. 1973, CONCANNON et al. 1978, KENAGY and PLACE 2000, BOONSTRA et al. 2001). The majority of sexual activity in European hedgehogs takes place between May and July and lasts until August, depending on region and latitude (REEVE 1994), and sexual behaviour starts directly after arousal from hibernation. Thus, increased cortisol levels due to sexual activity do not seem to match for female hedgehogs since (i) it is rather unlikely, that females are already lactating in March or April, when I measured significant differences between male and female hedgehogs, and (ii) the cortisol levels of females, as well as of males, did not vary throughout the year, while in the other studies there were clear increases in cortisol throughout the mating period. Although sexual behaviour was observed in the experimental population and females and males were mating as well as several females became pregnant, the successful rearing of the offspring did not occur. Possibly, this was caused by disturbance through other hedgehogs due to the high hedgehog density in my study (see chapter III.1.2), resulting in abandoning of the young.

Some studies indicate that females of various animal species, e.g. Siberian hamsters (*Phodopus sungorus*) or mice, show higher baseline cortisol levels than males, also outside of the mating season (BILBO and NELSON 2003, BILBO et al. 2003, MALISCH et al. 2007). Such female-biased higher glucocorticoid levels seem to be a general trend that appears to hold for most mammalian species (REEDER and KRAMER 2005). This effect is thought to result from females having a higher capacity to produce steroid-binding globulins, meaning that glucocorticoids can also bind to an extent to gonadal steroid-binding globulins, and therefore the total glucocorticosteroid concentration can be higher (BREUNER and ORCHINIK 2002, TOUMA and PALME 2005).

The results from my study indicate that European hedgehogs show similar sex-biased patterns in cortisol concentrations compared to other animal species. However, this is the first study with consistent hormone measurements over a period of three years in hedgehogs and therefore this is a new insight in the physiology of these animals.

The only anomaly in annual cortisol levels of the hedgehogs of my study were found in March and April 2007, with extremely high cortisol concentrations. In these months the stress hormone of female hedgehogs also correlated positively with the individual tick infestation weight, which did not occur in the other periods.

At the end of February 2007 the whole hedgehog garden was dug over with a rotovator over a period of two days. During this time hedgehogs were either moved to indoor enclosures or, when hibernating in nest boxes, locked in their nests, to prevent possible injuries. In February the majority of the animals were lightly aroused and therefore might have recognized the

disturbance. It seems that this was the main stressor leading to an increase in the cortisol levels in the hedgehogs and influencing the relationship between host and parasites in females. After recovering from the disturbance, ticks as single stressors were not correlated with cortisol levels of female hedgehogs anymore.

This seems to agree with the hypothesis that cortisol has an immunosuppressive effect with a simultaneous increase of parasite infection. The immunosuppressive effect of increased cortisol levels is considered to result, for example, in the inhibition of inflammation, macrophage and lymphocyte effects, changes of cytokine production and increase in monocyte apoptosis (LINDBERG and FRENKEL 1977, BARTON et al. 1987, MUEHLENBEIN 2006). Stressors increasing cortisol levels and decreasing the immunocompetence of an animal should therefore facilitate the infection with parasites. This was demonstrated in various studies. BELDEN and KIESECKER (2005) investigated the effect of environmental stressors on infections with *Alaria* sp. (Trematoda: Diplostomatidae) cercariae in grey treefrogs (*Hyla versicolor*). They treated tadpoles with exogenous corticosterone which resulted in increased infections with trematodes. Mice injected with corticosteroids prior to infection with *Giardia muris* suffered from higher trophozoite numbers than control animals treated with saline injections (NAIR et al. 1981).

In order to observe potential immunosuppressive effects of cortisol on hedgehogs, I tested for correlations (Pearson correlation) between cortisol levels and blood cells involved in immunity (leucocytes, lymphocytes, neutrophils, eosinophils, basophils, monocytes - for results see appendix V tables IX-X) but no significant correlations between the stress hormone and the other blood parameters could be detected, neither for female nor for male hedgehogs. So, it seems that cortisol does not have an immunosuppressive effect in hedgehogs, which facilitates the infection with ticks, or at least not on the parameters which I analyzed. Since I did not examine the effect of cortisol on all parameters of the immune system (e.g. cytokines), high stress levels in hedgehogs could still lead to a reduction of immunity. This explains the positive correlation between cortisol and the tick infestation level in association with an exogen, environmental stressor in female hedgehogs of my experimental population.

Not only stress hormones increase the risk of pathogen infections, parasites also increase stress levels in different organisms and therefore facilitate the infection with other parasites or pathogens. Calves of *B. taurus* infected with the nematode *Ostertagia ostertagi* developed higher cortisol levels than control animals (FLEMING 1998). CHAPMAN et al. (2007) tested for correlations between cortisol and endoparasite infection in red colobus monkeys (*Procolobus*

rufomitratus). High infection rates led to an increase in cortisol concentrations which were related to increased stress, as suggested by the authors.

In contrast to these studies, there is also data available showing no measurable effect of parasite infection on cortisol levels, as in the coral reef fish *Hemigymnus melapterus* (GRUTTER and PANKHURST 2000) and the rainbow trout *Oncorhynchus mykiss* (NOLAN et al. 2000). This shows that the response to acute parasite infection varies between different host species and cannot be generalized. An increase in cortisol due to parasitation, and as a result an eventually decreased immune response in some animal species might be counterproductive because it reduces the capacity of the individual to fight further parasite and pathogen infections. Therefore, some animal species, including the hedgehog, might react less sensitively to certain stressors, although responses to environmental stressors, such as disturbance of the female hedgehogs, might alter the organism's response to other stressors like ticks (ESCH et al. 1975). DUNLAP and SCHALL (1995) investigated the stress response of lizards to malaria infections. Unstressed animals, infected or uninfected, had the same basal corticosterone levels, but after adding and exogenous stressor, like capture and handling, infected animals showed significantly higher stress levels than uninfected animals.

Like females, the male hedgehogs from the present study did not show any variation in cortisol levels during the year, but I found more significant monthly correlations with tick infestation weight than in females. Interestingly there were no correlations in March 2007, the only period in which females showed significant correlations between cortisol levels and tick weight. This might be caused by the low sample size of ten animals and the high variability in cortisol in the group.

Different stressors have different effects and different responses to short- and long-term stress occur in different individuals, sexes or species (TILBROOK et al. 2000, BLANCHARD et al. 2001). Males and females often differ in the amount of stress they experience and the types of stressors they encounter (KLEIN 2004). In sockeye salmon (*Oncorhynchus nerka*) KUBOKAWA et al. (1999) found out that female fish had constantly higher cortisol levels than males and that they were not, in contrast to males, refractory to the stress of capture and handling during the breeding season. Male squirrel monkeys (*Saimiri sciureus*) manifest significantly higher cortisol levels after capturing and anaesthesia than females (COE et al. 1978). Female rats have higher basal corticosterone levels than males and they show higher responses to novel stressors (BEIKO et al. 2004). It is likely that females have, most of the time, a more robust stress response than males because of the central actions of the sexual hormones oestrogen

and the androgens. It seems that testosterone inhibits the HPA-axis while oestrogen enhances is function and therefore modulates the stress response (HANDA et al. 1994).

The differences between the sexes in relation to stress hormones and tick infestation of the hedgehogs of the experimental population seem to depend on the kind of environmental stressor the animals are exposed to. Both sexes had extremely high mean cortisol levels at the beginning of 2007 and the highest cortisol concentrations throughout 2006, indicating that females and males are stressed by the same factors. But since females showed correlations between tick weight and cortisol in March and April 2007, while males did not, and males showed correlations of stress hormones and ticks throughout 2006 and 2007 while females did not, these factors seem to influence the host-tick relationship differently between the sexes.

Social interactions serve as an important source of stress and are ubiquitous among mammalian species (BLANCHARD et al. 2001). ESCH et al. (1975) mentioned that, except for species with a highly structured social system or colonial organisms, there is generally an inverse relationship between group size and the well-being or the stress level of an individual. Hedgehogs, as solitary animals, are supposed to suffer from increasing population densities. In 2006 the mean density of hedgehogs in my population was 4.2 animals/ha, in 2007 3.3 animals/ha and in 2008 2.5 animals/ha, which is almost half of the density from 2006. The proportion of sexes (females: males) was 1:1.42 in 2006, 1:1.25 in 2007 and 1:0.92 in 2008. In the year with the highest cortisol levels, both for females and males, the population density and the proportion of males was the highest. This indicates higher intra- and intersexual interactions between the hedgehog individuals, which results in enhanced stress levels in these solitary animals.

Although both sexes showed increased hormone levels in 2006 and 2007 and the lowest levels in 2008, when the gender proportion was even and the population density was the lowest, the crowding influenced only the relation between cortisol levels and tick infestation in male hedgehogs and not in females. A study from LAVIOLA et al. (2002) showed differences in responses to crowding in female and male mice. They treated mice, which lived either under crowded or normal circumstances, with a light stressor such as the removal of sawdust from their home cages. While effects of crowding were absent in females, in males the crowding situation resulted in marked potentiating of cortisol release compared to the control group.

As mentioned previously, external stress from the disturbance caused by the rotovator increased the stress levels in both sexes, but only in females a positive correlation with tick infestation rates could be detected.

It is therefore obvious that both sexes in hedgehogs are stressed by the same factors (population density, disturbance), but for an alteration or facilitation of infection with ticks or other parasites and/or pathogens to occur, it depends on the type of stressor.
In the wild this could have major influence on population dynamics, since high stress might (i) decrease the reproductive success in females (see e.g. TILBROOK et al. 2000), and (ii) might facilitate infection with parasites and pathogens and therefore increase morbidity or even mortality. Anthropogenic influences like destruction or fragmentation of habitats might increase population densities of hedgehogs in certain areas and therefore increase stress (CHAPMAN et al. 2006) due to competition for natural resources (food, space) or sexual aggression, and the risk of being infected with ticks (male hedgehogs) and/or other parasites and pathogens (MCCALLUM and DOBSON 2002, CHAPMAN et al. 2006). Accordingly, for future hedgehog conservation efforts it is important to take environmental stressors and the resulting increase in parasites or pathogen infections into consideration.

2.4 Testosterone

2.4.1 Annual testosterone levels

The annual distribution of testosterone in hedgehogs with high levels in spring and early summer and low levels in late summer and autumn have been described in other studies (DUTOURNÉ and SABOUREAU 1983, SABOUREAU 1986, FOWLER 1988, EL OMARI et al. 1989). In hibernating animals, the duration of the breeding season is limited by the hibernation cycle. The vagina and the uterus of female hedgehogs remain small and inactive till the end of March and no recent corpora lutea (the endocrine structure involved in the production of progestogen, including progesterone) or ruptered follicles (pre-stages of corpora lutea) can be found from the start of October until the end of April (DEANESLY 1934). In males, the breeding season starts around March and ends in September/October. During this period the testis and epididymis size increase, the seminal vesicles increase in weight and full spermatogenesis is present (ALLANSON 1934). Peak plasma testosterone levels are found about one month before full spermatogenesis and return to basal values one month before the seminiferous tubules regress (SABOUREAU 1981, DUTOURNÉ and SABOUREAU 1983). Testosterone levels are closely related to melatonin concentrations, secreted from the pineal gland, with melatonin having a reversed concentration pattern to testosterone (FOWLER 1988). The pineal gland plays and important role in the responses of an organism to changes in photoperiod. Changes in photoperiod alter the secretion of melatonin and therefore have a

strong effect on the reproductive cycle, hibernation or other seasonal functions (PÉVET et al. 1989). In hedgehogs, elevated melatonin levels have no effect on testosterone levels during the breeding season, but depress testosterone secretion as early as September (FOWLER and RACEY 1990b). Testosterone itself also seems to be a controlling factor for the hibernation cycle. A study by HALL and GOLDMAN (1980) showed that testosterone had strongly inhibitory effects on hibernation in the Turkish hamster (*Mesocricetus brandti*). In addition, HALL et al. (1982) determined the role of the testis on hibernation in the same species. They found that the testicular cycle seems to influence the hibernation period by the secretion of androgens. In a study with golden-mantled ground squirrels (*Spermophilus lateralis*), males implanted with capsules filled with testosterone were prevented of entering hibernation (LEE et al. 1990). These studies indicate that elevated melatonin levels during winter are important for the regulation of endogenous endocrine cycles and that testosterone itself seems to be a regulatory factor for hibernation. This supports my results on annual testosterone levels, with testosterone being low just before hibernation starts.

2.4.2 Testosterone and tick infestation

The results from the three years reported here, showed no significant correlations between tick infestation and testosterone levels in the male hedgehogs from the experimental population, but a trend towards negative correlations. As mentioned previously (chapter III.2.2.1), testosterone is thought to have a suppressive effect on the immune system. This phenomenon was described by FOLSTAD and KARTER (1992) as the immunocompetence handicap hypothesis (ICHH), which views the cost of secondary sexual development from an endocrinological perspective. It sees testosterone as a double-edged sword which increases the sexual characteristics or behaviours of males while decreasing the immunocompetence and, therefore, increasing the risk of infection with pathogens and parasites. The hypothesis is supported by several studies on reptiles, birds and mammals (VERHULST et al. 1999, HUGHES and RANDOLPH 2001, ULLER and OLSSON 2003, MOUGEOT et al. 2004, COX and JOHN-ALDER 2007).

Immunosuppression might include the inhibition of transformation or proliferation of lymphocytes and antibody formation, or the increase of corticosteroids (WYLE and KENT 1977, DUFFY et al. 2000, EVANS et al. 2000, PETERS 2000). BELLIURE et al. (2004) manipulated the testosterone levels in two species of Mediterranean lacertid lizards (*Psammodrommus algirus* and *Acanthodactylus erythrurus*) and observed that the T cell-mediated immunity, which is important for healing wounds and resisting infections

(especially in the breeding season when male aggression is increased), was suppressed in animals with elevated testosterone levels. Additionally, they found that the individual variability in T cell-mediated responsiveness was negatively correlated with testosterone levels. HUGHES and RANDOLPH (2001) report that innate and acquired resistance to *I. ricinus* ticks were reduced in the natural rodent host *M. glareolus* when implanted with testosterone, unlike hosts which were implanted with inert oil.

Based on these studies, I also tested for correlations (Pearson correlation) between immunity related parameters (leucocyte concentration, lymphocytes, neutrophils, eosinophils, basophils, monocytes, cortisol) and testosterone levels in male hedgehogs (for results see appendix VI table XI and chapter III.1.5.3). I did not find any significant correlations during the investigation period, which indicates that testosterone has no effect on the immunity parameters of hedgehogs in my experimental population.

A variety of authors report the enhancing effect of testosterone on ectoparasite infestation in lizard species, as well as negative effects on haematological values such as haemoglobin and haematocrit and increasing mortality (SALVADOR et al. 1996, OLSSON et al. 2000, KLUKOWSKI and NELSON 2001, ULLER and OLSSON 2003, COX and JOHN-ALDER 2007). Similar observations were made for bird species such as barn swallows (*Hirundo rustica*) (SAINO et al. 1995), red-winged blackbirds (*Agelaius phoenicus*) (WEATHERHEAD et al. 1993) and house sparrows (*Passer domesticus*) (POIANI et al. 2000).

The problem with most studies dealing with immunocompetence and testosterone is that they are rather observational than experimental. ROBERTS et al. (2004) carried out a meta-analysis based on 22 studies which were done within 12 years after the ICHH was formulated. The studies used in the analysis had to be experimental because obersvational studies involving correlations are difficult to discuss in term of the ICHH, and the males in these studies had to be adults. Although the studies carried out since 1992 appeared to succeed in finding testosterone immunosuppressive when individual studies were used as a unit for the meta-analysis, when the analysis was conducted at species level the effect disappeared. The only taxonomic group showing a strong immunosuppressive effect of testosterone was the reptiles, but this was not the case for either birds or mammals, perhaps due to the smaller number of studies done compared to the other animal groups. The final results of the meta-analysis suggest a causal link between testosterone levels and immunosuppressive effects, but only in certain taxa within the Reptilia, demonstrating that the results from individual studies have to be treated carefully. Recent results from ROBERTS et al. (2007) indicate that high levels of testosterone and corticosterone in zebra finches (*Taeniopygia guttata*) lead to an enhanced

antibody response but that they have no immunosuppressive effect, and therefore disagree with the ICHH and the stress-linked ICHH (immunosuppressive effect of testosterone due to an increase of stress hormones). So it seems that the whole mechanism of androgenes influencing the immune system needs further clarification.

My analysis uses correlations which can not be used as causal evidence for the ICHH. However, from the results of the correlations it seems that the ICHH does not fit for hedgehogs, or at least not for the immunocompetence parameters that I investigated. Therefore, I conclude that increased testosterone levels in male hedgehogs: (i) do not lead to sex-biased parasitism, and (ii) do not support the ICHH, meaning that enhanced testosterone levels in male hedgehogs do not influence or facilitate infection, at least with ticks, but probably also with other parasites.

Since this is the first study done on the influence of testosterone on parasitism in the European hedgehog, and one of the few studies on mammals, it is important to support the results by experimental and field studies on wild populations in the future, in order to determine potential immunosuppressive mechanisms of testosterone and its influence on parasite infection. This would give us a better understanding of the ecology of hedgehogs and potentially improve conservation strategies for this protected animal.

2.5 Haematological values and regeneration

The results from the blood counts indicate that tick infestation can have significant, haematologically definable effects on European hedgehogs. High infestation rates force the animals to redirect energy resources from processes like reproduction and/or normal maintenance of bodily functions to regenerative processes like the production of new blood cells and immune defence. If the ticks were allowed to detach and the hedgehog had the possibility to recover without being infested again, the physiological status was normalized. The changes in the blood parameters from the differential blood count indicate that the anaemia caused by tick-induced blood loss was macrocytic, hypochromic and regenerative.

2.5.1 Blood count

Before I discuss the impact of ticks on the blood parameters it is important to define and to clarify the blood loss which a tick can induce.

A female *I. ricinus* weighs about 2-3 mg in the unengorged and 234.6-286 mg in the engorged state (LEES 1952, BOWESSIDJAOU et al. 1977, BROSSARD 1982), representing a 200 times

increase in weight during the blood meal. While engorging, the adult female imbibes about 0.45 ml of bodily fluids (blood, lymph, intra- and extracellular fluids) (HEATH 1951).

Females of *I. hexagonus* weigh between 2.3 and 3.8 mg before and about 115 mg after a blood meal (TOUTOUNGI et al. 1995). CARTER (1955) reports an amount of 1 ml of blood being spilled out at the abdomen of an engorged *I. hexagonus* female parasitizing a human. Compared to the weight of an engorged female, this amount seems to be rather unlikely and only a personal observation, considering that an average engorged *I. hexagonus* female weighs only about a tenth of the weight of 1 ml of blood (see TOUTOUNGI et al. 1995). To my knowledge there are no further reports on how much blood a female *I. hexagonus* ingests.

The weight gain of a tick does not reflect the total amount of blood it feeds on because during feeding a large part of the blood is digested, partly assimilated and excreted with the faeces (BALASHOV 1968, KOCH and SAUER 1984). Additionally excess liquid is regurgitated back into the host (SAUER et al. 1995, BOWMAN et al. 1997) leading to a concentration of the blood. KOCH et al. (1974) suggested concentration factors of 1.59 for larvae, 2.39 for nymphs and 2.78 for females based on data from four tick species (*Amblyomma americanum*, *Ixodes scapularis*, *Rhipicephalus sanguineus* and *Dermacentor variabilis*) with a blood volume imbided by *I. scapularis*, a species closely related to *I. ricinus*, being 0.51 ml (KOCH and SAUER 1984).

The blood volume of a hedgehog during its active period in the summer is about 8% of its body weight (ELIASSEN 1961); thus a hedgehog of 1 kg has about 80 ml of blood. According to the results for the mean hedgehog weight and the mean and maximum tick weight occurring on one hedgehog (see chapter III.1.3.1 and III.1.3.2), that the weight of female ticks preponderates in the weight of ticks infesting a hedgehog, and assuming that female *I. hexagonus* imbibe the same amount of blood as female *I. ricinus*, I calculate a maximum blood loss of about 23.06 ml (or 28.83% of the total hedgehog blood volume) per week.

A non-lethal haemorrhage occurs for a blood loss up to 20-25 ml/kg, a severe haemorrhage with the loss of vital signs is associated with a blood loss of about 40-50 ml/kg (STERN et al. 1993). My estimate for the maximum blood loss of a hedgehog is likely to be on the high side since the total tick load is normally lower. Potential additional blood loss caused by the feeding of hedgehog fleas is likely to be insignificant in the experimental population, as fleas were removed from a hedgehog if infestations were observed. Nevertheless, the quantity of blood removed by ticks, particularly on heavily infested animals, is likely to have major physiological effects potentially leading to mortality.

I noted a decrease of the erythrocyte values (erythrocyte concentration, haemoglobin, haematocrit) with an increase in total tick load. First, this indicates a tick-induced anaemia which has already been demonstrated in other animals infested with ticks such as rabbits (JELLISON and KOHLS 1938), cattle (RECHAV 1987) and lizards (DUNLAP and MATHIES 1993). This anaemia could be caused by the destruction (haemolysis) or loss (haemorrhage) of red blood cells by the suppression of erythropoiesis (formation of red blood cells), due to the suppression of bone marrow. To my knowledge, tick saliva does not contain any haemolytic agents which could be able to destroy the red blood cells. In contrast, the tick *Rhipicephalus* (*Boophilus*) *microplus* even excretes a protein in its saliva that prevents the lysis of erythrocytes (SAUER et al. 1995). Accordingly, it is more likely that the observed changes in the erythrocyte values are related to blood loss than to haemolysis. Additionally, haemorrhagic anaemia usually occurs during infestation with blood-feeding ectoparasites like fleas or ticks (TYLER and COWELL 1996).

Anaemia can also be described as regenerative, inadequately regenerative or non-regenerative. A regenerative anaemia is characterized by an increased erythropoietic response appropriate for the degree of anaemia, indicating that the erythropoietic tissues are healthy and the erythropoietic mechanisms are functioning (TYLER and COWELL 1996). The erythropoiesis results in a high production level of young red blood cells, the reticulocytes. This reticulocytosis is the most reliable indicator of a regenerative anaemia, because it consistently occurs during this kind of anaemia and is not caused by factors inducing a non-regenerative one (TYLER and COWELL 1996).

Due to continuous erythropoiesis, reticulocytes circulate in the peripheral blood of every healthy animal, but usually these concentrations are very low (CANFIELD 1998). I found an increase of the relative and absolute reticulocytes with increased tick weight, which indicates that the changes in the blood parameters can be associated with a regenerative anaemia.

The erythrocyte or corpuscular indices MCV, MCH and MCHC are further parameters to classify anaemia, so one can determine the cause and/or the aetiology of the anaemia.

The MCV is used to characterize the average size of the erythrocytes as normocytic (normal size), microcytic (decreased size) or macrocytic (increased size). Thus, my results show a macrocytic anaemia. This normally occurs during the regenerative response of the reticulocytosis (FERNANDEZ and GRINDEM 2000), when the concentration of reticulocytes, which are normally larger than mature red blood cells, increases since they have a higher cytoplasmic water content.

The MCHC is an estimate of the haemoglobin concentration in the circulating erythrocyte mass. The concentration can be defined as normal (normochromic), decreased (hypochromic) or increased (hyperchromic). My results show a decreased MCHC which is normally associated with regenerative anaemia. This hypochromic anaemia is caused by the high cytoplasmic water content and the lack of complete haemoglobin synthesis in the reticulocytes (TYLER and COWELL 1996).

The MCH is an estimate of the average haemoglobin mass in an erythrocyte. It is not routinely used for the classification of anaemia (TYLER and COWELL 1996). Parameters or states which increase the MCH normally also increase the MCV, e.g. regenerative anaemia.

The thrombocyte concentration of the experimental population correlates significantly positively with the tick infestation in 2007 as well as in the pooled years, but not in 2008. The outcomes in 2007 are in agreement with the anaemic state the animals are in, since inflammatory and anaemic stimuli support the release of thrombocytes from the bone marrow and spleen, which is defined as a secondary thrombocytosis (SANTHOSH-KUMAR et al. 1991, RIZZO et al. 2007). However, thrombocytes, like other haematological values, are not only influenced directly by blood loss or inflammation, but also by other factors including abiotic parameters (see chapter III.2.1) and also pathogens. Infections with *Anaplasma phagocytophilum*, the agent of anaplasmosis in animals and humans, can lead to haemolytic anaemia and also thrombocytopenia, caused by a severe reduction in thrombocyte concentration (BEXFIELD et al. 2005). Some 39.5% of examined ticks from the experimental hedgehog population were infected with *A. phagocytophilum* in 2007 (see SKUBALLA et al. in press), and therefore it is likely that, to a certain degree, the hedgehogs from the population were also infected. I have no data on the hedgehog infection rates with *A. phagocytophilum* from 2008, but it is likely that they were higher than in 2007, since the tick infestation rate in 2008 was also higher as well as the potential risk to become infected with the pathogen. Considering the antagonistic effects of the tick-induced anaemia and a potential *Anaplasma*-induced thrombocytopenia, this is a possible reason why I could not detect a positive correlation between the thrombocyte concentration and the tick infestation rate in 2008.

A decrease in lymphocytes with an increase in neutrophils at the same time can be an indicator of stress like inflammation or immune response to pathogen infections (PETERS and SCHWARZER 1985, THOMAS 2007). As already described in the introduction hedgehogs can harbour a variety of different pathogens, so the transmission of any one could lead to such an immunological response.

Several studies discuss the stress of handling as a cause of lymphocyte decrease. Thus several fish species (PICKERING et al. 1982, BARTON et al. 1987,), birds (GROSS and SIEGEL 1983, SCOPE et al. 2002) and mammals (SCHAEFER et al. 1997, CATTET et al. 2003, MONTANÉ et al. 2003), react with a lowered concentration of circulating lymphocytes to handling. Handling is an acute stress (rather than chronic, like in tick infestation) because the stimulus is removed before the response of the animal is complete (PICKERING et al. 1982). Therefore it is unlikely that the decrease in lymphocytes is a response to handling, since the hedgehogs were handled every day.

2.5.2 Regeneration

The regeneration experiment was conducted to support the results from the experimental population that tick-induced blood loss leads to a regenerative anaemia in hedgehogs. While the erythrocyte values, the corpuscular indices and the relative reticulocytes differed significantly between the R- and C-group on the first sampling date, when the R-group animals were infested with ticks, these values did not differ on the second or third sampling dates (without tick infestation). This adjustment to normalized blood values provides evidence for recovery from the tick-induced blood loss and for the hypothesis that the changes in blood parameters in the experimental population are really associated with the tick infestation and are not confounding effects due to other variables. It also seems that four to six weeks are enough time for the hedgehogs to recover from tick-induced blood loss (when all ticks are removed, and no new infestation occurs).

The results from the repeated measures ANOVA support the assumption that the hedgehogs recovered from blood loss. The erythrocytic values, as well as the corpuscular indices for the R-group, differed significantly between the first sampling date and the second and third sampling dates, indicating a regeneration process. Both relative and absolute reticulocytes did not differ between these three sampling dates, which indicates that the erythropoietic response is increased, even four to six weeks after the blood loss, so the regenerative process was not yet completed. In the C-group, the erythrocyte values were also lower on the first sampling date compared to the second and third sampling dates, and the relative and absolute reticulocytes decreased after four and six weeks, respectively, which also indicates regeneration. This can be explained by hedgehogs being natural hibernators, decreasing their metabolism, heart rate and breathing to a minimum during winter. In contrast to a hedgehog in the active season, which has a blood volume of 8% of its body weight, in the hibernating animal the blood volume decreases to 3% and increases again to 5.5% during arousal

(ELIASSEN 1961). Therefore, after arousal erythropoiesis is increased to normalize the blood volume and the blood cell values.

To the best of my knowledge there is no literature or data on the lifespan of a mature erythrocyte for hedgehogs. In humans the lifespan of a single mature erythrocyte is about 120 days. Approximately 0.8% of the red blood cells are thus replaced daily under normal conditions. Assuming an unimpaired regeneration rate, only about 24% of the erythrocytes in humans are replaced within 1 month. In 2009, due to the cold winter, the hedgehogs from both groups did not awake from hibernation until the beginning of April. The first blood samples were taken in the second week of April. Thus it is likely that the blood parameters of the C-group were different compared to the blood parameters from the active season, explaining the low erythrocyte values and the increased reticulocyte levels. The R-group had to deal: (i) with reduced blood volume after hibernation, and (ii) with blood loss due to tick infestation. This provides an explanation for the ongoing reticulocytosis even six weeks after the removal of the ticks. So it appears that in my experimental setup six weeks was too short a time for complete compensation of the lost blood to occur and also indicates that high tick infestation rates right after hibernation could increase morbidity in hedgehogs significantly.

2.5.3 Consequences of tick-induced blood loss

The tick-induced blood loss can be put on a level with energy loss. Due to this energy loss the hedgehog is forced to reallocate available energy from processes like growth or reproduction to the maintenance of bodily functions, in this case regeneration and immune responses. There is no data which describes mortality in hedgehogs caused by tick infestation but various sources have reported tick-associated mortality in other animal species. BOLTE et al. (1970) associated white-tailed deer (*Odocoileus virginianus*) fawn mortality with tissue destruction and secondary infections induced by the lone star tick *Amblyomma americanum*. A total of 34% of captured fawns were lost because of high tick infestation rates. In a desert chacma baboon (*Papio ursinus*) troop observed by BRAIN (1992), one of the major causes of infant mortality was tick infestation. SMITH and CHEATUM (1944) discussed the decline of a cottontail population on Fishers Island, New York due to heavy infestations with the tick species *Ixodes dentatus* and *Haemaphysalis leporispalustris*. The authors suggested tick-induced anaemia and/or bacterial infections caused the increased mortality rate. However, the reasons for the heavy tick infestations, such as habitat and extreme climatic changes or mast years, remained unclear.

According to these investigations it is possible that tick-induced blood loss can lead to increased mortality rates in hedgehogs. Certainly the studies mentioned all discuss increased mortality in relation to heavy tick infestation or to infestation of immature hosts, but not to moderate tick infestation rates in adult animals. I therefore suggest that normal tick infestation rates in the wild are not life-threatening to a healthy, adult hedgehog, but can have major negative effects on fitness and even survival ability of animals with already lowered or not yet fully developed immunity like young, old or sick hedgehogs.

Unlike other haemophagous arthropods, ixodid adults feed on their host for extended periods of up to two weeks. During this time the host responds to the infestation in different ways, including haemostatic responses and the activation of the innate and adaptive immune system. In order to attain a full blood meal, ticks counter these responses with bioactive compounds produced in their salivary glands (SGE = salivary gland extract) and secret them into their hosts (LAWRIE et al. 1999).

In chapter III.2.2.2 I mentioned acquired resistance as a response of the host to tick infestation. Acquired resistance to ticks is characterized by reduced, engorgement weight, longer feeding periods, decreased egg production, inhibited moulting and tick and egg mortality (see chapter III.2.2.2). Hosts showing acquired resistance often develop an influx of cells into the dermis and the epidermis surrounding the tick's mouthparts (WIKEL and BERGMAN 1997). As a cutaneous inflammatory response, infiltrates of basophils and eosinophils occur at the tick attachment site, called basophil hypersensitivity, leading to tick rejection by local basophil degranulation (BROWN et al. 1982). Basophil infiltrates also increase the vascular permeability at tick feeding sites, causing enhanced oedema formation (RIBEIRO 1989). The nutrients in the blood meal are then reduced, because only a protein-low serum is available at the oedema sites, leading to mortality or reduced moulting success in ticks. Additionally histamine inhibits tick salivation and engorgement (WIKEL 1996). Langerhans cells trap salivary antigens and migrate to the lymph nodes, where they act as antigen-presenting cells for specialized lymphocytes. Antibodies against tick-specific antigens are produced and contribute with the complement to acquired resistance (ALLEN et al. 1979, NITHIUTHAI and ALLEN 1985). T cells are also important for the resistance to ticks. T helper 1 (Th1) cells mediate hypersensitivity reactions, which are effectors of the basophil hypersensitivity reaction in the dermis and epidermis. Additionally cytokines like interferon γ (INF-γ) or interleukin 2 and 4 (IL-2, IL-4), produced by Th1 cells, can be determined at tick feeding sites (GANAPAMO et al. 1995). IL-2 is an autocrine growth factor, important for T cell activation, but also acts as a paracrine growth factor and signalling molecule, important for

the activation of T cells, B cells, natural killer cells (NK cells), monocytes, macrophages and more (GILLESPIE et al. 2001). IL-4 is an important factor for B cell activation, T cell proliferation and differentiation of CD4 and naive Th cells into Th2 cells.

A healthy immune system is therefore highly important for enabling the host to reject ticks. Thus, immunocompromised animals are not capable of responding properly to tick infestation. For hedgehogs this is important for juveniles which still need to establish a fully functioning immune system. High tick infestation rates might lower their chance to survive hibernation, since the ability to build up adequate fat reserves is reduced and available energy must be directed into maintenance of the immune system and physiological responses to tick infestation. This also holds for older animals.

Sick animals, in addition to lowered immunity, normally also show behavioural changes, like lethargy, anorexia and reduced grooming activity (HART 1988). Grooming is one of various parasite avoidance behaviours (HART 1992) and an experimental prevention of grooming can lead to an increased ectoparasite burden. For example, mice with limb disabilities have higher lice infestation rates than healthy mice (BELL et al. 1962), and cattle which were prevented from grooming by harnesses had a four time higher tick load with *R. (B.) microplus* than control animals (BENNETT 1969).

The tick densities in my population were experimentally elevated, and therefore the hedgehogs might have suffered from comparatively high blood loss. However, in my study other parasites occurring in wild populations were not taken into account. So while the tick-induced blood loss in wild hedgehog populations might be smaller than in my experimental population, the parasite species richness is higher, and, accordingly, the possible blood loss due to other parasites like the hedgehog flea *A. erinacei* or the trematode *B. erinacei* is increased. Additionally, the energy loss caused by other parasites – mite infestations can lead to hair loss or fungal infections, *Capillaria* spp. retrieve nutrients from the intestine – occur in wild populations, but were prevented in my experimental hedgehog population. So I suggest that tick infestations in combination with other co-stressors can have much more severe effects on hedgehogs in the wild, especially in immunocompromised ones, leading to increased morbidity and in stressful situations even to death.

Ticks need to overcome the host immune system. The SGE of ticks contains several immunosuppressive and immunomodulatory components, and the suppressive effect of tick saliva can be on the innate but also on the acquired immunity, as well as on various cell types (HANNIER et al. 2003). LEBOULLE et al. (2002) discovered a protein, expressed during feeding,

which they called Iris (*I. ricinus* immunosuppressor). Iris is capable of modulating T-lymphocyte and macrophage responsiveness by inducing a Th2-type response and inhibiting pro-inflammatory cytokines. Acquired resistance mediated by Th1-type immune response, involving IFN-γ production is suppressed.

During blood feeding, *I. ricinus* upregulates several proteins secreted in the saliva, amongst others IRAC I and II (*I. ricinus* anticomplement), which block the alternative complement pathway (DAIX et al. 2007, SCHROEDER et al. 2007). Further effects of SGE are suppression of the proliferation of NK cells, T cells, B cells, macrophages and neutrophils, a reduced production of cytokines like IL-10, IL-2, tumor-necrosis factor α (TNF-α), IFN-γ and modulation of the host immune response from Th1 to a Th2 cytokine profile (FERREIRA and SILVER 1999, KOPECKÝ et al. 1999, GILLESPIE et al. 2000, KOVÁŘ et al. 2002, MEJRI et al. 2002, BOPPANA et al. 2004, HANNIER et al. 2003, 2004).

The effect of SGE varies with the host and the ticks. LAWRIE et al. 1999 report that SGE of *I. hexagonus* inhibits the activity of the alternative complement pathway twice as strongly as SGE of *I. ricinus*. In my study the majority of ticks found on the hedgehogs were *I. ricinus,* but in the wild most of the ticks found on hedgehogs are *I. hexagonus* (see chapter IV.1.1.1). Accordingly, the immunosuppressive effect of SGE should be higher in wild populations, and therefore the risk of infection with other parasites/pathogens is increased, although WIKEL and BERGMAN (1997) suggest that tick-induced immunosuppression is not likely to influence the entire immune system of the host, since this would increase the likelihood of opportunistic infections, like endoparasites, and might deprive the tick from a potential food resource.

However, there are also several studies indicating the facilitation of pathogen transmission by tick saliva. KOPECKÝ et al. (1997) thought that the inhibitory effect of the elaboration of anti-inflammatory cytokines like IFN-γ increases the possibility of tick-transmitted pathogens. MEJRI et al. (2002) indicate that the impairment of the innate and acquired immune system of BALB/c mice by the SGE of *I. ricinus* leads to a facilitated transmission of tick-borne pathogens. HANNIER et al. (2004) suggest that a certain protein in the SGE of *I. ricinus* ticks facilitates the transmission of *B. burgdorferi* by preventing B cell activation.

As mentioned previously (see chapter I.2.4.2), hedgehogs can harbour a variety of pathogens, although it is not known how they react to infections with e.g. *Borrelia* spp.. The suppression of the immune system by ticks could also increases the risk of becoming infected with other parasites in hedgehogs. This increases potential fitness losses and leads to a redirection of energy away from reproduction, growth and preparation for hibernation to the maintenance of

bodily functions and the immune system. Especially in hedgehogs with lowered immunity this would decrease the chance of survival severely.

3. Summary

With this part of my project I wanted to investigate the negative influence of parasites on fitness-related parameters of the hedgehog for a specific parasite group by measuring the influence of ticks on the blood physiology of hedgehogs. Ticks were used, because, in comparison to endoparasites, their infestation rates are relatively easy to quantify and manipulate, and their direct impact on the physiology of their hosts is relatively easy to determine. In order to exclude confounding effects due to abiotic weather parameters I also tested for correlations between haematological values and tick density with temperature, relative humidity and rainfall.

I could not find consistent significant correlations between the haematological values or the stress or sexual hormones of hedgehogs with climate parameters. It is difficult to test for the influence of weather conditions on the physiological parameters of animals, because changing climate parameters can have short-term effects, for example on stress hormones or other blood parameters, which can be compensated rapidly by other factors. Additionally, weather often only acts as a co-stressor and does not have an influence when considered alone.

In order to determine whether climate parameters really have an impact on fitness-related parameters of hedgehogs, it will be necessary to conduct laboratory experiments in which the important parameters can be controlled appropriately, although this will not reflect natural conditions experienced by the wild populations.

I found significant correlations between *I. ricinus* density and temperature. These results suggest an autocorrelation with the natural developmental cycle of *I. ricinus*, with summer peaks for larvae and spring and autumn peaks for nymphs and females. The ambient climate does not play as important a role in the development of ticks as the microclimate. This applies to both investigated tick species. As long as the microclimate does not change over a longer period of time, ambient climatic changes will not have severe effects on tick populations.

In my experimental population I was not able to find evidence for sex-biased parasitism, such as that observed in other host-parasite systems. This might be due to the experimental setup in which possible sex-biased differences were compensated by the limited home range of the male host individuals and/or the high population density compared to wild hedgehog populations.

Increased cortisol levels are a non-specific way to cope with environmental and social stress and stress caused by parasite and pathogen infection. How strong an animal reacts to a stressor differs individually and also between the sexes. In my study some stressors seem to modulate the relationship between the hosts and the ticks differently between the sexes. Thus, while high population densities led to a positive correlation between cortisol and tick infestation rates in male hedgehogs, in females, although they also showed increased cortisol levels in years with high population densities compared to years with lower densities, no significant correlation between cortisol levels and tick infestation occurred. Compared to this, the disturbance by the rotovator in spring 2007 led to a positive correlation between the stress hormone and tick infestation rates in female hedgehogs, but not in males. Environmental stressors might therefore result in increased stress levels, leading, for example, to lower reproductive success, or because of the suppressed immune system, to increased parasite infections. In addition, anthropogenic influences like habitat fragmentation may also lead to increased hedgehog population densities and intraspecific aggression, which can also induce increased stress and increased parasite infections.

Testosterone concentrations of male hedgehogs showed seasonal fluctuations, with high values in spring and summer and a rapid decrease in autumn. These results support the suggestion that testosterone, along with other factors, plays an important, regulative role for the hibernation period of male hedgehogs.

I could not find significant correlations between testosterone levels and tick infestation or immunological parameters. This disagrees with the ICHH, in which the inhibiting effects of androgens on the immune system, and the resulting increased risk of parasite and pathogen infections, are hypothesized. However, it is important to recognize that my investigations were observational rather than experimental, and it is therefore important to support my work with studies from laboratory experiments, as well as from natural wild hedgehog populations.

My results from the correlations between the haematological parameters and the tick infestations of hedgehogs indicate that tick-induced blood loss causes a regenerative, haemorrhagic anaemia. This is characterized by a decrease in the erythrocyte values (erythrocyte and haemoglobin concentration, haematocrit) and an increased reticulocytosis with corresponding changes in the erythrocyte indices (MCV, MCH and MCHC). Additionally, signs of an immune reaction could be observed, characterized by an increased release of thrombocytes from the bone marrow and the spleen, lowered lymphocyte and higher neutrophil concentrations. Blood loss therefore leads to a reallocation of energy into processes like immune defence and regeneration and cannot be used for growth, reproduction

and other processes. This is a major threat for juvenile, old and sick hedgehogs, which are already weakened or which have immune systems that are not fully developed or recovered. However, tick-induced blood loss can also be of a major threat for healthy adult hedgehogs, especially in periods of high stress, like the rut and hibernation, during which the hedgehogs depend on their fat stores to survive.

If environmental conditions change in a way that favours the development of ticks and/or their transmission, e.g. habitat fragmentation leads to higher hedgehog population densities and as a result the risk of infection is increased, ticks could become a serious threat in particular because not only ticks, but also fleas and trematodes can cause anaemia in hedgehogs and therefore might intensify the energy loss. From the point of view of conservation, ticks and other haematophagous parasites are important factors affecting the health of individuals as well as populations of hedgehogs by influencing morbidity and indirectly mortality and reproduction.

To demonstrate that the results from the experimental population are based on the blood loss induced by ticks and not confounding effects I conducted a regeneration experiment. I was able to show that hedgehogs infected with ticks, need four to six weeks, without any further infestations, to recover from the blood loss and to establish normalized blood values again. A heavy tick infestation directly after arousal from hibernation challenges the hedgehog by: (i) the already reduced blood volume occurring during hibernation, and (ii) the tick-induced blood loss. As a consequence, a hedgehog that is freshly aroused from hibernation has to invest more energy in regeneration, which can also lead to an increased mortality risk.

The results from the experiment revealed a strong negative effect of ticks on the fitness of European hedgehogs, but also stress the complexity of host-parasite relationships by showing the importance of other abiotic and biotic factors.

IV. Hedgehog dissections

1. Results

1.1 Parasite distribution

1.1.1 Germany

The dissected hedgehogs originated from five regions in Germany including the catchment areas of several cities. Collections were made from 2005-2008: Berlin (N = 18, Berlin), Frankfurt on the Main (N = 50, Frankfurt, Wuppertal), Karlsruhe (N = 17, Karlsruhe, Forchheim, Ortenau, Steinfeld), Hamburg (N = 22, Hamburg, Nordtsrand, Hooksiel) and Munich (N = 30, Munich, Lottstetten). Numbers of hedgehogs, sexes, ages, locations and collection seasons (season 1 = December-April, season 2 = May-July, season 3 = August-November) are shown in table 39. Season 1 represents the hibernation period, season 2 the period after hibernation and the mating season, season 3 the period after the major breeding time and the time of preparation for hibernation.

Table 39: Number of German hedgehogs used for dissections (juveniles = 38, adults = 95). Animals are separated in age, sex, catchment area and collection date (S1 = December-April, S2 = May-July, S3 = August-November). F = females, M = males, B = both sexes, T = total number. Data for hoglets (N = 4) are not shown in the table.

	Berlin				Frankfurt				Karlsruhe				Hamburg				Munich			
	S1	S2	S3	T	S1	S2	S3	T	S1	S2	S3	T	S1	S2	S3	T	S1	S2	S3	T
adults																				
F	1	4	2	7	0	0	18	18	0	3	4	7	2	2	5	9	0	3	9	12
M	0	5	2	7	1	0	8	9	1	4	2	7	2	3	3	8	1	1	9	11
B	1	9	4	14	1	0	26	27	1	7	6	14	4	5	8	17	1	4	18	23
juveniles																				
F	0	1	0	1	2	0	7	9	0	1	1	2	1	0	2	3	0	1	1	2
M	1	2	0	3	3	1	8	12	0	0	0	0	0	0	1	1	1	0	4	5
B	1	3	0	4	5	1	15	21	0	1	1	2	1	0	3	4	1	1	5	7

I tested for differences in prevalence of the different parasite species between hedgehogs of different sex, age, collection date and location with a Fisher's exact test or a Chi-square test.
I found no significant differences except for fleas, with adults in Frankfurt having higher prevalences in season 1 than in season 2 ($p = 0.027$), *Capillaria aerophila* with adults in Munich having higher prevalences in season 1 than in season 2 ($p = 0.04$), *Capillaria* spp. with adults and juveniles in Frankfurt ($p = 0.025$) and Karlsruhe ($p = 0.028$) having higher

prevalences than hoglets. This is negligible since I dissected only two hoglets from Frankfurt and one from Karlsruhe. Therefore, real prevalences cannot be shown for hoglets.

For *Brachylaemus erinacei* I found differences between Frankfurt (prevalence 20%) and Munich (prevalence 53.3%) ($p = 0.022$).

The sum of *Plagiorhynchus cylindraceus* (peritoneal and intestinal *P. cylindraceus)* differed in Berlin between juveniles and adults ($p = 0.011$), with juveniles showing prevalences of 100% and adults of 21.4%. This was the same for *P. cylindraceus* from the body cavity ($p = 0.005$), with juveniles having prevalences of 100% and adults of 14.3%.

Since there are no obvious trends in differences in prevalences for the single parasite species I pooled sexes, seasons, ages and regions.

Differences in abundances were tested either with a Mann-Whitney U-test or a Kruskal-Wallis-test. The measured differences matched the differences found for prevalences.

For fleas I found higher abundances for adults in Frankfurt ($p = 0.025$) and in Karlsruhe ($p = 0.014$). In both cases the abundances were higher in season 1 than in season 2, although for Karlsruhe I dissected only two hedgehogs in season 1. For *C. striatum* abundances differed for Berlin ($p = 0.011$) with juveniles being more highly infected than adults and Frankfurt ($p = 0.09$) with adults being more highly infected than juveniles. For *C. aerophila* I found differences in Munich, with adults having higher nematode numbers in season 1 than in season 2 ($p = 0.007$). *Capillaria* spp. differed in Berlin with juvenile hedgehogs having more nematodes than adults ($p = 0.008$).

B. erinacei showed differences between Frankfurt and Munich ($p = 0.002$), and Karlsruhe and Munich ($p = 0.023$). In both cases hedgehogs from Munich had higher trematode numbers.

The sum of *P. cylindraceus* differed in Berlin with juveniles having higher abundances than adults ($p = 0.002$). The same was found for peritoneal *P. cylindraceus* ($p = 0.001$). Additionally, in Munich adults had higher abundances in season 1 than in season 2 ($p = 0.029$).

No obvious trends were detected and regarding the number of tests made and given an α-level of 0.05 these results can be handled as a type 1 error. Therefore, I pooled sexes, seasons, ages and regions. Table 40 shows the parasite distribution of all dissected hedgehogs from Germany, table 41 shows the same for the tick distribution.

Table 40: Macroparasite prevalences, abundances, intensities and ranges of dissected hedgehogs from Germany. Hedgehog sexes, seasons (month of collection) and regions are pooled. J = juveniles, A = adults, All = all ages, N = number of samples, SD = standard deviation, prevalence range indicates range from the different regions. Hoglets (N = 4) are not represented in the table.

Parasites	Age	N	Prevalence % (range)	Abundance (SD)	Intensity (SD)	Range
Fleas	J	38	31.6 (25-50)	1.95 (7.49)	6.17 (12.67)	0-46
	A	95	26.3 (7.1-34.8)	2.89 (10.29)	11 (17.95)	0-91
	All	133	27 (11.8-50)	2.62 (9.56)	9.43 (16.4)	0-91
Crenosoma striatum	J	38	71.1 (14.3-100)	15.5 (32.54)	21.81 (36.93)	0-149
	A	95	67.4 (50-85.7)	23.03 (61.95)	34.19 (73.07)	0-415
	All	133	66.4 (47.1-88.9)	20.88 (55.15)	30.52 (64.52)	0-415
Capillaria aerophila	J	38	44.7 (33.3-75)	7.68 (13.63)	17.18 (16.01)	0-48
	A	95	41.1 (23.5-50)	3.92 (7.33)	9.54 (8.83)	0-31
	All	133	40.9 (31.8-50)	4.99 (9.66)	11.86 (11.88)	0-48
Capillaria spp. intestine	J	38	86.8 (50-100)	375.53 (462.6)	432.42 (471.23)	0-1245
	A	95	83.2 (70.6-92.9)	95.8 (144.86)	115.2 (151.74)	0-755
	All	133	81.8 (72.7-90)	175.72 (301.69)	208.67 (318.27)	0-1245
Brachylaemus erinaceus	J	38	34.2 (19-75)	9.21 (20.05)	26.92 (26.88)	0-73
	A	95	35.8 (21.4-52.2)	25.23 (95.96)	70.5 (151.47)	0-735
	All	133	34.4 (20-53.3)	20.65 (81.99)	58.45 (130.52)	0-735
Plagiorhynchus cylindraceus body cavity	J	38	21.1 (9.5-100)	1.34 (3.43)	6.38 (5.04)	0-14
	A	95	8.4 (4.3-14.3)	0.15 (0.58)	1.75 (1.16)	0-4
	All	133	11.7 (3.3-33.3)	0.49 (1.96)	4.06 (4.27)	0-14
P. cylindraceus intestine	J	38	5.3 (0-25)	0.34 (1.95)	6.5 (7.78)	0-12
	A	95	8.4 (0-14.3)	0.15 (0.58)	1.75 (1.16)	0-4
	All	133	7.3 (3.3-16.7)	0.2 (1.15)	2.7 (3.43)	0-12
P. cylindraceus sum	J	38	21.1 (0-100)	1.68 (4.94)	8 (8.43)	0-26
	A	95	14.7 (5.9-28.6)	0.29 (0.99)	2 (1.84)	0-7
	All	133	16.1 (6.7-38.9)	0.69 (2.82)	4.18 (5.88)	0-26

Table 41: Tick prevalences, abundances, intensities and ranges of dissected hedgehogs from Germany. Hedgehog sexes, seasons (month of collection) and regions are pooled. J = juveniles, A = adults, All = all ages, N = number of samples, SD = standard deviation, prevalence range indicates range from the different regions. Hoglets (N = 4) are not represented in the table.

	Age	N	Prevalence % (range)	Abundance (SD)	Intensity (SD)	Range
Total tick numbers	J	38	52.6 (42.9-100)	20.12 (66.79)	38.3 (89.2)	0-46
	A	95	63.2 (23.5-85.7)	62.46 (216.82)	98.9 (266.9)	0-1922
	All	133	58.4 (27.3-88.9)	50.37 (187.34)	83.75 (236.25)	0-1922
Total *Ixodes ricinus* numbers	J	38	15.8 (0-100)	2.87 (10.91)	18.17 (23.38)	0-51
	A	95	27.4 (11.8-57.1)	2.81 (16.08)	10.27 (29.87)	0-155
	All	133	23.4 (10-66.7)	2.83 (14.75)	11.75 (28.59)	0-155
Total *Ixodes hexagonus* numbers	J	38	47.4 (25-75)	17.29 (64.99)	36.5 (91.93)	0-398
	A	95	57.9 (23.5-85.7)	59.66 (215.07)	103.05 (275.61)	0-1903
	All	133	53.3 (22.7-83.3)	47.56 (185.72)	86.64 (244.54)	0-1903
Larvae *I. ricinus*	J	38		1.5 (6.54)	19 (17.09)	0-35
	A	95		0.33 (1.48)	4.43 (3.64)	0-11
	All	133		0.66 (3.72)	8.8 (11.1)	0-35
Nymphs *I. ricinus*	J	38		1 (3.83)	9.5 (8.58)	0-21
	A	95		1.77 (10.44)	9.88 (23.57)	0-100
	All	133		1.55 (9.05)	9.81 (21.34)	0-100
Females *I. ricinus*	J	38		0.34 (1.07)	2.6 (1.82)	0-5
	A	95		0.6 (4.03)	4.38 (10.46)	0-39
	All	133		0.53 (3.45)	3.89 (8.87)	0-39
Larvae *I. hexagonus*	J	38		13.39 (62.28)	56.56 (123.25)	0-380
	A	95		36.28 (167.69)	104.45 (274.33)	0-1532
	All	133		29.74 (145.67)	94.19 (249.19)	0-1532
Nymphs *I. hexagonus*	J	38		3.18 (6.38)	7.56 (8.06)	0-29
	A	95		19.2 (65.35)	35.76 (86.16)	0-442
	All	133		14.62 (55.72)	29.03 (76.06)	0-442
Females *I. hexagonus*	J	38		0.68 (2.64)	3.71 (5.47)	0-16
	A	95		3.54 (16.24)	10.18 (26.55)	0-151
	All	133		2.72 (13.84)	9.05 (24.28)	0-151
Total tick weight	J	38		0.12 (0.26)	0.23 (0.32)	0-1.3
	A	95		0.48 (1.5)	0.76 (1.83)	0-11.98
	All	133		0.38 (1.28)	0.62 (1.61)	0-11.98

	Age	N	Prevalence % (range)	Abundance (SD)	Intensity (SD)	Range
Total	J	38		0.04 (0.12)	0.25 (0.22)	0-0.56
I. ricinus	A	95		0.07 (0.45)	0.27 (0.87)	0-4.32
weight (g)	All	133		0.06 (0.38)	0.26 (0.78)	0-4.32
Total	J	38		0.08 (0.23)	0.17 (0.31)	0-1.3
I. hexagonus	A	95		0.41 (1.44)	0.71 (1.85)	0-11.98
weight (g)	All	133		0.32 (1.23)	0.58 (1.62)	0-11.98

In table 42, the species richness for dissected hedgehogs from Germany is listed. Sexes, seasons and regions were pooled. I could not find any significant differences between juvenile and adult hedgehogs using a Mann-Whitney U-test. Species richness only includes the macroparasites found in and on the hedgehogs. Due the problems involved with quantifying infestation rates, mites were not included in the species richness. Only a few percent of hedgehogs were parasite free or harboured only a single parasite species. Hedgehogs with three parasite species were the most common, followed by four, two and five species. No hedgehog harboured all detected parasite species. The mean species richness for juveniles is 3.53 (SD = 1.66), for adults 3.52 (SD = 1.55) and for all animals 3.52 (SD = 1.57).

Table 42: Species richness of dissected hedgehogs from Germany (N = 133, juveniles N = 38, adults = 95). Different tick species and life stages are accounted for one species. No differentiation is made between peritoneal and intestinal *Plagiorhynchus cylindraceus*. Hedgehog sexes, seasons (month of collection) and regions are pooled.

Species number	0	1	2	3	4	5	6	7
Frequency % (juveniles)	5.3	2.6	18.4	26.3	21.1	18.4	7.9	0
Frequency % (adults)	3.2	5.3	17.9	31.6	20	16.8	5.3	0
Frequency % (all ages)	6.6	4.4	17.5	29.2	19.7	16.8	5.8	0

1.1.2 UK

Hedgehogs from the UK were collected in 2006 and 2009 and came from the catchment areas of Ayrshire (N = 5), Wales (N = 4), Hull (N = 14), Durham (N = 4) and Uist (N = 2). The origin of one hedgehog remained unclear. Due to the low sample size I pooled hedgehogs from different regions and collection dates. Only differences between the sexes and ages of the animals were compared (Fisher's exact test for prevalences and Mann-Whitney U-test for abundances). Numbers of hedgehogs, sexes and ages are shown in table 43.

Table 43: Number of British hedgehogs used for dissections (juveniles = 14, adults = 16). Animals are separated in age, sex and catchment area. F = females, M = males, B = both sexes, nk = not known.

	Ayrshire	Wales	Hull	Durham	Uist	nk
adults						
F	1	2	2	0	0	0
M	2	1	6	0	1	1
B	3	3	8	0	1	1
juveniles						
F	1	1	0	2	1	0
M	1	0	4	2	0	0
nk	0	0	2	0	0	0
B	2	1	6	4	1	0

I found no differences for sex or age in the prevalences of the different parasites. Therefore, these data were pooled. Abundances did not differ for sexes and ages except for intestinal *Capillaria* spp. which were higher in juveniles than in adults ($p = 0.031$, abundance juveniles = 373.64, abundance adults = 79.56) based on three juveniles with very high *Capillaria* spp. numbers (717, 772, 1855). Table 44 shows the parasite distribution for all dissected hedgehogs from the UK, table 45 shows the tick distribution.

Table 44: Macroparasite prevalences, abundances, intensities and ranges of dissected hedgehogs from the UK. Hedgehog sexes, seasons (month of collection) and regions are pooled. J = juveniles, A = adults, All = all ages, N = number of samples, SD = standard deviation.

Parasites	Age	N	Prevalence %	Abundance (SD)	Intensity (SD)	Range
Fleas	J	14	0	0	0	
	A	16	0	0	0	
	All	30	0	0	0	
C. striatum	J	14	78.6	21.93 (30.55)	27.91 (32.09)	0-91
	A	16	62.5	8.63 (10.95)	13.8 (10.97)	0-33
	All	30	70	14.83 (22.93)	21.19 (24.92)	0-91
C. aerophila	J	14	35.7	1.86 (2.91)	5.2 (2.39)	0-8
	A	16	18.8	0.56 (1.26)	3 (1)	0-4
	All	30	26.7	1.17 (2.25)	4.38 (2.2)	0-8
Capillaria spp. intestine	J	14	92.9	373.64 (500.5)	402.38 (508.77)	0-1855
	A	16	87.5	79.56 (130.69)	90.93 (136.36)	0-432
	All	30	90	216.8 (378.67)	240.89 (392.32)	0-1855
B. erinaceus	J	14	57.1	13.43 (26.17)	23.5 (31.65)	0-92
	A	16	50	18.13 (44.39)	36.25 (58.92)	0-156
	All	30	53.3	15.93 (36.49)	29.88 (46.16)	0-156
P. cylindraceus body cavity	J	14	14.3	2.29 (6.6)	16.0 (11.31)	0-24
	A	16	0	0	0	
	All	30	6.7	1.07 (4.57)	16.0 (11.31)	0-24
P. cylindraceus intestine	J	14	14.3	0.29 (0.73)	2 (0)	0-2
	A	16	25	0.25 (0.45)	1 (0)	0-1
	All	30	20	0.27 (0.58)	1.33 (0.52)	0-2
P. cylindraceus sum	J	14	28.6	2.57 (6.54)	9 (10.39)	0-24
	A	16	25	0.25 (0.45)	1 (0)	0-1
	All	30	26.7	1.33 (4.54)	5.0 (8.04)	0-24

Table 45: Tick prevalences, abundances, intensities and ranges of dissected hedgehogs from the UK. Hedgehog sexes, seasons (month of collection) and regions are pooled. J = juveniles, A = adults, All = all ages, N = number of samples, SD = standard deviation.

	Age	N	Prevalence %	Abundance (SD)	Intensity (SD)	Range
Total tick numbers	J	14	42.9	11.21 (34.71)	26.17 (51.61)	0-131
	A	16	50	35.44 (94.18)	70.88 (127.04)	0-369
	All	30	46.7	24.13 (72.66)	51.71 (101.2)	0-369
Total *I. ricinus* numbers	J	14	0	0	0	
	A	16	12.5	0.56 (1.55)	4.5 (0.71)	0-5
	All	30	6.7	0.4 (1.15)	4.5 (0.71)	0-5
Total *I. hexagonus* numbers	J	14	35.7	11.07 (34.76)	31 (56.16)	0-131
	A	16	43.8	34.88 (94.39)	79.71 (134.55)	0-369
	All	30	40	23.77 (72.77)	59.42 (107.94)	0-369
Larvae *I. ricinus*	J	14		0	0	
	A	16		0	0	
	All	30		0	0	
Nymphs *I. ricinus*	J	14		0	0	
	A	16		0.19 (0.75)	3 (0)	0-3
	All	30		0.1 (0.55)	3 (0)	0-3
Females *I. ricinus*	J	14		0	0	
	A	16		0.19 (0.54)	1.5 (0.71)	0-2
	All	30		0.1 (0.4)	1.5 (0.71)	0-2
Larvae *I. hexagonus*	J	14		10 (34.38)	70 (83.44)	0-129
	A	16		10.69 (29.5)	85.5 (16.26)	0-97
	All	30		10.37 (3.31)	77.75 (49.89)	0-129
Nymphs *I. hexagonus*	J	14		0.5 (0.94)	1.75 (0.96)	0-3
	A	16		16.69 (51.33)	44.5 (80.12)	0-204
	All	30		9.13 (37.82)	27.4 (63.67)	0-204
Females *I. hexagonus*	J	14		0.64 (1.6)	2.25 (2.5)	0-6
	A	16		7.5 (19.39)	30 (31.29)	0-68
	All	30		4.3 (14.41)	16.13 (25.35)	0-68
Total tick weight (g)	J	14		0.01 (0.03)	0.04 (0.04)	0-0.1
	A	16		0.14 (0.31)	0.027 (0.041)	0-1.24
	All	30		0.08 (0.24)	0.19 (0.35)	0-1.24

	Age	N	Prevalence %	Abundance (SD)	Intensity (SD)	Range
Total *I. ricinus* weight (g)	J	14		0	0	
	A	16		0.02 (0.06)	0.15 (0.06)	0-0.2
	All	30		0.01 (0.04)	0.15 (0.06)	0-0.2
Total *I. hexagonus* weight (g)	J	14		0.01 (0.03)	0.04 (0.04)	0-0.1
	A	16		0.12 (0.31)	0.24 (0.41)	0-1.24
	All	30		0.67 (0.23)	0.17 (0.35)	0-1.24

In table 46 the species richness for hedgehogs from the UK is listed. Sexes and ages showed no significant differences and could therefore be pooled. No animal harboured no, six or more different parasite species. The majority had three parasite species following four, two, five and one species. The mean species richness was 3.36 (SD = 1.34) for juveniles, 2.94 (SD = 0.85) for adults and 3.13 (SD = 1.11) for all animals.

Table 46: Species richness of dissected hedgehogs from the UK (N = 30, juveniles N = 14, adults N = 16). Different tick species and life stages are accounted for one species. No differentiation was made between peritoneal and intestinal *Plagiorhynchus cylindraceus*. Hedgehog sexes, seasons (month of collection) and regions are pooled.

Species number	0	1	2	3	4	5	6	7
Frequency % (juveniles)	0	14.3	7.1	28.6	28.6	21.4	0	0
Frequency % (adults)	0	6.3	18.8	50	25	0	0	0
Frequency % (all ages)	0	10	13.3	40	26.7	10	0	0

1.1.3 New Zealand

For the statistical analysis I used 205 hedgehogs from different catchment areas in New Zealand including Palmerston North (N = 31) and Auckland (N = 36) from the North Island and Molesworth (N = 38), Twizel (N = 55) and Macraes Flat (N = 45) from the South Island. Animals were caught and killed from February-April in 2005 (Molesworth) and from November-December in 2007 and January-February in 2007 and 2008. For the analysis the South and the North Island were treated as separate regions but catchment areas and death years were pooled. Numbers of hedgehogs, sexes, ages and locations are shown in table 47.

Table 47: Number of New Zealand hedgehogs used for dissections (South Island: juveniles = 45, adults = 94; North Island: juveniles = 20, adults = 46). Animals are separated in age, sex, and catchment area, collection. F = females, M = males, B = both sexes.

	South Island			North Island	
	Macraes Flat	Molesworth	Twizel	Auckland	Palmerston North
adults					
F	9	11	7	9	13
M	29	13	25	12	12
B	38	24	32	21	25
juveniles					
F	3	8	11	4	1
M	4	7	12	11	4
B	7	15	23	15	5

Table 48 shows prevalences and abundances for the macroparasites found in and on hedgehogs in New Zealand.

For fleas there were differences both in prevalence ($p = 0.011$) and abundance ($p = 0.01$) for adults on the North Island with higher numbers and prevalences in February than in the other months. These results from the fact that I only had two animals which died in February and on one of these animals only two fleas were found. Assuming that these are not the real prevalences occurring in the wild, I ignored these results and pooled all months.

I found ticks (8 females, 2 nymphs) of *Haemaphysalis longicornis* on one animal from the North Island. *H. longicornis* is known as the bush tick or the New Zealand cattle tick. It is normally found on cattle but also occasionally on other mammals.

Prevalences and abundances for *C. striatum* differed both for juvenile (prevalence: $p = 0.005$, abundance: $p = 0.004$) and adult (prevalence: $p = 0.009$, abundance: $p = 0.006$) hedgehogs from the South Island dependent on the month of collection. For juveniles I found the highest prevalences in March (50%), for adults in March (42.1%) and April (50%). Abundances were highest in March for juveniles and in February, March and April for adults.

For *C. aerophila* I found differences in prevalence ($p = 0.001$) and abundance ($p = 0.001$) for adults from the South Island dependent on the month of collection. Prevalences of 25% were found in December with a total of two from eight investigated hedgehogs showing *C. aerophila* infections. In all other months the prevalences were 0%. The mean abundance in

December was 2.5 with one hedgehog having 19 worms and one hedgehog having only a single worm.

For *Capillaria* spp., animals from the South Island and North Island differed in prevalence (South Island: $p = 0.005$, North Island: $p = 0.001$) and abundance (South Island: $p = 0.004$, North Island: $p = 0.001$). In both cases juveniles showed lower prevalences and abundances than adult hedgehogs.

No differences could be detected for trematodes. The trematodes found in New Zealand differed morphologically from *B. erinacei* from Europe, however, because of the state of the worms it was not possible to determine their species or genus.

Prevalences ($p = 0.025$) and abundances ($p = 0.008$) of peritoneal *P. cylindraceus* and abundances ($p = 0.043$) of the sum of intestinal and peritoneal *P. cylindraceus* differed between ages on the North Island, with juveniles being more highly infected than adults. Acanthocephalans from the body cavity ($p = 0.032$) and sum of acanthocephalans ($p = 0.01$) differed in prevalences between the regions, and abundance of acanthocephalans from the body cavity ($p = 0.008$) and sum of all acanthocephalans ($p = 0.008$) also differed between regions. In all cases the hedgehogs from the North Island showed higher prevalences and abundances than hedgehogs from the South Island. However, as there were only four animals with infections the sample size is too low to draw definite conclusions. Therefore ages and regions were pooled. Tables 48-50 show the macroparasite distribution for juvenile, adult and all dissected hedgehogs from New Zealand.

Table 48: Macroparasite prevalences, abundances, intensities and ranges of dissected juvenile hedgehogs from New Zealand. Hedgehog sexes, months of death and regions were pooled. N = number of samples, SD = standard deviation.

Parasites	Region	N	Prevalence %	Abundance (SD)	Intensity (SD)	Range
Fleas	South Island	45	0	0	0	
	North Island	20	0	0	0	
	Both Islands	65	0	0	0	
Ticks	South Island	45	0	0	0	
	North Island	20	0	0	0	
	Both Islands	65	0	0	0	
C. striatum	South Island	45	13.3	0.44 (1.74)	3.33 (3.88)	0-11
	North Island	20	20	3.95 (15.41)	19.75 (33)	0-69
	Both Islands	65	15.4	1.52 (8.68)	9.9 (21.05)	0-69
C. aerophila	South Island	45	0	0	0	
	North Island	20	0	0	0	
	Both Islands	65	0	0	0	
Capillaria spp. intestine	South Island	45	8.9	0.69 (2.93)	7.75 (7.27)	0-18
	North Island	20	15	5.5 (19.12)	36.67 (41.93)	0-85
	Both Islands	65	10.8	2.17 (10.93)	20.14 (29.18)	0-85
Trematodes	South Island	45	0	0	0	
	North Island	20	0	0	0	
	Both Islands	65	0	0	0	
P. cylindraceus body cavity	South Island	45	0	0	0	
	North Island	20	15	0.4 (1.35)	2.67 (2.89)	0-6
	Both Islands	65	4.6	0.12 (0.76)	2.67 (2.89)	0-6
P. cylindraceus intestine	South Island	45	0	0	0	
	North Island	20	5	0.1 (0.45)	2	0-2
	Both Islands	65	1.5	0.03 (0.25)	2	0-2
P. cylindraceus sum	South Island	45	0	0	0	
	North Island	20	15	0.5 (1.47)	3.33 (2.52)	0-6
	Both Islands	65	4.6	0.15 (0.83)	3.33 (2.52)	0-6

Table 49: Macroparasite prevalences, abundances, intensities and ranges of dissected adult hedgehogs from New Zealand. Hedgehog sexes, months of death and regions are pooled. N = number of samples, SD = standard deviation.

Parasites	Region	N	Prevalence %	Abundance (SD)	Intensity (SD)	Range
Fleas	South Island	94	0	0	0	
	North Island	46	4.3	0.07 (0.33)	1.5 (0.71)	0-2
	Both Islands	140	1.4	0.02 (0.19)	1.5 (0.71)	0-2
Ticks	South Island	94	0	0	0	
	North Island	46	2.2	0.22 (1.47)	10	0-10
	Both Islands	140	0.7	0.07 (0.85)	10	0-10
C. striatum	South Island	94	19.1	0.85 (2.48)	4.44 (4.08)	0-13
	North Island	46	28.3	0.89 (1.82)	3.15 (2.15)	0-8
	Both Islands	140	22.1	0.86 (2.27)	3.9 (3.42)	0-13
C. aerophila	South Island	94	2.1	0.21 (1.96)	10 (12.73)	0-19
	North Island	46	0	0	0	
	Both Islands	140	1.4	0.14 (1.61)	10 (12.73)	0-19
Capillaria spp. intestine	South Island	94	39.9	4.6 (16.43)	14.9 (27.15)	0-147
	North Island	46	69.6	20.57 (35.58)	29.56 (39.53)	0-159
	Both Islands	140	43.6	9.84 (25.45)	22.59 (34.73)	0-159
Trematodes	South Island	94	0	0	0	
	North Island	46	2.2	0.2 (1.33)	9	0-9
	Both Islands	140	0.7	0.06 (0.76)	9	0-9
P. cylindraceus body cavity	South Island	94	0	0	0	
	North Island	46	0	0	0	
	Both Islands	140	0	0	0	
P. cylindraceus Intestine	South Island	94	0	0	0	
	North Island	46	2.2	0.02 (0.15)	1	0-1
	Both Islands	140	0.7	0.01 (0.08)	1	0-1
P. cylindraceus sum	South Island	94	0	0	0	
	North Island	46	2.2	0.02 (0.15)	1	0-1
	Both Islands	140	0.7	0.01 (0.08)	1	0-1

Table 50: Macroparasite prevalences, abundances, intensities and ranges of dissected hedgehogs of all ages from New Zealand. Hedgehog sexes, months of death, age of hedgehogs and regions were pooled. N = number of samples, SD = standard deviation.

Parasites	Region	N	Prevalence %	Abundance (SD)	Intensity (SD)	Range
Fleas	South Island	139	0	0	0	
	North Island	66	3	0.05 (0.27)	1.5 (0.71)	0-2
	Both Islands	205	1	0.01 (0.16)	1.5 (0.71)	0-2
Ticks	South Island	139	0	0	0	
	North Island	66	0.66	0.15 (1.23)	10	0-10
	Both Islands	205	2.05	0.05 (0.7)	10	0-10
C. striatum	South Island	139	17.3	0.72 (2.27)	4.17 (3.97)	0-13
	North Island	66	25.8	1.82 (8.59)	7.06 (16.13)	0-69
	Both Islands	205	20.0	1.07 (5.22)	5.37 (10.74)	0-69
C. aerophila	South Island	139	1.4	0.14 (1.61)	10.00 (12.73)	0-19
	North Island	66	0	0	0	
	Both Islands	205	1	0.1 (1.33)	10 (12.73)	0-19
Capillaria spp. intestine	South Island	139	23.7	3.33 (13.71)	14.03 (25.61)	0-147
	North Island	66	53.0	16 (32.12)	30.17 (39.15)	0-159
	Both Islands	205	33.2	7.41 (22.16)	22.34 (34.01)	0-159
Trematodes	South Island	139	0	0	0	
	North Island	66	1.5	0.14 (1.11)	9	0-9
	Both Islands	205	0.5	0.04 (0.63)	9	0-9
P. cylindraceus body cavity	South Island	139	0	0	0	
	North Island	66	4.5	0.12 (0.75)	2.67 (2.89)	0-6
	Both Islands	205	1.5	0.04 (0.43)	2.67 (2.89)	0-6
P. cylindraceus Intestine	South Island	139	0	0	0	
	North Island	66	3.0	0.05 (0.27)	1.5 (0.71)	0-2
	Both Islands	205	1	0.01 (0.16)	1.5 (0.71)	0-2
P. cylindraceus sum	South Island	139	0	0	0	
	North Island	66	6.1	0.17 (0.83)	2.75 (2.36)	0-6
	Both Islands	205	2	0.05 (0.48)	2.75 (2.36)	0-6

In New Zealand, as in Germany, I also found seven different macroparasite species, although the species richness was very different (table 51). The majority of all hedgehogs had no or only one macroparasite species. A minority had two or three species. Four or more species did not occur at all. I used a Mann-Whitney U-test to test for differences in species richness. I

found species differences between ages both for the South Island (p = 0.004) and the North Island (p = 0.002) with juveniles having a lower species richness than adults in both cases. For the South Island the mean species richness for juveniles was 0.22 (SD = 0.56), for adults 0.52 (SD = 0.68) and for all animals 0.42 (SD = 0.66). For the North Island the mean species richness for juveniles was 0.6 (SD = 0.76), for adults 1.09 (SD = 0.66) and for all animals 0.91 (SD = 0.74). Pooling both regions the mean species richness for juveniles was 0.31 (SD = 0.64), for adults 0.71 (SD = 0.72) and for all animals 0.58 (SD = 0.72).

Table 51: Species richness of dissected hedgehogs from New Zealand. No differentiation was made between peritoneal and intestinal *Plagiorhynchus cylindraceus*. Hedgehog sexes, death months and regions of origin are pooled. North Island N = 66 (juveniles N = 20, adults N = 46), South Island N = 139 (juveniles N = 45, adults N = 96).

	Region	Species number							
		0	1	2	3	4	5	6	7
Frequency % (juveniles)	South Island	84.4	8.9	6.7	0	0	0	0	0
	North Island	65	20	15	0	0	0	0	0
	Both Islands	78.5	12.3	9.2	0	0	0	0	0
Frequency % (adults)	South Island	58.5	30.9	10.6	0	0	0	0	0
	North Island	15.2	63	19.6	2.2	0	0	0	0
	Both Islands	44.3	41.4	13.6	0.7	0	0	0	0
Frequency % (all ages)	South Island	66.9	23.7	9.4	0	0	0	0	0
	North Island	30.3	50	18.2	1.5	0	0	0	0
	Both Islands	55.1	32.2	12.2	0.5	0	0	0	0

1.1.4 Comparison of the investigation areas

To compare abundances of parasites and species richness I used either a Kruskal-Wallis test or a Mann-Whitney U-test depending on the number of independent groups. I used a Chi-square-test or a Fisher's-exact-test to test for differences in prevalences. For prevalences and abundances of parasites and species richness from the different investigation areas see chapters IV.1.1.1-IV.1.1.3.

Fleas:

Prevalences differed between the investigation areas ($p = 0.001$). Germany showed higher prevalences than the UK ($p = 0.001$), the South Island ($p = 0.001$) and the North Island ($p = 0.001$). The other areas did not differ from each other. Abundances of fleas also differed significantly between the investigation areas ($p = 0.001$). I found higher abundances in Germany compared to the UK ($p = 0.001$), the South Island ($p = 0.001$) and the North Island of New Zealand ($p = 0.001$). The UK did not differ from either of the New Zealand areas but the South Island differed significantly from the North Island ($p = 0.04$) which had higher abundances. Figure 37 shows the distribution of flea numbers for Germany and the North Island of New Zealand.

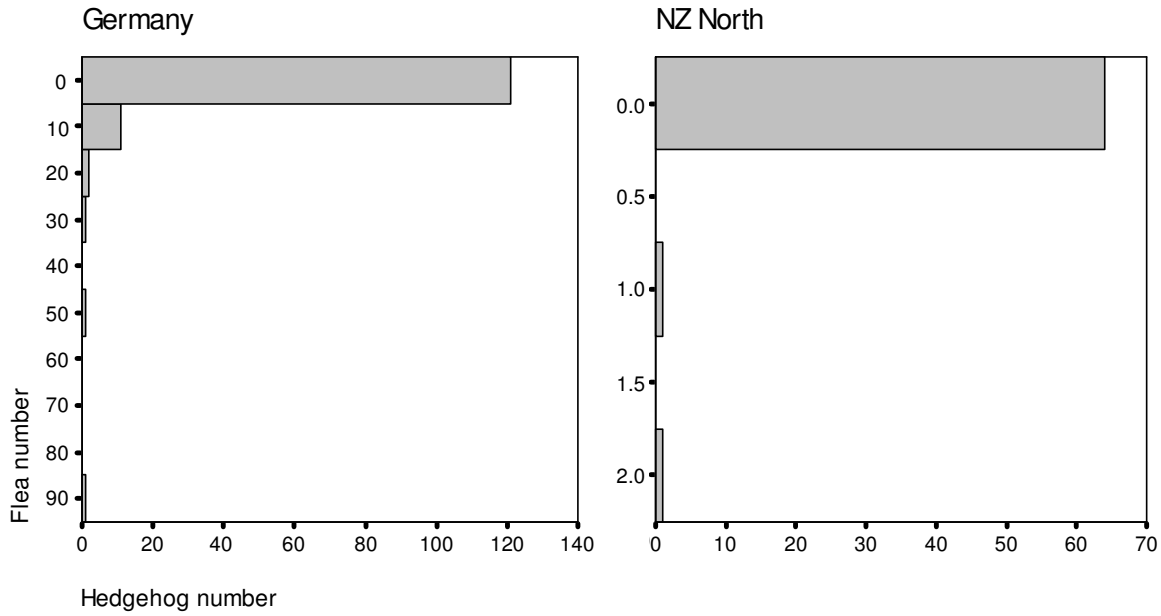

Figure 37: Distribution of flea numbers in the investigation areas Germany (N = 133) and the North Island of New Zealand (NZ North, N = 66). Hedgehog sexes, ages and collection dates are pooled. Note: fleas found in Germany were *Archaeopsylla erinacei*, in New Zealand *Ctenocephalides felis felis*.

Crenosoma striatum:

Prevalences of *C. striatum* differed between the investigation areas (p = 0.001). Germany showed higher prevalences than the South Island and the North Island of New Zealand (p = 0.001). I found the same pattern for the UK which had higher prevalences than the South and North Island (p = 0.001). The areas also differed in abundances (p = 0.001) with both Germany and the UK having higher nematode numbers than either New Zealand islands. Figure 38 shows the distribution of *C. striatum* numbers for Germany, the UK and New Zealand.

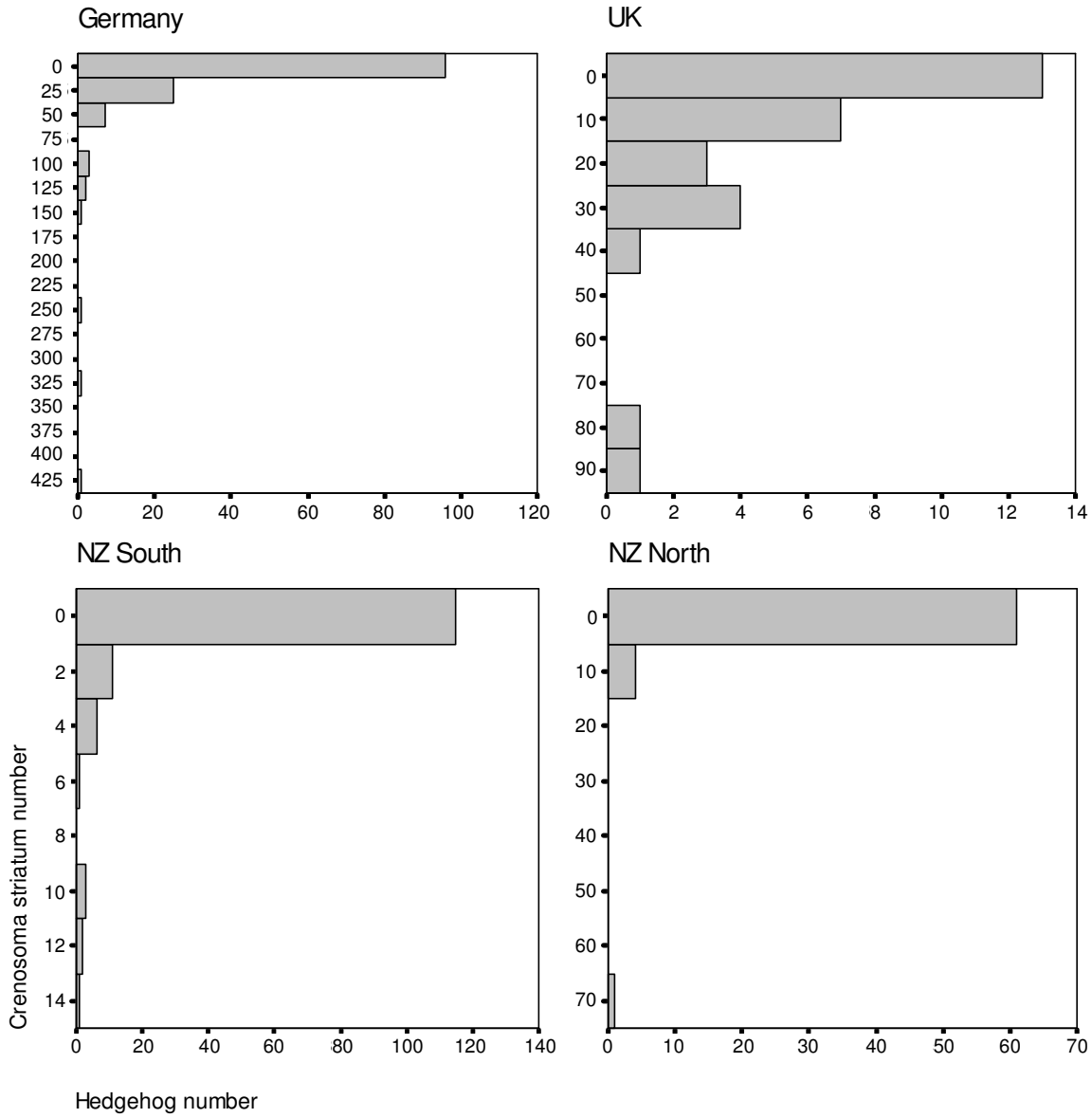

Figure 38: Distribution of *Crenosoma striatum* numbers in the investigation areas Germany (N = 133), the UK (N = 30), the South Island (NZ South, N = 139) and the North Island (NZ North, N = 66) of New Zealand. Hedgehog sexes, ages and collection dates are pooled.

Capillaria aerophila:

Prevalences of *C. aerophila* differed significantly between the investigated areas (p = 0.001). Germany and the UK showed higher prevalences than both islands of New Zealand (p = 0.001). Germany did not differ from the UK and there were no significant differences between the South and the North Island of New Zealand. For abundances I found the same results. Figure 39 shows the distribution of *C. aerophila* numbers for Germany, the UK and the South Island of New Zealand.

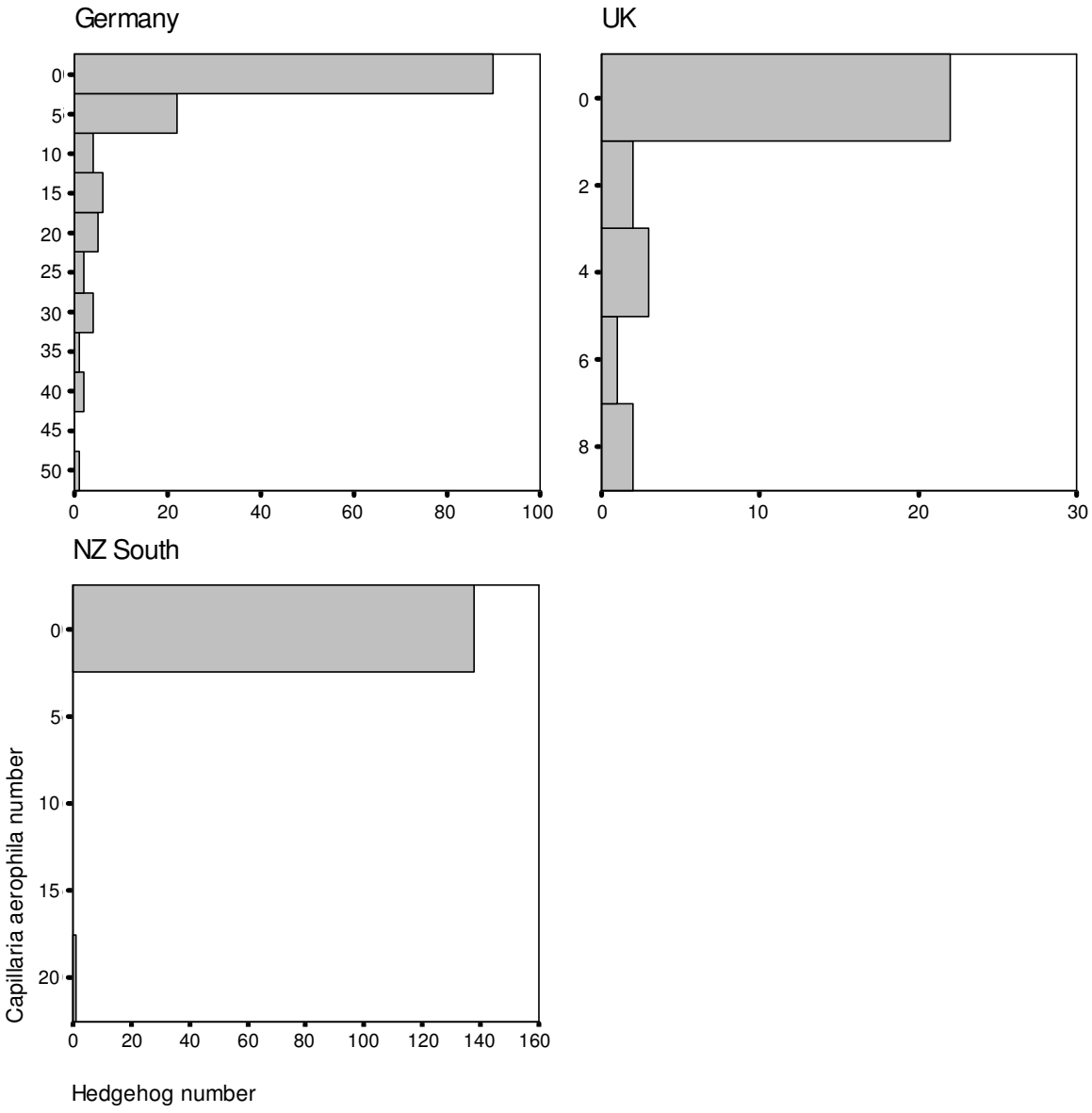

Figure 39: Distribution of *Capillaria aerophila* numbers in the investigation areas Germany (N = 133), the UK (N = 30) and the South Island of New Zealand (NZ South, N = 139). Hedgehog sexes, ages and collection dates are pooled.

Capillaria spp.:

Compared to other parasite species, intestinal *Capillaria* spp. had the highest prevalences in all investigation areas. The prevalences in Germany and the UK were higher than in New Zealand (p = 0.001), but the North Island also showed higher prevalences than the South Island (p = 0.001). The results for abundances are the same. The distributions of intestinal Capillaria spp. numbers are presented in figure 40.

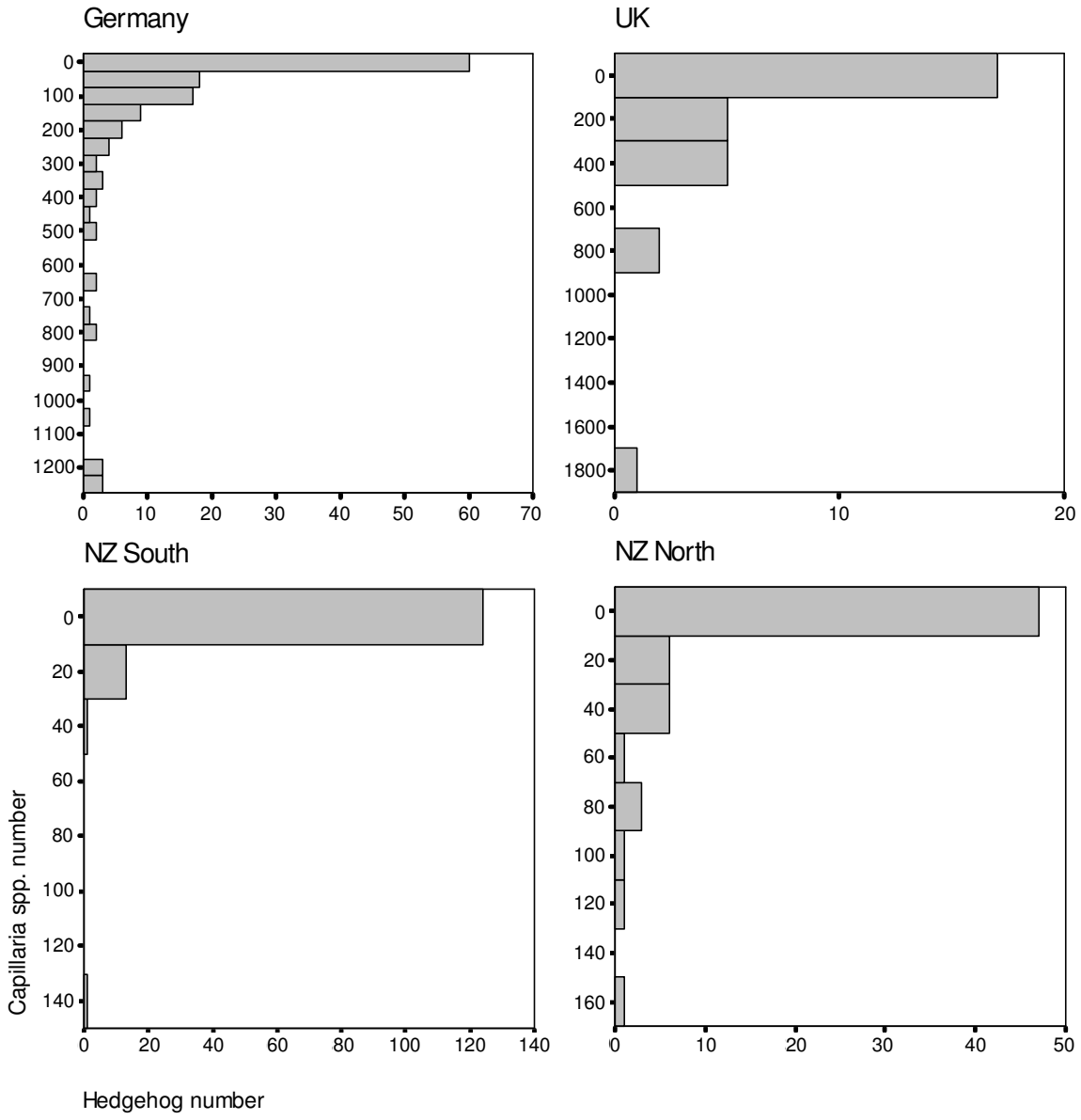

Figure 40: Distribution of intestinal *Capillaria* spp. numbers in the investigation areas Germany (N = 133), the UK (N = 30), the South Island (NZ South, N = 139) and the North Island (NZ North, N = 66) of New Zealand. Hedgehog sexes, ages and collection dates are pooled.

Trematodes:

The trematode species found in New Zealand did not match with *B. erinacei* from Europe. Both prevalences and abundances for trematodes were higher in Germany and the UK than in New Zealand (p = 0.001). Germany and the UK did not differ from each other, nor did the islands of New Zealand. Figure 41 shows the distribution of trematode numbers of the intestine for Germany, the UK and the North Island of New Zealand.

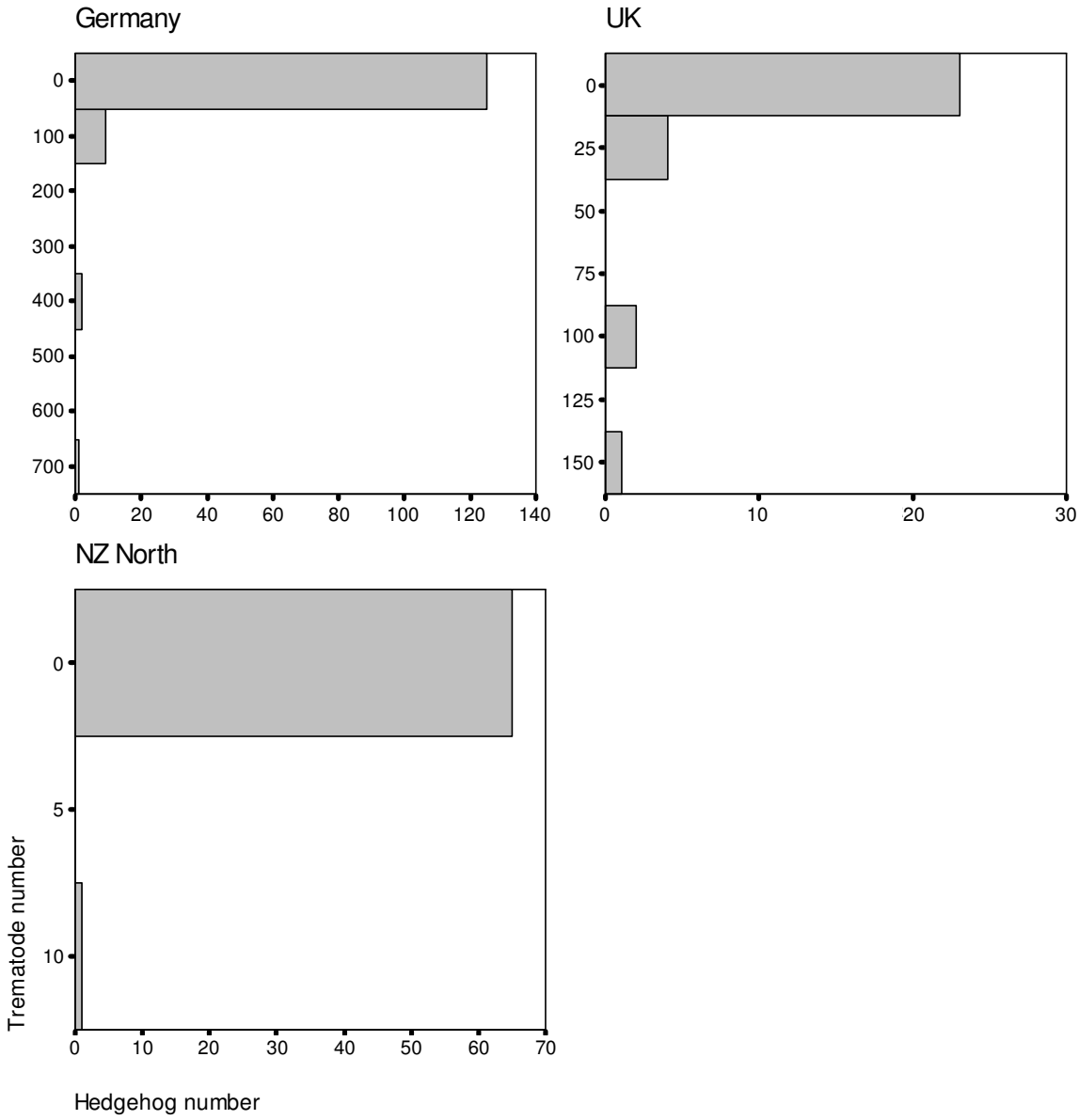

Figure 41: Distribution of trematode numbers in the investigation areas Germany (N = 133), the UK (N = 30) and the North Island of New Zealand (NZ North, N = 66). Hedgehog sexes, ages and collection dates are pooled. Note: trematodes found in Europe belong to the species *Brachylaemus erinacei*, while trematodes found in New Zealand could not be determined to species or genus.

Plagiorhynchus cylindraceus:

Prevalences for acanthocephalan infections (body cavity, intestine, sum) differed significantly between the investigation areas ($p = 0.001$). Germany showed higher prevalences than the South Island of New Zealand ($p = 0.001$). No differences were found between Germany and the North Island and the UK, except for intestinal *P. cylindraceus* for which the UK showed higher prevalences than Germany ($p = 0.043$). The UK also had higher prevalences than the South Island ($p = 0.001$) and the North Island (body cavity $p = 0.031$, intestine and sum $p = 0.001$). The North Island showed higher prevalences than the South Island for peritoneal *P. cylindraceus* ($p = 0.032$) and the sum of acanthocephalans ($p = 0.01$). Abundances also differed between the investigation areas ($p = 0.001$). Germany had higher abundances than the South Island ($p = 0.001$). For intestinal acanthocephalans Germany had lower abundances than the UK ($p = 0.037$) and for the sum of acanthocephalans higher abundances than the North Island ($p = 0.046$). The UK had higher abundances than the South Island (body cavity $p = 0.002$, intestine and sum $p = 0.001$) and the North Island (intestine $p = 0.006$, sum $p = 0.005$). The North Island showed higher abundances than the South Island (body cavity $p = 0.012$, intestine $p = 0.04$, sum $p = 0.003$). Figures 42-44 show the distribution of acanthocephalan numbers for Germany, the UK and the North Island of New Zealand.

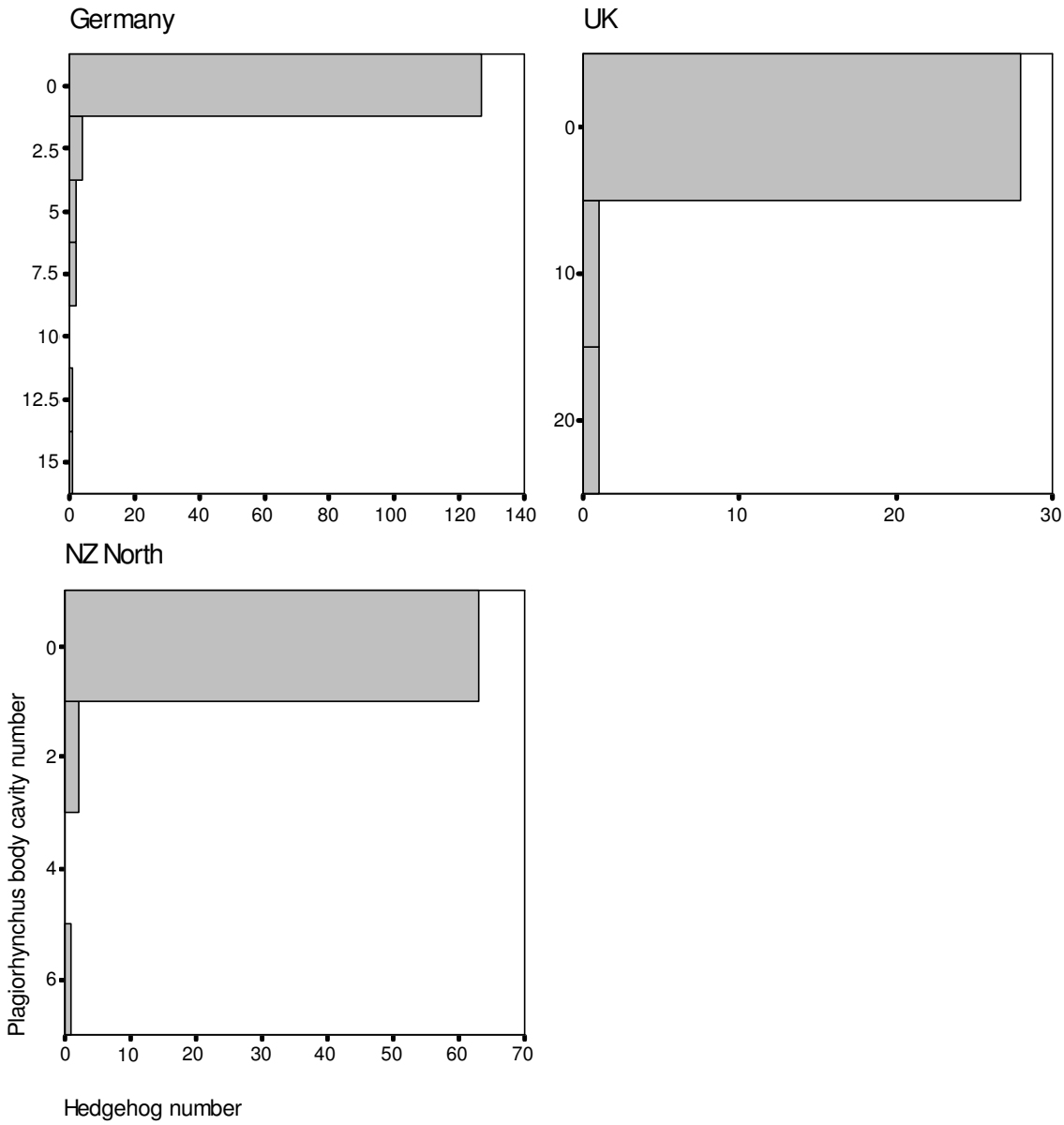

Figure 42: Distribution of peritoneal *Plagiorhynchus cylindraceus* numbers in the investigation areas Germany (N = 133), the UK (N = 30) and the North Island of New Zealand (NZ North, N = 66). Hedgehog sexes, ages and collection dates are pooled.

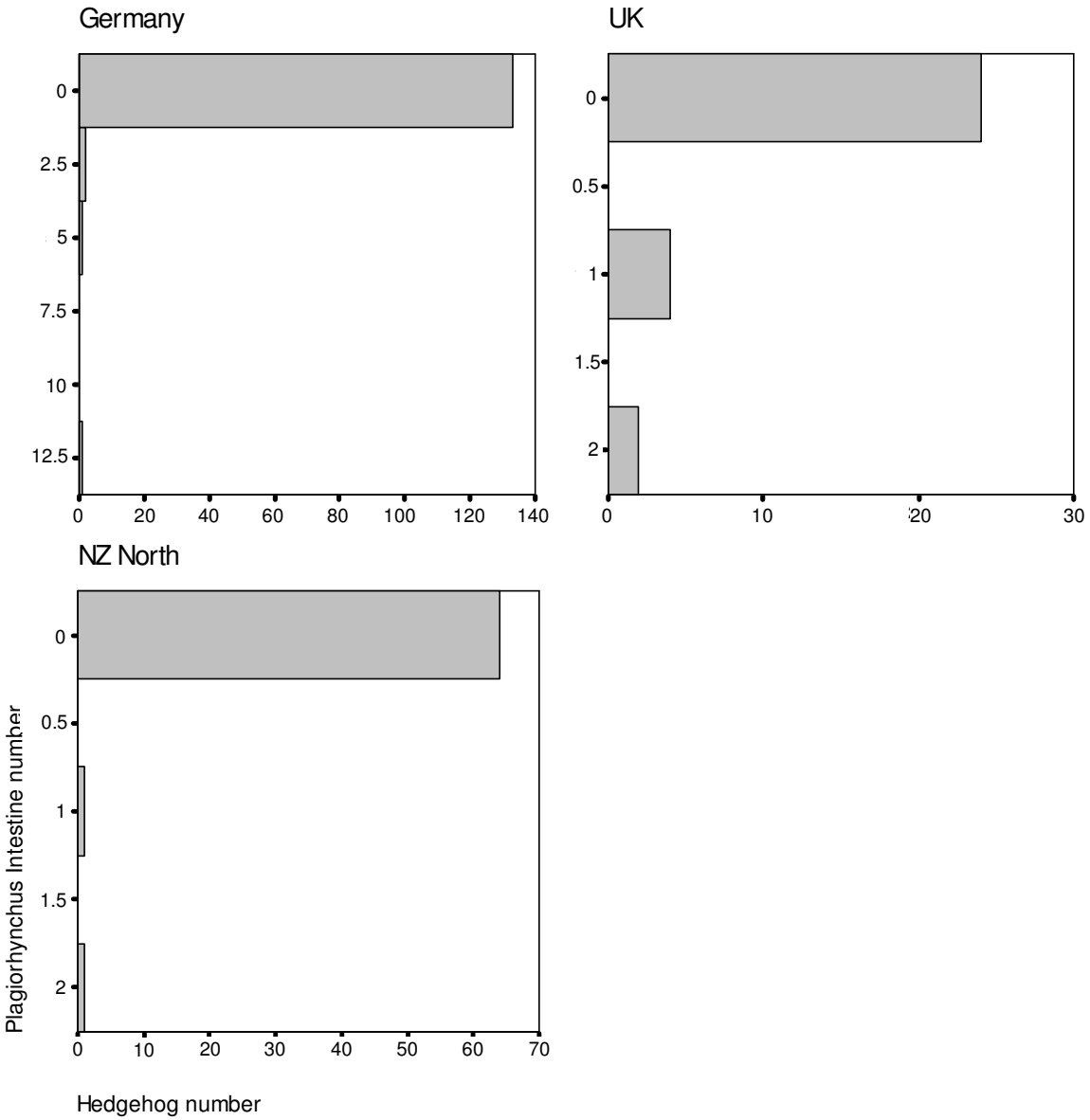

Figure 43: Distribution of intestinal *Plagiorhynchus cylindraceus* numbers in the investigation areas Germany (N = 133), the UK (N = 30) and the North Island of New Zealand (NZ North, N = 66). Hedgehog sexes, ages and collection dates are pooled.

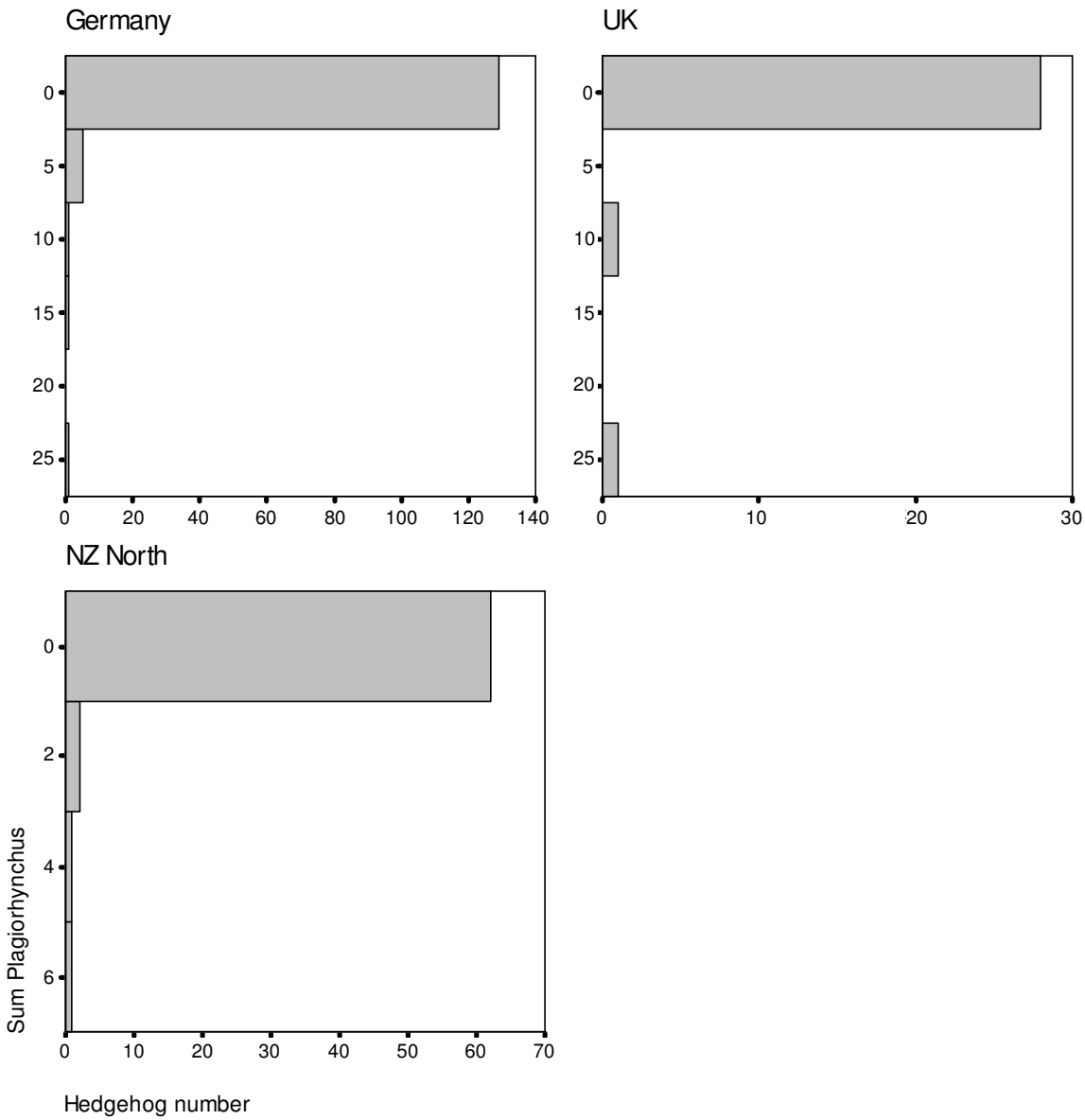

Figure 44: Distribution of all *Plagiorhynchus cylindraceus* in the investigation areas Germany (N = 133), the UK (N = 30) and the North Island of New Zealand (NZ North, N = 66). Hedgehog sexes, ages and collection dates are pooled.

Species richness:

Species richness differed significantly between the investigation areas (p = 0.001). Both Germany and the UK had a higher mean species richness than New Zealand (p = 0.001). Germany and the UK did not differ from each other and there were no differences between the islands of New Zealand. Figures 45 and 46 show the mean species richness for all investigation areas, separated by ages and for all hedgehogs.

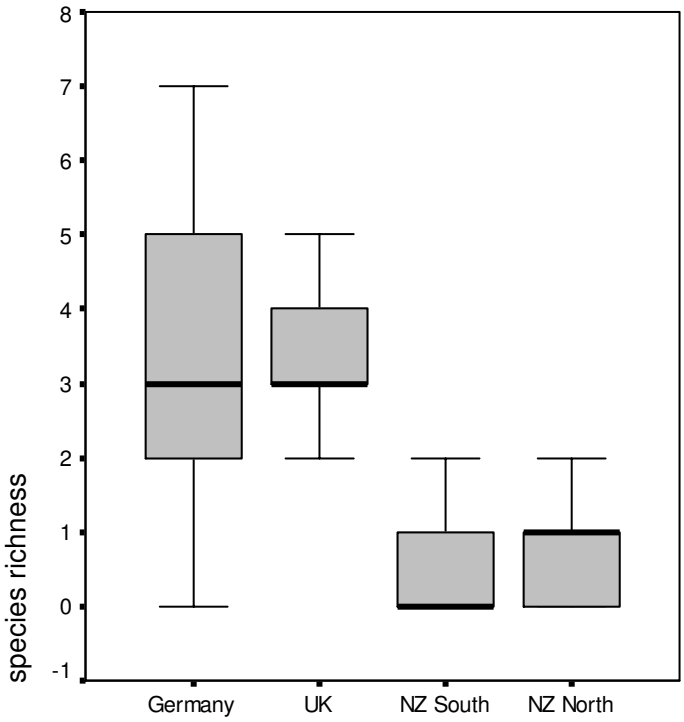

Figure 45: Species richness for the different investigation areas. The black bars indicate the median, lower and upper grey bars the 25% and 75% percentile and the error bars the lowest and highest non extreme value. Germany (N = 133), UK (N = 30), South Island (NZ South, N = 139), North Island (NZ North, N = 66) of New Zealand. Hedgehog sexes, ages and collection dates are pooled.

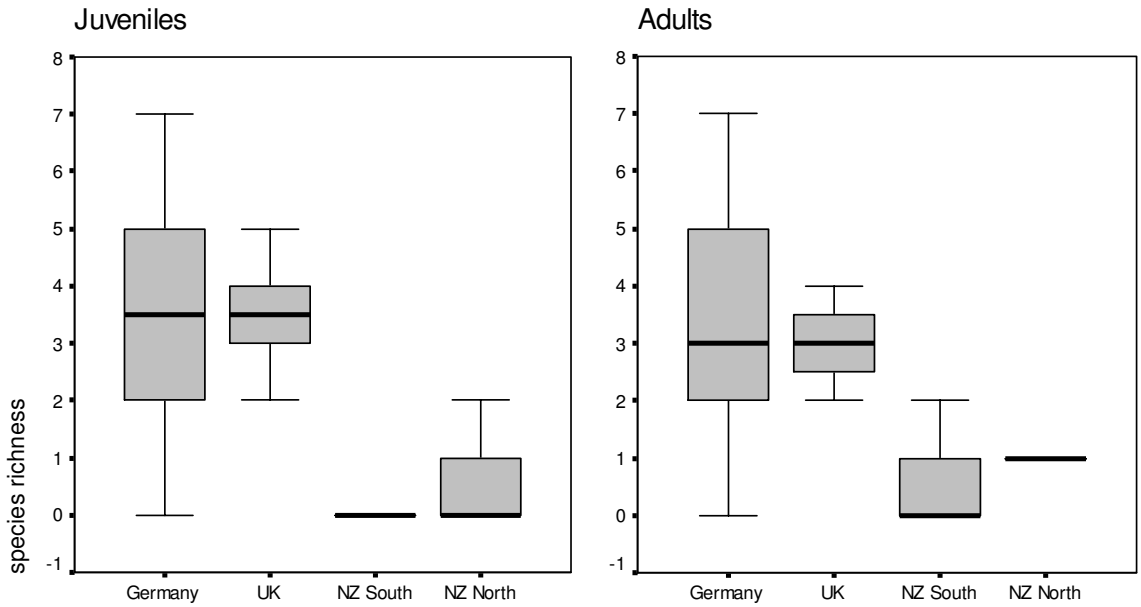

Figure 46: Species richness for the age groups in the different investigation areas. The black bars indicate the median, lower and upper grey bars the 25% and 75% percentile and the error bars the lowest and highest non extreme value. Juveniles: Germany (N = 38), UK (N = 14), South Island (NZ South, N = 45), North Island (NZ North, N = 20) of New Zealand. Adults: Germany (N = 95), UK (N = 16), South Island (NZ South, N = 94), North Island (NZ North, N = 46) of New Zealand. Hedgehog sexes and collection dates are pooled.

Ticks:

I found only one hedgehog on the North Island infested with eight females and two nymphs of *H. longicornis*. This species does not occur in Europe. Therefore I did not compare hedgehogs from New Zealand with hedgehogs from Europe in relation to tick prevalences or abundances. Germany and the UK did not differ in prevalence of total tick infestation and infestation with *I. hexagonus* but in infestation with *I. ricinus* ($p = 0.045$) with Germany having higher prevalences. According to tick numbers I found no significant differences for total, species or life stage numbers (differentiated after species) except for total *I. ricinus* numbers with Germany having higher abundances than the UK ($p = 0.047$). The total tick weight from German hedgehogs was also higher than that of the British ones ($p = 0.021$). Figures 47-49 shows the distribution of total tick weight and *I. ricinus* and *I. hexagonus* weight for Germany and the UK.

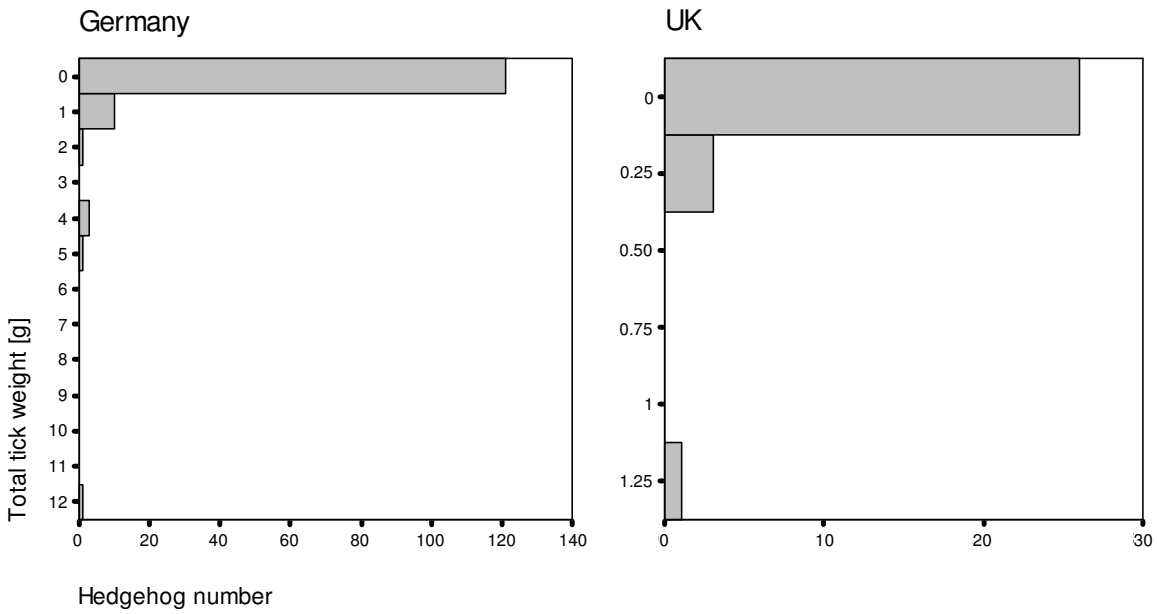

Figure 47: Distribution of total tick weight (g) (all species, all life stages) in the investigation areas Germany (N = 133) and the UK (N = 30). Hedgehog sexes, ages and collection dates are pooled.

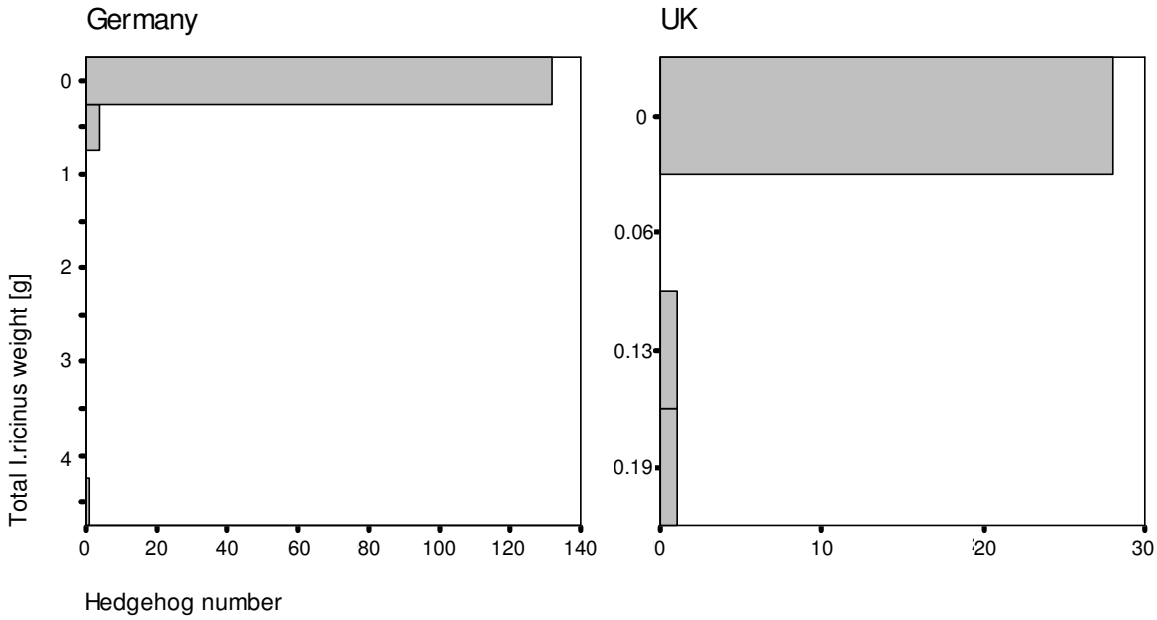

Figure 48: Distribution of total *Ixodes ricinus* weight (g) (all life stages) in the investigation areas Germany (N = 133) and the UK (N = 30). Hedgehog sexes, ages and collection dates are pooled.

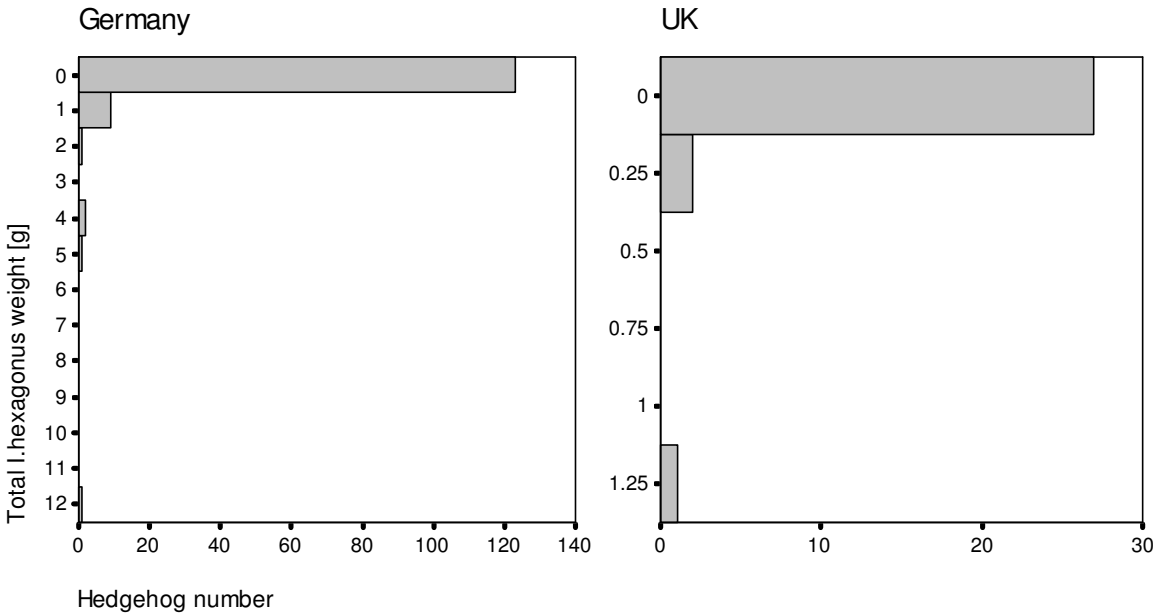

Figure 49: Distribution of total *Ixodes hexagonus* weight (g) (all life stages) in the investigation areas Germany (N = 133) and the UK (N = 30). Hedgehog sexes, ages and collection dates are pooled.

1.2 Parasites and fitness related parameters

1.2.1 Condition factor

In order to define the health status of the dissected hedgehogs, it was necessary to calculate a condition factor. Therefore, I first tested for correlations between hedgehog length in cm and hedgehog weight in grams. The investigation areas and hedgehog ages were treated separately. To calculate the condition factor I also used those animals which were treated with anthelmintica, and those from which the place of origin was not known and which were not used to investigate the geographical distribution of the parasites.

At first I tested for differences in weight/length ratio (w/l ratio) between hedgehog sexes, separated by seasons (season 1 = December-April, season 2 = May-July, season 3 = August-November). For German hedgehogs I found no differences for adults (season 1 $p = 0.476$, season 2 $p = 0.104$, season 3 $p = 0.101$) or juveniles (season 1 $p = 0.578$, season 2 $p = 0.459$, season 3 $p = 0.415$). Therefore I pooled sexes for both ages.

Because of the low sample size of the British animals I was not able to test for differences in seasons for both ages. Results for adults in seasons 1 showed no differences between sexes ($p = 0.231$) as well as for juveniles in season 1 ($p = 0.510$) and season 3 ($p = 0.143$). Thus, I also pooled sexes of the British hedgehogs. Hedgehogs from New Zealand were separated by islands, but since the animals were all trapped within the same season it was not necessary to

separate between collecting dates. The animals from Molesworth were excluded from these tests to prevent false effects, since these animals had been stored in the freezer for three years and their muscles had already dried out at the time of dissection. I found no differences between sexes for adults (South Island p = 0.294, North Island p = 0.254) or juveniles (South Island p = 0.285, North Island p = 0.494). Therefore I also pooled sexes for New Zealand.

After pooling the sexes, tests for correlations between weight and length were conducted using a Pearson correlation. For German hedgehogs there were no correlations between weight and length (season 1 r = 0.396, p = 0.116; season 2 r = 0.157, p = 0.263; season 3 r = -0.005, p = 0.967). In addition, no differences for w/l ratio between the different seasons could be observed (ANOVA, p = 0.365), so I decided to pool all adults from Germany. For adults from the UK – because of the low sample size all seasons were pooled – I found similar results (r = 0.128, p = 0.636). As there were no significant correlations I decided to use the w/l ratio as the condition factor for adults from Germany and the UK.

For juveniles from Germany, significant correlations between weight and length could be detected (season 1 r = 0.724, p = 0.005; season 2 r = 0.721, p = 0.067; season 3 r = 0.806, p = 0.001). Although there was no significant correlation in season 2, there was an obvious trend to positive correlations. The w/l ratios from season 1 and 2 differed significantly from the w/l ratios of season 3 (p = 0.002), with juveniles from season 3 having a lower w/l ratio. Because of this I calculated the condition factor for juveniles from Germany by separating the seasons.

For juveniles from the UK no significant positive correlations could be measured although the probability tended to significance (r = 0.494, p = 0.061). But since the sample size, with N = 15, was very small and there was also a positive trend, I decided to treat the juveniles as if there was a significant correlation. The w/l ratios from the different seasons did not differ significantly (ANOVA, p = 0.580), so all juveniles from the UK were pooled

In New Zealand there were positive correlations for adults (South Island r = 0.293, p = 0.012; North Island r = 0.427, p = 0.001) and for juveniles (South Island r = 0.5, p = 0.001; North Island r = 0.79, p = 0.001). The w/l ratio from adults did not differ between the two islands (t-test, p = 0.165), whereas the w/l of juveniles differed significantly between the islands (t-test, p = 0.016). So for calculating the condition factor, all adults from New Zealand were pooled, but juveniles were treated separately for the different islands.

The regression for juveniles from Germany was y = 14.611x+6.4852 for season 1 and 2 and y = 19.023x–144.6 for season 3 (figure 50).

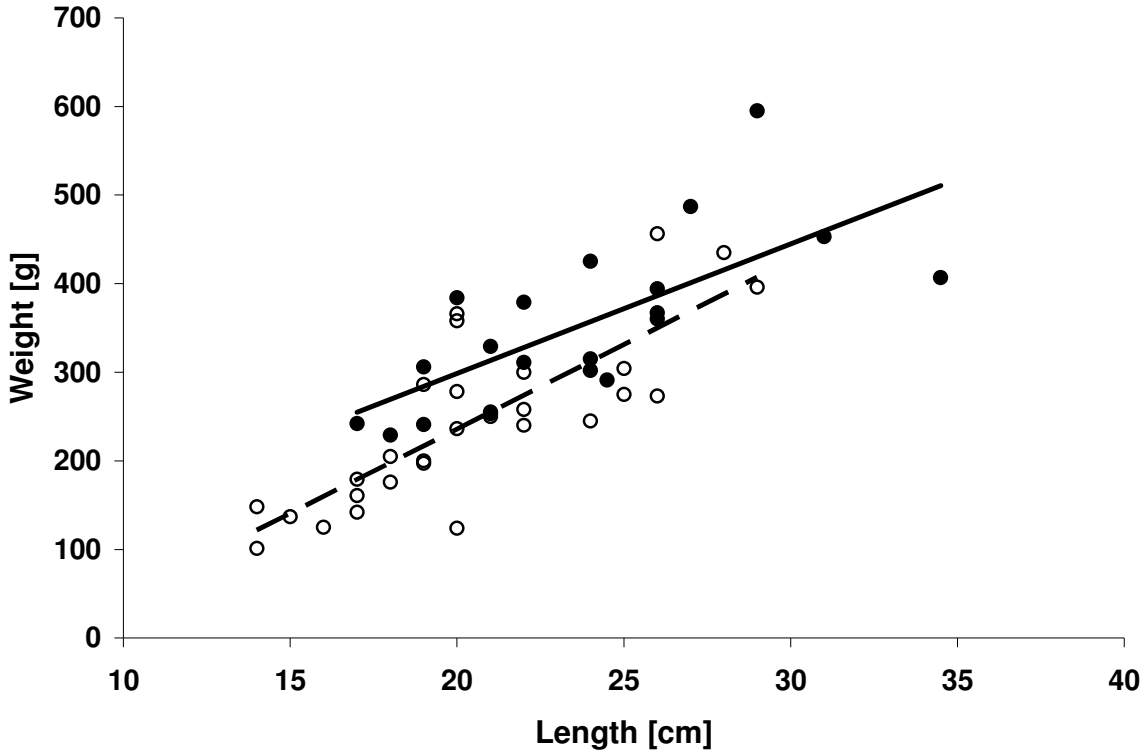

Figure 50: Relationship between body weight (g) and body length (cm) of juvenile hedgehogs from Germany (season 1 and 2 N = 20,●; season 3 N = 29,○). Coefficient of determination R^2 for season 1 and 2 = 0.506,——, for season 3 = 0.65,– –. Sexes and regions are pooled.

For juveniles from the UK the regression was y = 8.4992x+120.03 (figure 51).

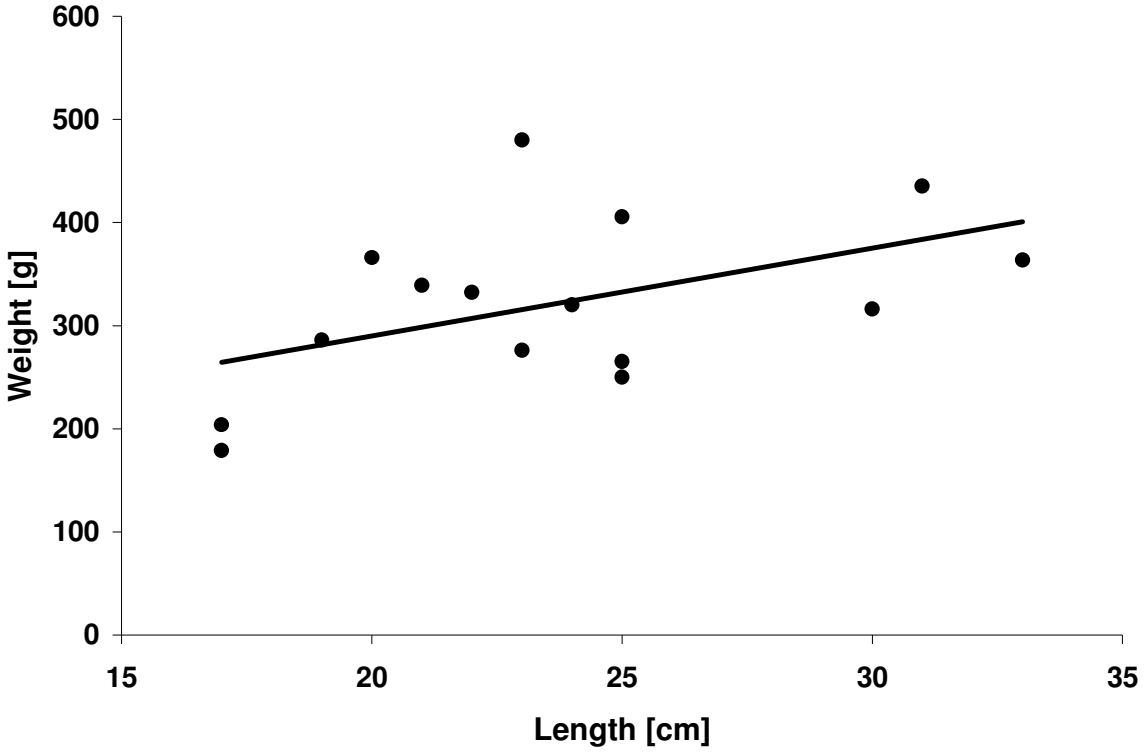

Figure 51: Relationship between body weight (g) and body length (cm) of juvenile hedgehogs from the UK (N = 15). Coefficient of determination $R^2 = 0.244$. Sexes and regions are pooled.

The regression for New Zealand adults was y = 12.642x+253.24 (figure 52).

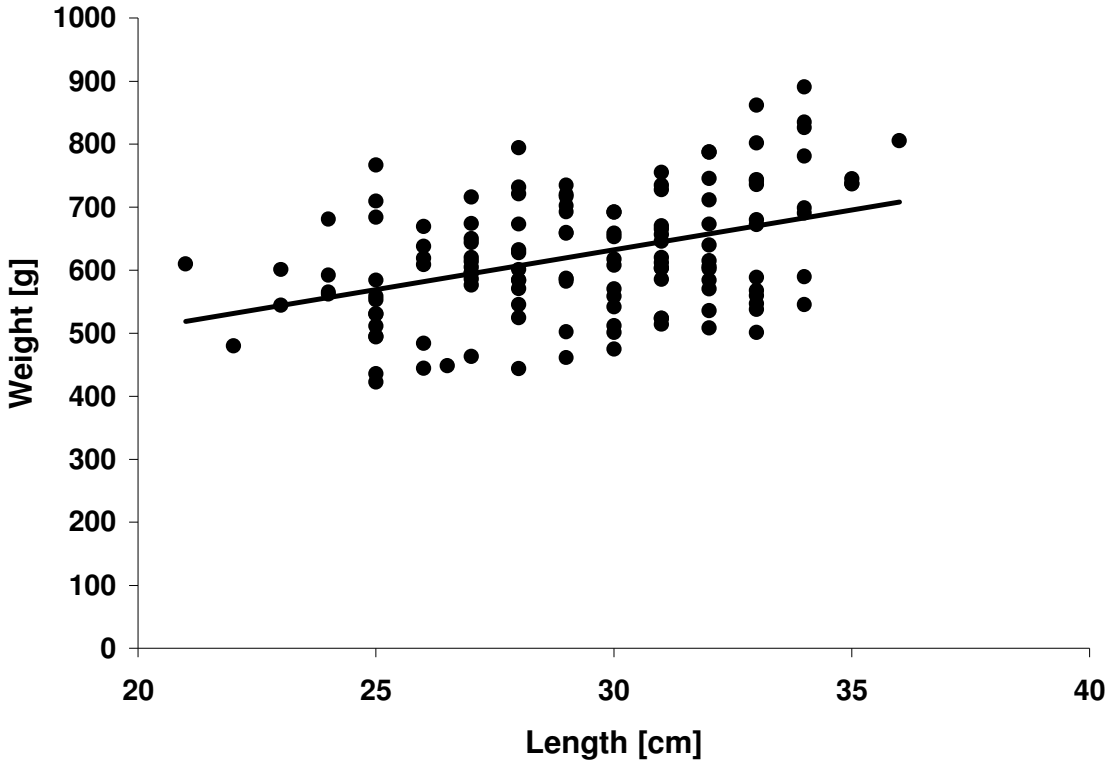

Figure 52: Relationship between body weight (g) and body length (cm) of adult hedgehogs from New Zealand (N = 131). Coefficient of determination $R^2 = 0.173$. Sexes and regions are pooled.

The regression for juveniles from the South Island was y = 8.5031x+156.16, for juveniles from the North Island y = 14.175x+4.815 (figure 53).

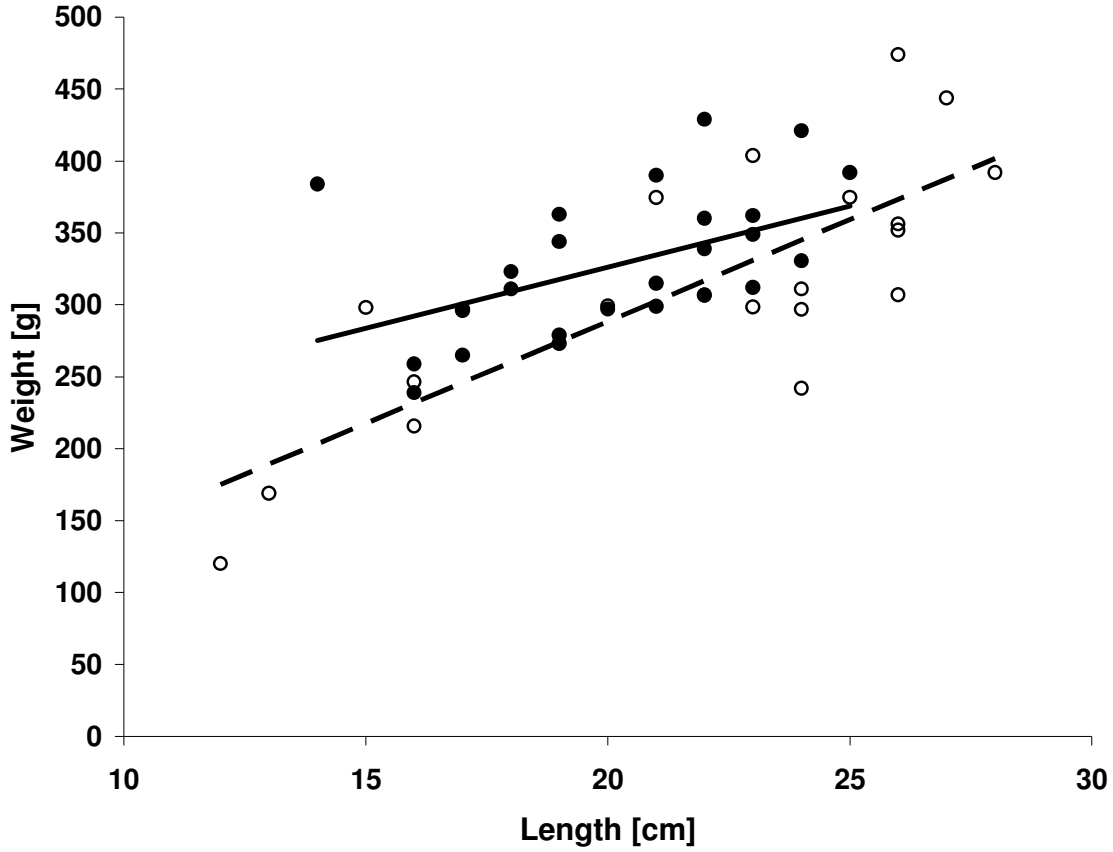

Figure 53: Relationship between body weight (g) and body length (cm) of juvenile hedgehogs from New Zealand (South Island N = 27, ●; North Island N = 19, ○). Coefficient of determination R^2 for the South Island = 0.25, ——, for the North Island = 0.624, – –. Sexes and regions are pooled.

1.2.2 Organs

To test for the influence of parasites on condition factor and organ weight I used a stepwise multiple regression with an α-value of 0.05. As criterion variables I chose either the condition factor or the organ weights and as predictor variables I chose the parasite numbers and the total tick weight (species and life stages pooled). For organ weight I used parasite numbers, total tick weight and the condition factor as predictor variables. Fleas were not used as a predictor variable, because I was not confident that my estimates of flea numbers were correct since fleas usually leave their host immediately after its death (IOFF 1941), while, for example feeding ticks need longer to detach and leave the host. Since I found only one hedgehog in New Zealand infested with ticks, I did not use total tick weight as a predictor variable for

New Zealand hedgehogs. Peritoneal and intestinal *P. cylindraceus* were not treated as single predictor variables, but the sum of all acanthocephalans was used.

Condition factor:

Using the stepwise method, a significant model emerged for adult hedgehogs from Germany ($F_{3, 90}$ = 6.378, p = 0.001, adjusted R^2 = 0.148), and the North Island of New Zealand ($F_{1, 44}$ = 7.134, p = 0.011, adjusted R^2 = 0.12). The significant variables are shown in table 52.

Table 52: Significant predictor variables for the multiple regression analysis of the condition factor and the parasite numbers and total tick weight (g) for adult hedgehogs from Germany (N = 94) and the North Island of New Zealand (N = 46). Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability.

Predictor variable	Beta	p
Germany		
Capillaria spp.	-0.373	0.001
Species richness	0.232	0.028
C. aerophila	0.213	0.047
North Island		
Capillaria spp.	-0.374	0.011

Capillaria spp. showed the strongest significant correlation with the condition factor for adults from Germany and from the North Island. Both correlations were negative, indicating that increasing *Capillaria* numbers reduce the health status in adult hedgehogs. *C. aerophila* numbers as well as species richness correlate positively with the condition factor for German hedgehogs.

There was no significant model for adult hedgehogs from the UK (N = 15) or the South Island (N = 70), although I found a strong trend towards negative correlations between the w/l ratio and the number of *Capillaria* spp. for British hedgehogs (r = -0.434, p = 0.053). A higher sample size might have strengthened this effect and brought it into line with that from Germany. If I compare the different investigation sites, *Capillaria* spp. have a strong, negative effect on condition of adult hedgehogs.

I found no significant models for juvenile hedgehogs from Germany (N = 38) on either New Zealand island (South Island N = 30, North Island N = 20), but I did for juveniles from the UK ($F_{1, 12}$ = 8.796, p = 0.012, adjusted R^2 = 0.375). The significant predictor variable was *B. erinaceus* numbers (Beta = 0.65, p = 0.012).

These results indicate that increasing trematode numbers also increase with the condition factor of juvenile hedgehogs from the UK. Those results did not occur in other countries,

although trematodes also occurred there. Thus, the results from the UK could be interpreted as false effects, due to low sample size.

Kidney:

For kidney weight, I used the weight of both single kidneys, including the suprarenal glands. I found significant models for adult hedgehogs from Germany ($F_{1, 92} = 8.557$, $p = 0.004$, adjusted $R^2 = 0.075$), from the South Island of New Zealand ($F_{1, 68} = 38.149$, $p = 0.001$, adjusted $R^2 = 0.35$) and the North Island ($F_{1, 42} = 18.31$, $p= 0.001$, adjusted $R^2 = 0.287$). The significant predictor variables for these models are presented in table 53. No significant model was found for adults from the UK.

Table 53: Significant predictor variables for the multiple regression analysis of the kidney weight (g) and the parasite numbers, total tick weight (g) and condition factor for adult hedgehogs from Germany (N = 94), the South Island (N = 70) and the North Island of New Zealand (N = 44). Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability, w/l = weight (g)/length (cm).

Predictor variable	Beta	p
Germany		
w/l	0.292	0.004
South Island		
Condition factor	0.599	0.001
North Island		
Condition factor	0.551	0.001

In all investigation areas, except for the UK, the condition factor of adults correlated positively with the kidney weight, indicating that the kidney depends strongly on the body weight and therefore the condition of the hedgehog.

There was also a significant model for juvenile hedgehogs from Germany ($F_{2, 35} = 8.099$, $p = 0.001$, adjusted $R^2 = 0.277$). The significant predictor variables were *Capillaria* spp. (Beta = 0.468, $p = 0.002$) and the condition factor (Beta = 0.375, $p = 0.012$). This indicates that the kidney weight increases with body weight. This fits with the results from the adult hedgehogs. No significant models were found for the UK and New Zealand.

Liver:

For liver weight of adult hedgehogs I found significant models for the UK ($F_{2, 12} = 15.32$, $p = 0.001$, adjusted $R^2 = 0.672$), the South Island ($F_{1, 68} = 30.032$, $p = 0.001$, adjusted $R^2 = 0.296$) and the North Island ($F_{3, 42} = 10.525$, $p = 0.001$, adjusted $R^2 = 0.388$). The significant

predictor variables for these models are presented in table 54. No significant model was found for adult hedgehogs from Germany.

Table 54: Significant predictor variables for the multiple regression analysis of the liver weight (g) and the parasite numbers, total tick weight (g) and condition factor for adult hedgehogs from the UK (N = 15), the South Island (N = 70) and the North Island of New Zealand (N = 46). Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability.

Predictor variable	Beta	p
UK		
C. aerophila	-0.789	0.001
B. erinacei	-0.499	0.008
South Island		
Condition factor	0.553	0.001
North Island		
Condition factor	0.634	0.001
C. striatum	0.306	0.014
Capillaria spp.	0.289	0.029

The models obviously differ from each other. In the UK I found negative correlations with *C. aerophila* and *B. erinacei*. Those could not be found in New Zealand. Here, I found positive correlations with the condition factor on both islands, indicating that liver weight depends on body weight. I also found positive correlations with lungworms and intestinal *Capillaria* spp. on the North Island, indicating an increase in liver weight with increasing parasite numbers.
Significant models were found for juvenile hedgehogs from Germany ($F_{1, 35} = 13.225$, $p = 0.001$, adjusted $R^2 = 0.254$), the UK ($F_{1, 12} = 5.035$, $p = 0.044$, adjusted $R^2 = 0.237$) and the North Island ($F_{1, 18} = 7.551$, $p = 0.013$, adjusted $R^2 = 0.256$). The significant predictor variables are presented in table 55. No significant model was found for the South Island.

Table 55: Significant predictor variables for the multiple regression analysis of the liver weight (g) and the parasite numbers, total tick weight (g) and condition factor for juvenile hedgehogs from Germany (N = 37), the UK (N = 14) and the North Island of New Zealand (N = 20). Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability.

Predictor variable	Beta	p
Germany		
Condition factor	0.524	0.001
UK		
Condition factor	0.554	0.044
North Island		
Species richness	0.544	0.013

The condition factor correlated positively with the liver weight from juvenile hedgehogs in Germany and the UK. This was also observed for adults of New Zealand, but not from adults in Europe .The liver weight of juvenile animals from the North Island correlated positively with the species richness.

Lung:

For lung weight the only significant model I found was for adult hedgehogs from Germany ($F_{1, 91}$ = 9.216, p = 0.003, adjusted R^2 = 0.082). The significant predictor variable was *P. cylindraceus* numbers (Beta = 0.303, p = 0.003). No such trend could be observed in the other investigation areas.

I found significant models for juvenile hedgehogs from Germany ($F_{2, 35}$ = 7.228, p = 0.002, adjusted R^2 = 0.252), the UK ($F_{3, 10}$ = 18.222, p = 0.001, adjusted R^2 = 0.799) and for the North Island ($F_{1, 18}$ = 45.189, p = 0.001, adjusted R^2 = 0.699). The significant predictor variables are presented in table 56. No significant model was found for the South Island.

Table 56: Significant predictor variables for the multiple regression analysis of the lung weight (g) and the parasite numbers, total tick weight (g) and condition factor for juvenile hedgehogs from Germany (N = 38), the UK (N = 14) and the North Island of New Zealand (N = 20). Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability.

Predictor variable	Beta	p
Germany		
Condition factor	0.484	0.002
Capillaria spp.	0.308	0.038
UK		
Species richness	0.593	0.001
Condition factor	0.410	0.008
Total tick weight (g)	0.385	0.016
North Island		
C. striatum	0.846	0.001

Both in Germany and the UK the lung weight correlated positively with the condition factor. For juvenile hedgehogs from Germany the intestinal *Capillaria* spp. numbers correlated positively with the lung weight. In the UK it was species richness and the total tick weight and on the North Island lungworm numbers.

Spleen:

There were significant models for adult hedgehogs from Germany ($F_{2, 88} = 19.021$, $p = 0.001$, adjusted $R^2 = 0.286$), the UK ($F_{1, 13} = 10.476$, $p = 0.006$, adjusted $R^2 = 0.404$) and the South Island ($F_{1, 67} = 11.587$, $p = 0.001$, adjusted $R^2 = 0.135$). The significant predictor variables are presented in table 57. No significant model was found for the North Island.

Table 57: Significant predictor variables for the multiple regression analysis of the spleen weight (g) and the parasite numbers, total tick weight (g) and condition factor for adult hedgehogs from Germany (N = 91), the UK (N = 15) and the South Island of New Zealand (N = 69). Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability, w/l = body weight (g)/body length (cm).

Predictor variable	Beta	p
Germany		
w/l	0.399	0.001
P. cylindraceus	0.361	0.001
UK		
C. striatum	-0.668	0.006
South Island		
Condition factor	0.384	0.001

Both in Germany and on the South Island I found positive correlations between spleen weight and condition factor. Although it was not included into a model, I found a significant positive correlation for spleen weight and condition factor also on the North Island ($r = 0.298$, $p = 0.026$). This indicates that the spleen weight depends on the hedgehog's body weight. An influence occurred only in the European countries. In Germany *P. cylindraceus* numbers correlated positively with spleen weight, while in the UK lungworm numbers correlated negatively.

I found significant models for juvenile hedgehogs from Germany ($F_{1, 35} = 5.309$, $p = 0.027$, adjusted $R^2 = 0.107$) and the North Island ($F_{1, 18} = 5.829$, $p = 0.027$, adjusted $R^2 = 0.203$). For Germany the significant predictor variable was total tick weight (Beta = 0.363, $p = 0.027$) and for the North Island it was species richness (Beta = 0.495, $p = 0.027$). No significant models were found for the UK and the South Island.

Heart:

For heart weight I found significant models for adult hedgehogs from Germany ($F_{1, 91} = 4.031$, $p = 0.048$, adjusted $R^2 = 0.042$) and the UK ($F_{1, 13} = 5{,}183$, $p = 0.04$, adjusted $R^2 = 0.230$). For Germany the significant predictor variable was *C. aerophila* (Beta = -0.206, p = 0.048), for the UK species richness (Beta = -0.543, p = 0.04). No significant models were found for New Zealand.

I found significant models for juvenile hedgehogs from all investigation areas. In Germany ($F_{1, 36} = 7.735$, $p = 0.009$, adjusted $R^2 = 0.154$) the predictor variable was *Capillaria* spp. (Beta = 0.421, p = 0.009), in the UK ($F_{1, 12} = 10.416$, $p = 0.007$, adjusted $R^2 = 0.42$) it was the condition factor (Beta = 0.682, p = 0.009), on the South Island ($F_{1, 28} = 5.75$, $p = 0.023$, adjusted $R^2 = 0.141$) and on the North Island ($F_{1, 18} = 37.836$, $p = 0.001$, adjusted $R^2 = 0.66$) the predictor variable was the lungworm *C. striatum* (South Island Beta = 0.413, p = 0.023; North Island Beta = 0.823, p = 0.001).

1.2.3 Sexual Organs

In case of the sexual organs of hedgehogs I tested for differences between the different seasons (see chapter IV.1.2.1) with a Kruskal-Wallis and a Mann-Whitney U-test for animals from Germany before conducting the multiple regressions analysis.

For adults the testicle weight (p = 0.046) and the prostate weight (p = 0.023) differed significantly between seasons. Testicle weight was higher in season 2 compared to season 1 (p = 0.073) and season 3 (p = 0.021). Season 1 did not differ from season 3 (p = 0.773). Although season 1 did not differ significantly from season 2 there is a trend with animals from season 2 having larger testicles. Therefore, I pooled season 1 and 3 and treated season 2 separately for the multiple regression analysis. Similar results could be found for the prostate. Season 1 and season 3 did not differ from each other (p = 0.551). Season 2 and season 3 differed significantly (p = 0.008) and season 2 was also not different from season 1 (p = 0.157). But since I had only two animals to compare with in season 1, I pooled season 1 and 3 and treated season 2 separately, as for testicle weight.

The uterus (p = 0.028) and penis weight (p = 0.009) of juveniles differed between seasons, with animals from season 3 showing lower organ weights than those from season 1 (uterus p = 0.032, penis p = 0.012) and season 2 (uterus p = 0.052, penis p = 0.026). Season 1 and season 2 did not differ from each other (uterus p = 0.564, penis p = 0.297). Because of this I pooled the animals from season 1 and 2 for the multiple regression analysis for uterus and penis weight and treated season 3 separately.

Uterus and ovaries:

For the weight of the female sexual organs I used the weight of the uterus and the associated ovaries.

I found significant models for adult hedgehogs from Germany ($F_{1, 49} = 7.682$, $p = 0.008$, adjusted $R^2 = 0.118$), from the South Island ($F_{1, 14} = 5.615$, $p= 0.033$, adjusted $R^2 = 0.235$) and the North Island ($F_{1, 20} = 6.7$, $p= 0.018$, adjusted $R^2 = 0.228$). In all cases the w/l ratio or the condition factor were the significant predictor variables (Germany Beta = 0.368, $p = 0.008$; South Island Beta = 0.535, $p = 0.033$, North Island Beta = 0.501, $p = 0.018$). This indicates that the uterus weight depends on the body weight of the female hedgehog. I found no significant model for hedgehogs from the UK. But with a sample size of five females this would not be representative anyway.

For juveniles I only found one significant model from the North Island ($F_{1, 2} = 0.004$, $p = 0.004$, adjusted $R^2 = 0.989$) with the significant predictor variable being *Capillaria* spp. (Beta = 0.996, $p = 0.004$). Since I only had four females in this group, it is not possible to make a robust conclusion. Looking at the uterus weights from Germany, without separating data into seasons, and at New Zealand without separating into islands, I did not find any significant models, so I suggest that the results from the North Island are based on false effects.

Penis weight:

For penis weight I found significant models for adult hedgehogs from Germany ($F_{4, 38}$= 9.742, p= 0.001, adjusted R^2= 0.454), the UK ($F_{2, 7}$= 13.583, p= 0.004, adjusted R^2= 0.737) and the South Island ($F_{1, 52}$= 4.934, p= 0.031, adjusted R^2= 0.069). The significant predictor variables are shown in table 58. No significant model was found for the North Island.

Table 58: Significant predictor variables for the multiple regression analysis of the penis weight (g) and the parasite numbers, total tick weight (g) and condition factor for adult hedgehogs from Germany (N = 43), the UK (N = 10) and the South Island of New Zealand (N = 54). Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability, w/l = body weight (g)/body length (cm).

Predictor variable	Beta	p
Germany		
w/l	0.368	0.005
P. cylindraceus	0.298	0.013
Capillaria spp.	-0.371	0.006
Total tick weight (g)	0.272	0.027
UK		
C. aerophila	-0.743	0.003
Species richness	-0.440	0.037
South Island		
Condition factor	0.294	0.031

There seems to be no clear trend, except maybe for the condition factor, which correlates positively both in Germany and on the South Island and indicates the connection between penis weight and body weight.

I found significant models for German juvenile hedgehogs from season 1 and 2 ($F_{1, 6}$ = 8.123, p = 0.029, adjusted R^2 = 0.504), season 3 ($F_{1, 11}$ = 5.726, p = 0.036, adjusted R^2 = 0.283) and for all seasons pooled ($F_{1, 19}$ = 24.127, p = 0.001, adjusted R^2 = 0.536). Additionally I found significant models for the South Island ($F_{1, 14}$ = 191,665, p = 0.001, R^2 = 0.927) and the North Island ($F_{2, 11}$ = 15.09, p = 0.001, adjusted R^2 = 0.684). The significant predictor variables are given in table 59. No significant model was found for the UK.

Table 59: Significant predictor variables for the multiple regression analysis of the penis weight (g) and the parasite numbers, total tick weight (g) and condition factor for juvenile hedgehogs from Germany season 1/2 (N = 8), season 3 (N = 13), pooled seasons (N = 21), the South Island (N = 16) and the North Island (N = 14) of New Zealand. Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability.

Predictor variable	Beta	p
Germany season 1/2		
Total tick weight (g)	0.758	0.029
Germany season 3		
Condition factor	0.585	0.036
Germany all seasons		
Total tick weight (g)	0.748	0.001
South Island		
C. striatum	0.965	0.001
North Island		
Capillaria spp.	0.507	0.025
C. striatum	0.448	0.043

There seems to be no certain trend apparent in the investigation areas, but it is noticeable that the parasite species observed (ticks, lungworms, *Capillaria* spp.) all correlate positively with the penis weight.

Testicles:

For German adult hedgehogs I found significant models for season 1 and 3 ($F_{2, 26} = 9.954$, p = 0.001, adjusted $R^2 = 0.39$), season 2 ($F_{3, 8} = 69.906$, p = 0.001, adjusted $R^2 = 0.949$) and for all seasons pooled ($F_{2, 38} = 32.658$, p = 0.001, adjusted $R^2 = 0.613$). I also found significant models for the UK ($F_{2, 7} = 10.237$, p = 0.008, adjusted $R^2 = 0.672$) and the South Island ($F_{1, 52} = 5.785$, p = 0.02, adjusted $R^2 = 0.083$). The significant predictor variables are shown in table 60. No significant models were found for the North Island.

Table 60: Significant predictor variables for the multiple regression analysis of the testicle weight (g) and the parasite numbers, total tick weight (g) and condition factor for adult hedgehogs from Germany of season 1/3 (N = 29), season 2 (N = 12), pooled seasons (N = 41), the UK (N = 10) and the South Island of New Zealand (N = 54). Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability, w/l = body weight (g)/body length (cm).

Predictor variable	Beta	p
Germany season 1/3		
w/l	0.446	0.01
Capillaria spp.	-0.345	0.04
Germany season 2		
Total tick weight (g)	0.975	0.001
w/l	0.752	0.001
C. aerophila	-0.434	0.004
Germany all seasons		
Total tick weight (g)	0.621	0.001
w/l	0.531	0.001
UK		
Species richness	-0.740	0.006
w/l	0.505	0.033
South Island		
Condition factor	0.316	0.02

The only connection between the three investigation areas is the positive correlation of testicle weight and condition factor. Endoparasites and species richness have a negative effect on testicle weight, while ticks have a positive one.

For juvenile hedgehogs I found significant models from Germany ($F_{1, 18} = 16.098$, p = 0.001, adjusted R^2 = 0.443) with species richness being the significant predictor variable (Beta = 0.687, p = 0.001), the South Island ($F_{1, 14} = 322.319$, p = 0.001, adjusted $R^2 = 0.955$) with *C. striatum* being the significant predictor variable (Beta = 0.979, p = 0.001) and the North Island ($F_{1, 11} = 37{,}88$, p = 0.001, adjusted $R^2 = 0.755$) with *Capillaria* spp. being the significant predictor variable (Beta = 0.88, p = 0.001). In all cases I found increasing testicle weights with increasing parasite numbers.

Seminal vesicles:

The seminal vesicles of juveniles are poorly developed, and thus it is difficult to detect them during a dissection. Therefore I only conducted multiple regression analyses for adult hedgehogs.

I found significant models for Germany ($F_{1, 32} = 17.178$, $p = 0.001$, adjusted $R^2 = 0.329$), the UK ($F_{2, 6} = 14.169$, $p = 0.005$, adjusted $R^2 = 0.767$), the South Island ($F_{1, 50} = 7.13$, $p = 0.01$, adjusted $R^2 = 0.107$) and the North Island ($F_{1, 21} = 18.592$, $p = 0.001$, adjusted $R^2 = 0.444$). The significant predictor variables are presented in table 61.

Table 61: Significant predictor variables for the multiple regression analysis of the seminal vesicle weight (g) and the parasite numbers, total tick weight (g) and condition factor for adult hedgehogs from Germany (N = 34), the UK (N = 9), the South Island (N = 52) and the North Island of New Zealand (N = 23). Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability, w/l = body weight (g)/body length (cm).

Predictor variable	Beta	p
Germany season		
w/l	0.591	0.001
UK		
Species richness	-0.785	0.004
Total tick weight (g)	0.532	0.021
South Island		
Condition factor	0.353	0.01
North Island		
Condition factor	0.685	0.001

In all investigation areas, except for the UK, the seminal vesicles correlated positively with the condition factor of the hedgehog, indicating the weight of the seminal vesicles depend on the body weight of the hedgehog. In the UK this was not the case, perhaps because of the low sample size.

Prostate:

Like for the seminal vesicles, I only conducted a multiple regression analysis for adult hedgehogs, since the prostate is poorly developed in immature animals.

For Germany I found significant models for season 1 and 3 ($F_{1, 15} = 7.387$, $p = 0.016$, adjusted $R^2 = 0.285$), season 2 ($F_{2, 6} = 15.142$, $p = 0.005$, adjusted $R^2 = 0.78$) and for pooled seasons ($F_{1, 24} = 7.68$, $p = 0.011$, adjusted $R^2 = 0.211$). I also found significant models for the South Island ($F_{3, 47} = 11.596$, $p = 0.001$, adjusted $R^2 = 0.389$) and the North Island ($F_{1, 19} = 13.341$,

p = 0.002, adjusted R^2 = 0.382). The significant predictor variables are shown in table 62. Because of the low sample size I did not conduct a multiple regression analysis for the UK.

Table 62: Significant predictor variables for the multiple regression analysis of the prostate weight (g) and the parasite numbers, total tick weight (g) and condition factor for adult hedgehogs from Germany of season 1/3 (N = 17), season 2 (N = 9), pooled seasons (N = 41), the South Island (N = 51) and the North Island of New Zealand (N = 21). Hedgehog sexes, collection dates and catchment areas are pooled. Beta = standardized regression coefficient, p = probability, w/l = body weight (g)/body length (cm).

Predictor variable	Beta	p
Germany season 1/3		
w/l	0.574	0.016
Germany season 2		
P. cylindraceus	0.642	0.009
B. erinacei	-0.573	0.014
Germany all seasons		
w/l	0.492	0.011
South Island		
Condition factor	0.496	0.001
C. striatum	-0.277	0.016
Capillaria spp.	0.236	0.039
North Island		
Condition factor	0.642	0.002

2. Discussion

Most studies on the prevalence and abundance of parasite infections in European hedgehogs were conducted in the late 1970s and 1980s (see e.g. TIMME 1980, BARUTZKI et al. 1984, 1987, MAJEED et al. 1989). This study is therefore the most recent outlining the infection of European hedgehogs in three different investigation areas, Germany, the UK and New Zealand. In fact, this is the first study with detailed results on the macroparasite fauna of *E. erinaceus* in its novel range of New Zealand. I will discuss the results from the European hedgehog populations from my study with results from former studies and outline the differences in the macroparasite fauna between the native and the novel range.

This is also the first study to examine the influence of parasites on body condition and organ size as fitness parameters in order to determine the effect of parasites on individual animals as well as potentially on populations of European hedgehogs.

2.1 Parasite distribution

As for tick infestation in the experimental population, I could not find any trend for sex-biased parasitism in the dissected hedgehogs, independently of parasite species or country investigated. This could result from my European samples being biased in the direction of sick animals, which are more likely to be parasitized than healthy animals thus masking the influence of certain sex differences described in chapter III.2.2.1. However, no sex-biased parasitism occurred in New Zealand too, where hedgehog samples were randomly collected. This indicates that the European results are probably not biased and that sex-biased parasitism in hedgehogs does not occur naturally.

I compared the prevalence of parasites from my European samples with results from other authors. In most of these studies egg and larval counts from faecal samples were used to determine parasite prevalence. DÖPKE (2002) took faecal samples from dead animals, but only from the colon and not from the whole intestine; therefore infections with adults from *Capillaria* spp. or *B. erinaceus* might have not been detected.

The only study I could compare tick prevalences with was carried out by EGLI (2004) from Switzerland, who did her research on living animals from rural, suburban and urban areas. With 58.5%, she found slightly higher prevalences of *I. hexagonus* than I did with 53.3% in Germany and 40% in the UK. She found prevalences for *I. ricinus* of 11.1% which are lower than the prevalences I found in Germany (23.4%) but higher than those from the UK (6.7%). The abundance and population density of ticks depends on habitat and also on available host

species, thus, the infestation rate of the hedgehogs changes with location. It is therefore not possible to generalize infestation rates for certain parasites, but both my results from Germany and the UK seem to reflect natural conditions and suggest that the two countries differ in tick community structure for hedgehogs.

Flea infestation prevalences were much higher in the study from EGLI (2004) (43.7%) and from VISSER et al. (2001) (84.2%) than in my study (Germany = 27%, UK = 0%). If dead hedgehogs were not frozen immediately after their death, it is likely that a high number of fleas left the host before I was able to collect them, while for example feeding ticks stay longer on the dead hosts before they detach. This makes it difficult to compare results from dissections with results from living animals. I did not find any fleas on animals from the UK, although it is a common parasite there (BAKER and MULCAHY 1986), and studies from Germany suggest that every hedgehog is, to a greater or lesser extent, infested with fleas (BECK and CLARK 1997, BECK et al. 2005). This indicates that flea prevalences from dissected hedgehogs are likely to turn out to be smaller than under natural conditions.

Crenosoma striatum and *Capillaria aerophila* prevalences were comparable with those of other authors (TIMME 1980, BARUTZKI et al. 1984, 1987, BAUER and STOYE 1984, MAJEED et al. 1989, EPE et al. 1993, DÖPKE 2002, EGLI 2004, PANTCHEV et al. 2005). The prevalences of intestinal *Capillaria* spp. were higher in my study (Germany= 81.8%, UK= 90%) compared to findings from other studies. In most of these studies faecal samples were examined and it is not clear whether the authors took collective samples from an animal or only a single sample. Faecal egg counts sometimes have unknown or variable levels of specificity and sensitivity (WILSON et al. 2006) and collective samples are important to ensure whether an infection is present or not, especially since *Capillaria* eggs are not shed daily. TIMME's study (1980) on hedgehogs which died because of disease was the only one I could compare with the results from my study. He reported prevalences only half as high as mine (40.4%). This is the same for *B. erinaceus*, for which I detected prevalences of 34.3% in Germany and 53.3% in the UK. TIMME (1980) only measured prevalences of 0.6%, and the highest prevalences found by another author were 10.4% (EGLI 2004) from hedgehog faecal samples from Switzerland. The occurrence of the trematode seems to vary significantly between investigation areas. SCHÜTZE (1980) detected prevalences of 80% around Berlin, 20% in Bremen and only 1% in Central Hesse (reports from hedgehogs treated in veterinary practices). In my study, a similar pattern occurred. Prevalences of animals from Munich were significantly higher than those of the catchment areas of Frankfurt. This indicates that there are clear regional differences in *Brachylaemus* distribution.

My work on macroparasite infections is the most recent in this area, and my results show explicitly that parasites are very common in hedgehog populations and therefore potentially play an important role in population dynamics of their hosts.

To my knowledge, this is the first study which describes infections with *P. cylindraceus* from Germany, an intestinal parasite of passerine birds, which sporadically occurs in the intestinal tract of mammals (see SKUBALLA et al. 2010). Occasionally, findings from European hedgehogs have been reported, for example by EDELENYI and SZABO (1963) from Hungary and KEYMER et al. (1991) from the UK. Although the hedgehog acts as an ecological sink for this acanthocephalan, which means the parasite cannot reproduce inside the animal, or at the most a paratenic host, it is assumed that it causes diarrhoea, abdominal swelling, peritonitis and sometimes even mortality (SKUBALLA et al. 2010). Reports from wildlife rescue centres from the UK indicate that infections in juvenile animals occur more often than in adult hedgehogs (SKUBALLA et al. 2010). This can be due to differences in dietary preferences. Hedgehogs are very flexible concerning their diet, which mostly depends on prey availability (REEVE 1994), but also on age. Young hedgehogs are more prone to consume unpalatable food like woodlice, the intermediate hosts for *P. cylindraceus*, than adults (DIMELOW 1963), which increases their risk of becoming infected. REEVE (1994) published a list of prey eaten by hedgehogs of different ages, which showed that mainly suburban hedgehogs younger than one year had the highest mean numbers of woodlice per gut as prey.

This is also the first study which describes the macroparasite community of hedgehogs from New Zealand in detail. The European hedgehog was first introduced from Great Britain to Canterbury on the South Island of New Zealand in 1869 (BROCKIE 1975). The fate of this first pair remains unknown. The next introductions were made between 1871 and 1892. In 1910 the first hedgehogs were introduced to the North Island. The natural spread of hedgehogs in New Zealand was slow, but due to human transfers they extended from human settlements to surrounding country districts (BROCKIE 1975).

Although most potentially invasive species fail in colonizing their new habitats, those which succeed in establishing may achieve high population densities. For example populations of the bivalve mollusc *Potamocorbula amurensis*, native to China, Japan and Korea, increased and spread rapidly only two years after its invasion in the San Francisco Bay (CARLTON et al. 1990, NICHOLS et al. 1990). The North American racoon (*Procyon lotor*) was successfully introduced to Germany in 1934 and since then its populations have increased rapidly with up to 100 animals/100ha in the city area of Bad Karlshafen (Northern Hesse). This is comparable to densities of urban populations in North America (HOHMANN et al. 2002).

The enhanced performance of an invasive species in its new environment can be explained by three ecological factors: (i) lack of competition, (ii) better environmental conditions and food resources, and (iii) absence of natural enemies and parasites (TORCHIN et al. 2001), also referred to as the enemy release (ERH) or parasite release hypothesis (PRH). These hypotheses propose that invasive species lose their parasites during the process of invasion, leading to higher demographic success (TORCHIN et al. 2003, PRENTER et al. 2004). In a study from 2003, TORCHIN et al. compared parasite infections of 26 host species of various taxa in their new and their native ranges. They reported an average of 16 parasite species infecting native populations. Of these, only an average of three parasite species accompanied the host into its introduced range.

In my study I found parasite species in New Zealand hedgehogs, which also occurred in European samples, such as *C. striatum*, *C. aerophila*, *Capillaria* spp. and *P. cylindraceus*, but prevalences differed significantly, also between both New Zealand islands. The hedgehog flea *A. erinacei*, the ticks *I. hexagonus* and *I. ricinus* and the trematode *B. erinacei* were lacking, although I found another trematode species infecting one hedgehog from the North Island and in addition one animal was infected with an acanthocephalan which was detected the first time in the European hedgehog in this country (SMALES et al. 2010).

Fleas occurred only on two animals on the North Island, but all specimens were cat fleas (*Ctenocephalides felis felis*) and not *A. erinacei*. The cat flea *C. felis felis* was able to establish in New Zealand and its occurrence is reported by various authors (see GUZMAN 1984, TENQUIST and CHARLESTON 2001, KELLY et al. 2005) and the infestation of hedgehogs with cat fleas is also known (BROCKIE 1958 cited from TENQUIST and CHARLESTON 2001). All hedgehogs with fleas originated from the catchment area of Auckland, were the contact between a hedgehog and a cat is more likely, than in more rural areas.

Haemaphysalis longicornis, the tick species which I sampled from one hedgehog and which can usually be found on cattle, has also been reported previously from hedgehogs and other mammals in New Zealand (TENQUIST and CHARLESTON 2001).

Plagiorhynchus cylindraceus was only found on hedgehogs from the North Island while *C. aerophila* was only found in animals from the South Island. It is obvious that the occurrence of certain parasite species depends on the area from which the host originated (ZETLMEISL et al. in press). The hedgehog populations from the two New Zealand islands are considered to be independent from each other, since they mostly originate from spatially and temporarily separated introduced animals, and, although the populations from the Manawatu region on the

North Island originated from animals transferred from the South Island (PARKES 1975), the remainder of both populations probably never mixed.

Most of the parasites from hedgehogs are very host specific and it is not known whether they have adequate hosts beside the hedgehog, or suitable living conditions in New Zealand. Thus, the actual parasitation of the animals depends: (i) on the occurrence of other suitable definitive hosts, (ii) the susceptibility to infection with new parasites, and (iii) on the parasite fauna which was brought with the introduced hedgehogs from Europe or Great Britain, respectively, as well as (iv) on their success of establishing in their new environment. CRUMP et al. (2001) suggest that several factors have limited the range of zoonoses and parasites to New Zealand. This includes the small number of animal sources transported, while in case of livestock only healthy animals were chosen for transport. So the extended voyage to New Zealand during early European settlement was a limiting factor for parasites and pathogens. Only those that could persistently circulate within the crowded transport conditions or which were able to persist within their animal hosts could be introduced (CRUMP et al. 2001). Although nothing is known of the parasites brought with hedgehogs to New Zealand, it is likely that ticks and fleas were not introduced because: (i) only uninfected animals were transported, (ii) the parasites were not able to complete their developmental cycle during the ship journey, or (iii) because of the low host number in the new environment or certain abiotic factors the ectoparasites were not able to establish in their new habitat.

Ixodes hexagonus seems to mate only within the nest of its host and male ticks are only occasionally found on hedgehogs (PFÄFFLE et al. unpublished). A possible lack of mates to fertilize engorged females might also have lowered the chance of these ectoparasites to establish in its new range.

In contrast to fleas and ticks, the specific hedgehog mite *Caparinia tripilis* established successfully in New Zealand and parasitizes hedgehogs on both the North and the South Island (SWEATMAN 1962, SPAIN and LUXTON 1971, GORTON 1998). Additionally, it is associated, both in Europe and New Zealand, with the skin fungus *Trichophyton mentagrophytes* var. *erinacei* which can also infect humans (SWEATMAN 1962, QUAIFE 1966, SMITH 1968b). The life cycles of other mite species which belong, like *C. tripilis*, to the family Psoroptidae occur completely on their host. All life stages of *Otodectes cynotis* develop within the ear canals of carnivores (OTRANTO et al. 2004) and *Psorptes ovis* in the ear canals of sheep (SANDERS et al. 2000). The developmental cycle of *C. tripilis* was not investigated yet, but it is likely that its whole development also occurs on the hedgehog and

does not involve other habitats. This would have facilitated the establishment of this mite in New Zealand.

The *Capillaria* species found in the hedgehog are not strictly host specific. *C. aerophila* does not only parasitize the lungs of hedgehogs, but is also a common parasite of red foxes *V. vulpes* (SMITH 1978, RICHARDS et al. 1995, SRÉTER et al. 2003) and has also been detected in other carnivorous mammals such as cats *Felis catus* (VANPARIJS and THIENPONT 1973, NOLAN and SMITH 1995), bobcats *Lynx rufus* (STONE and PENCE 1978), dogs *Canis lupus familiaris* (SHAW et al. 1996), martens *Martes* spp. (BUTTERWORTH and BEVERLEY-BURTON 1980) and racoons *P. lotor* (RICHARDSON et al. 1992). Infections in cats have also been reported from New Zealand (MCKENNA 1997, 2009). In addition, *C. erinacei* from the intestine of hedgehogs have been detected in cats, dogs and pigs from New Zealand (COLLINS 1973, MCKENNA 1997, 2009).

The longevity of adult *Capillaria* spp. inside their hosts is about 10-11 months (ECKERT 2000), and the eggs are extremely resistant and persistent due to their stable and sticky envelope (SAUPE and SCHICHT-TINBERGEN 2008). These factors and the independence from intermediate hosts might have facilitated the successful establishment of various *Capillaria* species from hedgehogs in New Zealand.

The longevity of a *C. striatum* infection in hedgehogs has, to my knowledge, not yet been investigated. But I and other authors detected the parasite in the lungs of hedgehogs from New Zealand (BROCKIE 1958 cited from MCKENNA 1997, 2009, GORTON 1998), indicating that the parasite survived the journey of the early European settlement to New Zealand. Furthermore, known suitable intermediate hosts like the grove or brown-lipped snail *Cepaea nemoralis* (CAIN and SHEPPARD 1953) or the European amber snail *Succinea putris* (syn. *Helix putris*) (POWELL 1933) were successfully introduced to New Zealand which enables the lungworm to go through its developmental cycle.

Only one hedgehog on the North Island was infected with trematodes. Unfortunately, it was not possible to determine the species or genus, but they differed significantly from *B. erinacei* in morphology. Additionally, *B. erinacei*, although using *Succinea* species amongst others as intermediate hosts, has never been reported from New Zealand previously and therefore has likely never been introduced or was not able to establish. In contrast, other trematode species like *Agadistomum pusillum*, *Eupryphium melis* and *Harmostomum* spp. have been detected in New Zealand hedgehogs (SMITH 1964, 1968a). One of these species might have infected the hedgehog I found, but since it was not possible to determine the species morphologically this remains unclear.

As mentioned above, *P. cylindraceus* is a parasite of passerine birds and avian species like the European starling (*Sturnus vulgaris*), the black bird (*Turdus merula*), the Australian magpie (*Gymnorhina tibicens*) and the American robin (*Turdus migratorius*). These have played important roles in the establishment of this parasite in its novel ranges of East Asia, North America, South Africa and Australia (SKUBALLA et al. 2010). Whether it was introduced to New Zealand via its avian hosts or isopod intermediate hosts remain unclear. In addition to *P. cylindraceus*, I also found a late stage acanthella of a putative species of *Polymorphus* (SMALES et al. 2010), which represents rather an occasional, than a common infection, since these acanthocephalans also predominantly infect birds.

2.2 Comparison of investigation areas

Hedgehogs are a pest organism in New Zealand where they reach high population densities (PARKES 1975, COWAN and TYNDALE-BISCOE 1997). As in Europe, they have few natural predators (http://www.invasivespecies.net/database/species/ecology.asp?si=176&fr=1&sts=, 19.8.2010). A comparison of parasite prevalences, abundances and species richness between all investigated areas supports the PRH (parasite release hypothesis). Species richness of both European countries did not differ significantly for juveniles, adults and pooled ages. The mean species richness was about 3-3.5 species/animal. In contrast, the mean species richness on the North Island was only about 1 and on the South Island, with 0.5, was even lower. On average the animals from New Zealand were less frequently parasitized than the native populations in Europe. Hedgehogs from Europe showed significantly higher prevalences and abundances of the investigated parasite species than New Zealand hedgehogs. This fact makes it possible to investigate the potential influence of parasites on fitness related parameters of hedgehogs using the New Zealand populations, as a control group compared to the European populations.

One of the most common features of macroparasites is their tendency to occur aggregated or over-dispersed (POULIN 1993), creating a negative binominal distribution within their host population. SHAW et al. (1998) analysed 49 different wildlife host-macroparasite systems, from which 90% fitted this distribution. The degree of parasite aggregation within the host population is of great importance. Macroparasites, for example, are more likely to regulate their host populations in a stable way when a large proportion of the parasite population is concentrated in a small proportion of the host population (TOMPKINS et al. 2006). Looking at the distribution of the investigated parasites within the hedgehog populations from Europe and New Zealand, over-dispersion for the different parasite species is common, and invariably

the case with sufficiently large sample sizes. This means that, although hedgehogs from Europe were biased towards sick and more parasitized animals, my investigated populations reflect natural parasite distributions, and can therefore be used to determine the potential influence of parasites on fitness related parameters. This information can be used as a basis for investigations on the influence of parasites on host population dynamics.

2.3 Parasites and organs

The models resulting from the multiple regression analyses, which I performed to determine the influence or effect of parasites on organ weights and the condition of hedgehogs showed high variances in their outcomes. Therefore, it was difficult to interpret these results and distinguish between real and false effects. Studying parasitic effects in the field but also on dissected animals is always problematic, since the pre-infection condition of the hosts is generally unknown (ARNOTT et al. 2000). My studies were also more observational than experimental, whereby certain effects caused by one or more parasite species could possibly not be detected. Nevertheless, the observations which I made can be supportive for further experimental setups and/or investigations on living animals in the field.

To summarize, for most organs there was no clear pattern of influence of parasites when comparing the different investigation areas. For example, my results showed that the liver weight of adult hedgehogs was positively correlated with the number of *Capillaria* spp. and *C. striatum* on the North Island of New Zealand, while in the UK it was negatively correlated with *C. aerophila* and *B. erinacei*. Spleen weight for adults was positively correlated with the condition factor in Germany and on the South Island and with *Plagiorhynchus* numbers in Germany and negatively correlated with *C. striatum* in the UK.

Juveniles showed also, not clearly definable patterns similarly to adults. Lung weight, for example, was positively correlated with *Capillaria* spp. and condition factor in Germany, with species richness and tick weight in the UK, and with *C. striatum* on the North Island. Heart weight was positively correlated with *Capillaria* spp. in Germany, with the condition factor in the UK and with *C. striatum* on both New Zealand islands. These are just a few examples to show the differences between the investigation areas. Assuming that one parasite species should have the same effect on its host, independently of the area from which the host originates, my findings are interesting and hypotheses can be made as to whether they can be used as facts or just co-effects resulting from other environmental circumstances.

Parasites impose energetic costs upon their hosts and parasite-induced alterations in physiology and metabolism may have life-history consequences (GÉRARD and THÉRON 1997).

For example, the maintenance of immunocompetence and of mounting an immune response to parasite and pathogen infection are nutritionally demanding processes that result in trade-offs among competing energy demands for growth, reproduction, temperature regulation and survival (DERTING and COMPTON 2003).

The spleen plays a major role in pathogen resistance because it is the major site for lymphocyte recirculation and differentiation, supporting immune surveillance, antibody production, formation of parts of the complement system, development of macrophages, phagocytosis and destruction of antigens, immune complexes and parasitized blood cells and production of the tetrapeptide tuftsin which facilitates granulocytosis and immunogenesis (JOHN 1994). In various bird species spleen size is used as a measure of immunological defence and/or capability. BROWN and BOMBERGER-BROWN (2002) compared spleen sizes of individual cliff swallows (*Petrochelidon pyrrhonota*) from parasite-free colonies with those from infested sites and found that spleen size increased whenever the birds were exposed to large numbers of ectoparasites. Infections with nematodes, but not trematodes or cestodes, also lead to increased spleen sizes, suggesting that the avian spleen is important for resisting nematode infection (JOHN 1995, FIGUEROLA et al. 2005). This is supported by lymphocytes accounting for most of the volume of avian spleens, suggesting that the spleen size is a good indicator of the strength of the immune response mounted against parasites and of its capacity to deal with potential infections (MORAND and POULIN 2007). The assumption that avian spleen size and immunocompetence are positively correlated with each other was made despite the lack of knowledge about the physiology of the avian spleen (SMITH and HUNT 2004). Investigations on wild lesser snow geese (*Chen caerulescens caerulescens*) could not support this theory, although even weak associations should have been detected due to the large sample size (SHUTLER et al. 1999).

The effect of parasites on spleen size has also been investigated in several mammal species. Experiments on laboratory and wild mice (*Mus musculus*) conducted by KRISTAN and HAMMOND (2000, 2003) and KRISTAN (2002) revealed that animals suffering from infection with the nematode *Heligmosomoides polygyrus* developed larger spleen masses than uninfected mice. Wild-derived common voles (*Microtus arvalis*) experimentally infected with the rat flea *N. fasciatus* had larger spleen sizes than uninfected animals (DEVEVEY and CHRISTE 2009), and white-toothed shrew (*Crocidura russula*) showed higher spleen masses when suffering from higher nematode intensities (GOÜY DE BELLOCQ et al. 2007b). In contrast, spleen size and parasite load are negatively associated in red deer (VICENTE et al. 2007, CORBIN et al. 2008).

As mentioned previously, the spleen weight of my investigated hedgehogs correlated positively with acanthocephalans (sum of all peritoneal and intestinal *P. cylindraceus*) in adults from Germany and negatively with *C. striatum* in adults from the UK. In juvenile hedgehogs the spleen mass correlated positively with total tick weight in Germany, but negatively with *C. aerophila* in the UK. From these results it is difficult to determine the role of the (mammalian) spleen in parasite infections, suggesting that other factors play a dominant role.

One problem is that the spleen undergoes seasonal variations (JOHN 1994, MØLLER et al. 2003, FÉRNANDEZ-LLARIO et al. 2004). This has also been reported for hedgehogs (BIÖRCK et al. 1956, ELIASSEN 1961), but only little is known about intraspecific variation in spleen size (BROWN and BOMBERGER-BROWN 2002). Other factors like stress or environmental variables such as climatic conditions might have confounding effects on organ size (HARA et al. 1981, MØLLER and ERRITZØE 2003, FÉRNANDEZ-LLARIO et al. 2004). In contrast to avian spleens, those from mammals are important as sites for the production and storage of red blood cells, leading to short-term variations in volume, which is a major factor in spleen mass variation (CORBIN et al. 2008). Therefore, the patterns found in birds might be less striking and more difficult to identify in mammals (NUNN 2002, GOÜY DE BELLOCQ et al. 2007a).

For most mentioned studies, only nematodes, but not cestodes or trematodes, had an effect on spleen size, perhaps because the latter remain largely in the digestive tract and cause less internal trauma. They therefore induce a lower immune reaction by the spleen than nematodes, which often migrate through tissue, potentially causing significant trauma (COWAN et al. 2009). The nematodes from hedgehogs also remain mainly in the intestine or the lung, respectively, and do not penetrate tissues. They might therefore have no significant effect on spleen size.

According to my and other studies it seems that the effect of parasite infection on spleen mass in hedgehogs and other mammals, and the mechanisms involved, are not fully understood and need further investigation.

As for the spleen, I found no consistent patterns of the influence of certain parasites on other organ masses when comparing the different investigation areas, neither for juvenile nor for adult hedgehogs. However, various authors have found such relationships between parasite infection and the mass of other organs.

The liver, an important organ for vertebrate metabolism, is enlarged in female three-spined sticklebacks (*Gasterosteus aculeatus*) infected with the cestode *Schistocephalus solidus*. In sticklebacks, the liver size is usually an indicator of energy reserves which are normally

stored by females before the breeding season. Whether the enlargement of the liver is associated with a response by the host or is caused by parasite manipulation remains unclear (ARNOTT et al. 2000). RALOFF (2007) reports a new not yet identified protozoan parasite, for which heavy infections cause the liver of *Rana* spp. tadpoles to triple its size, and causes the total destruction of liver cells. For mammals, hepatomegaly occurred in deer mice (*Peromyscus maniculatus*) infected with the trematode *Schistosomatium douthitti*, with eggs becoming trapped in the liver (SCHWANZ 2006), and the nematode *Capillaria hepatica*, which is a liver inhabiting parasite and whose eggs remain in the liver until the host dies (MEAGHER 1998). In both cases, the liver tissue is caused direct mechanical damage and the liver enlargement reflects scar tissue formation and regeneration of the organ. Additionally, there are a many studies concerning hepatomegaly in humans caused by different parasite species like *Schistosoma* spp. (STEPHENSON et al. 1985, ZWINGENBERGER et al. 1988) and *Ascaris lumbricoides* (CHA et al. 2002).

When investigating the potential influence of a parasite on the physiology and morphology of its host, the duration of the infection is also an important factor. In the case of oldfield mice (*Peromyscus polionotus*) from the United States infested with the nematode *Trichinella spiralis*, which leads to enlargement of the liver in humans and rats, the infection had no effect on liver size (MEAGHER and DUDEK 2002). The authors suggest that a hepatomegaly occurs predominantly in the acute phase of infection, and that the mice were dissected in an earlier stage, where changes in organ size had not occurred yet.

Changes in kidney size were shown for three-spined sticklebacks infected with *S. solidus*. Males increase their kidney size before the breeding season, since the kidney produces spiggin, a protein glue important for building sticklebacks nests. Infected males showed reduced kidney development, which might reflect an energy deficit caused by the parasite, which in turn might affect the reproductive success of the males (RUSHBROOK and BARBER 2006, RUSHBROOK et al. 2007). House mice (*Mus musculus*) infected with *H. polygyrus* showed an increase in kidney size, but only when they were exposed to low temperatures acting as a co-stressor. Parasitized mice under normal temperatures had the same kidney sizes as unparasitized mice (KRISTAN and HAMMOND 2003).

Also heart and lung size can be affected by parasite infections. Increased lung size in mice infected with *H. polygyrus* was associated with an increased ventilation response that correlates with a greater resting metabolic rate. This occurs during parasite infection (KRISTAN and HAMMOND 2000). Heart size of lesser snow geese is reduced when the animals suffer from high nematode loads (SHUTLER et al. 1999). Although the heart is not directly

associated with the immune status of animals, the cardiac output, and therefore the size of the organ, might be affected by helminth-induced stress. A flea-induced increase in heart size in male common voles (*Microtus arvalis*) was demonstrated by DEVEVEY and CHRISTE (2009). Voles were experimentally infected with the rat flea *N. fasciatus* and the organs removed on the 98th day post infection. The body mass of infected animals was decreased compared to control animals, but they had a relatively larger heart mass than uninfected voles. The authors associated this cardiomegaly with a higher metabolic rate and therefore a higher cardiac output in response to anaemia.

The problem of investigating the effect of parasites on organs in wild animals is that it is not possible to control all variables. The animals are not anatomically and physiologically stable over time. Organ sizes can vary between seasons and several morphological structures show drastically changes in size and appearance within an individual's lifetime (PIERSMA and LINDSTRÖM 1997). For example, various bird species show hypertrophy of organs during migration, because an increase in the size of organs involved in digestion and nutrient assimilation increases the ability to process nutrients (PIERSMA et al. 1999, PIERSMA 2002). The change in relative organ size in response to different life-cycle stages can occur very rapidly, showing flexibility and implying that it is costly for organisms to maintain unused capacities in both supply and demand organs (RICKLEFS and WIKELSKI 2002). In a few cases, the change in organ size occurs within a few days following a shift in activity or diet. BUCHMANN (1986) showed that the liver of the Baltic cod (*Gadus morhua*) decreases as a function of progressing maturity and that liver size is presumably associated with the infection with the acanthocephalan *Echinorhynchus gadi* and the diet of the fish.

The kidney is one of the most energetically demanding organs in a mammalian body. HAMMOND and JANES (1998) report an increase in kidney mass with an increased protein intake, showing that kidney weight increases with elevated energy demands. Also, heart size can be diminished in migratory birds as a result of a disproportional decrease of blood viscosity with a decreasing haematocrit, which leads to a reduction of the energy expenditure by the heart (JENNI et al. 2006).

These few examples show how the size of an organ is influenced by factors other than parasites, which makes it difficult in wild animals to distinguish between parasite and confounding effects.

For wild populations, animals which died naturally are often not suitable for terminal measurements, since the causes of death may bias the analysis or are often not even known (PIERSMA and LINDSTRÖM 1997). The hedgehogs I investigated originated from different

populations and therefore differed in life history backgrounds. Possible effects of certain parasite species on organ sizes might therefore not be noticed because of confounding effects like diet, stress, or abiotic factors. Nevertheless, field data enables the investigation of animals in their natural environment and provides a much more accurate picture than carefully controlled laboratory studies (RANDOLPH and NUTTALL 1994). Therefore, the data presented in this thesis, in spite of all of the uncertainties involved, represents a reasonably accurate picture of what is found in natural populations.

The negative effect of parasites on host condition has been demonstrated in various studies. DAWSON and BORTOLOTTI (2000) investigated the influence of hematozoan parasites on the body condition of American Kestrels (*Falco sparverius*) during the breeding season. Parasite-reduced fitness in females occurred only during egg incubation but nor prior to egg laying, suggesting that the parasites' effect might have been masked by the high variation in mass resulting from egg laying. Intestinal nematodes reduced the yearly body condition of horses from the Shackelford Banks, North California (RUBENSTEIN and HOHMANN 1989). The authors discuss these results with the assumption that larvae of nematodes cause tissue damage while migrating to their final destination and adult worms can lead to anaemia and usurpation of hosts nutrients and vitamins. The removal of ectoparasites caused an increase in weight gain during lactation in female ground squirrels (*Spermophilus columbianus*), increasing the overall condition (NEUHAUS 2003).

By using multiple regression analysis to test for influences of parasites on the body condition, measured as the condition factor in juveniles from all investigation areas and adults from New Zealand, and the weight/length ratio in adults from Europe no trends for correlations were found for juvenile hedgehogs.

Young animals face other physiological and morphological constraints than full-grown animals. They may, for example, respond to demands in their environment by using energy that would otherwise be allocated to growth. Such demands include harsh weather, predation risk, and availability of food or parasite infection (KRISTAN 2000). Additionally, size at weaning may influence the manner in which an animal copes with these demands because there might be differences in the absolute amount of energy reserves potentially available and demands can be different for animals of different sizes. Furthermore, maternal condition can affect the growth rate of the offspring (DUFVA 1996, KRISTAN 2000).

For juveniles, parasite infection does not always have to result in a lowered body condition, measured as the relation between size and weight. KRISTAN (2000) investigated the effect of

the early infection with *H. polygyrus* on mice pups. Uninfected and infected animals showed no significant differences in body mass, but did in body composition. An infection led, for example, to an increased liver, kidney, spleen but smaller intestine mass. The results may indicate a change in energy allocation to organs during growth, or may simply reflect systemic morphological changes owing to parasite pathology. It can be assumed that: (i) similar mechanisms to those mentioned by KRISTAN (2000) also apply for juvenile European hedgehogs, (ii) there might be a threshold for parasite infection below which the animals escape the influence of parasites at the morphological and physiological levels, or (iii) that there is no true relationship between the tested variables in juvenile European hedgehogs.

The latter is unlikely, since I found a definitive negative relationship between body condition and the intensity of *Capillaria* spp. infection in adults from Germany and the North Island of New Zealand and a trend towards a negative correlation in the UK. It is more likely that juveniles cope with parasite infection in other ways than adults, and that smaller or infected juveniles show a kind of compensatory growth, which also occurs in some rodent species (KRISTAN 2002). This enables them to use the energy for fast growth, potentially to reach reproductive ability early and thereby modulate parasite effects (SORCI and CLOBERT 1995).

As mentioned previously, the only constant pattern I found was the negative relationship between the numbers of intestinal *Capillaria* spp. and the body condition of adult European hedgehogs. For adults from the UK I only found a trend for the effect of the nematodes on body condition ($r = -0.434$, $p = 0.053$). The sample size of 15 might have been to low to show significant effects. I also did not find a significant correlation for *Capillaria* spp. and the condition factor in adults from the South Island of New Zealand. The effect of *Capillaria* spp. within a population might only be measured within a certain threshold below which the population escapes the influence of the parasites. For instance, except for the South Island, the prevalence of *Capillaria* spp. exceeded 50% in all other investigated populations. Furthermore, the abundances and intensities were the lowest on the South Island, supporting this theory.

The hedgehogs from Europe might be biased to sick and already weakened animals, which could have strengthened the effect of *Capillaria* spp. on the condition, since only severely parasitized animals were dissected. However, the results from the North Island, where the hedgehogs were more randomly sampled and were not biased to sick animals, correspond to the multiple regression analysis models from Europe. This indicates that *Capillaria* spp. has a severe effect on the body condition of hedgehogs. For individuals, this is of importance especially during periods of high stress and hibernation. For adult hedgehogs in natural

populations the mortality during winter, which is much higher than at other times of the year; varies from 20–43% (HOECK 1987, KRISTIANSSON 1990). Winter survival depends predominantly on the fat reserves hedgehogs store in the pre-hibernating period. As described in chapter III.2.5.3, every factor which influences the ability of a hedgehog to store fat before winter increases the mortality risk of the animal.

A fitness decrease with negative effects on hibernation survival was shown by ARNOLD and LICHTENSTEIN (1993) in alpine marmots (*Marmota marmota*) infected with the mite *Echinonyssus blanchardi*. The mass loss during hibernation increased with the number of ectoparasites found in the previous summer and the probability of winter survival was significantly reduced in marmot families with increased ectoparasite loads. Since *Capillaria* spp. have a significant negative effect on body weight of hedgehogs it seems likely that they might also have a strong influence on survival of the animal, especially during hibernation. NEWEY et al. (2004, 2005) discussed the effect of the nematode *Trichostrongylus retortaeformis* on mountain hare populations (*Lepus timidus*). Nematode infections reduced the body condition of the animals significantly. The authors suggested that the influence of *T. retortaeformis* would cause a destabilizing effect, which leads to the regulation of mountain hare populations. It is possible that *Capillaria* spp. also have the potential to regulate hedgehogs, not only at an individual level by reducing body condition, but also at a population level by increasing mortality rates especially during winter. In addition, together with certain environmental factors, which increase parasite numbers and therefore also pathogenicity, or which increase the susceptibility of the host to parasite infection, *Capillaria* spp. might be of significance for hedgehog conservation. An important factor is habitat destruction or fragmentation which leads to a concentration of organisms in an ecosystem and an increase in potential parasite transmission due to the higher contact rate between individuals (HOLMES 1996). A pathogen or parasite which regulates a host population in a large ecosystem, might act as an agent of extinction in shrinking ecosystems (HOLMES 1996). Fragmented habitats are also, like other ecosystems, affected by human toxins, which have the ability to inhibit the immune system, making animals more susceptible to infection (HOLMES 1996). Additionally climatic changes challenge the adaptability of many organisms (SCHINDLER et al. 1990) which might increase the potential for disease. Considering these facts, a future task would be to investigate of the role of *Capillaria* spp. in wild hedgehog population dynamics, taking into account environmental factors and also the density of other parasites.

2.4 Parasites and host reproduction

Various studies discuss the impact of parasites on the host's reproduction, either due to disturbance of the hormonal balance or by damaging gonad tissue. The biggest effect is definitely due to parasitic castration, occurring in various host-parasite relationships either as direct castration in intermediate hosts or indirect and hormonal castration in intermediate and final hosts (e.g. WILSON and DENISON 1980, LAFFERTY 1993, ARNOTT et al. 2000, LIMA et al. 2007). The reduction of a host's reproductive ability is not always connected with total castration, but can result in a diminished reproductive success, for example due to lowered productivity because of lowered size of the gonads. A parasite-induced reduction in gonad size in mammals has predominantly been observed in rodent hosts. SEED et al. (1978) reported a decreased gonad weight in male *Microtus montanus* infected with *Trypanosoma brucei gambiense*. The estradiol level of male inbred Balb/c mice infected with *Taenia crassiceps* was increased to 200 times their normal values and testosterone levels were 90% lower than normal (LARRALDE et al. 1995). This resulted in a significant reduction in the seminal vesicle weight. In addition, female mice showed slightly increased estradiol levels and increased uterus weights. The authors suggested that the parasite either stimulates the host's endocrine system towards abnormal female hormone levels, or it favours its own growth by producing own estrogens. Male oldfield mice infected with the nematode *Trichinella spiralis* showed a decrease in testis and seminal vesicle weight, which was negatively correlated with infection intensity (MEAGHER and DUDEK 2002). However, it was not clear whether this decrease was associated with a reallocation of energy from reproductive function to the immune response or to higher cortisone levels caused by a stress response, infection, starvation or inflammation, which in turn caused direct gonad damage.

In my study, no steady trends which showed a relation between parasite infection and the size of hedgehog's sexual organs, either in juveniles or in adult animals occurred. This indicates that the parasite species investigated have no direct influence on gonad size and therefore on reproduction. As discussed for the other organs, the gonads also underlie the influence of various environmental factors (including season, which was excluded by statistical analysis – see IV.2.4), intraspecific and also individual variations throughout a certain period of time. Therefore, it is most likely that possible parasite-induced effects on hedgehog gonads might have been masked by other influences and could therefore not be detected. Furthermore, although I was not able to discover a direct relationship between parasite infection and gonad size, a negative influence on reproductive success cannot be excluded, since parasite infection could have an effect on the sperm production of males or the probability of abortion or

successful birth and upbringing of the offspring by females. Unfortunately, I was not able to measure this using my experimental setup, but it should definitely be in the subject of further experiments or investigations on wild hedgehog populations.

However, I found significant positive correlations between the condition factor and the uterus, testicle, seminal vesicle and prostate weights of adults from all investigation areas, except for the UK (no significant correlation between condition factor and uterus, seminal vesicles, prostate - this could be connected with the low sample size), and the North Island of New Zealand (no significant correlation between condition factor and testicle weight). No significant correlations were found for juveniles, but ALLANSON (1934) has shown that there is no regular relationship between testis and body weight in immature hedgehogs anyways.

My results indicate that animals, that are "fit" enough and store enough fat, can invest more energy into their reproductive organs, which might also increase their reproductive success. Considering the negative effect of *Capillaria* spp. on body condition, in other words the body weight of hedgehogs, the energy investment into reproductive tissues should be decreased with infection intensity. High *Capillaria* spp. infections could therefore indirectly cause a lowered pregnancy or birth rate in hedgehog populations and in females with decreased body condition also a diminished success in raising their offspring. Hence, I hypothesize that *Capillaria* spp. infections have the potential to regulate wild hedgehog populations by reducing the fitness of animals, which is likely to lead to increased winter mortality and/or reduced reproductive success.

3. Summary

In the second part of my study I investigated the influence of parasites on fitness parameters of hedgehogs at a general level by measuring the macroparasite infection rates in dissected hedgehogs from highly infected (Germany and the UK) and poorly infected populations (New Zealand). This represents a more natural situation than focusing only on one parasite group or species. Quantification of the actual parasite infection load of an animal is easier to measure in dead animals than in living ones, and although it is not possible to control confounding effects, and the pre-infection condition of animal is not known in most cases, the examination of dead animals gives an insight into natural conditions.

My results from the dissections of hedgehogs from different populations show the high prevalences and intensities of infection by various parasite species in European hedgehogs, indicating their potential importance for the individual host as well as for host populations.

Not all of the findings on parasite infections in the dissected hedgehogs can be compared to infection rates of wild populations. For example, flea abundances and prevalences in my study might not reflect the natural infestation rates of wild hedgehogs, since it is likely that a large proportion of fleas left the host before or directly after death and could therefore not be counted. However my results for the other parasites reflect natural infections of wild hedgehogs, and considering the high prevalences for various parasite species, it is obvious that parasites are common in and on hedgehogs and might therefore have the potential to influence hedgehog populations.

P. cylindraceus, which is predominantly a parasite of passerine birds, can have a severe negative effect on health of hedgehogs, mainly on juveniles, which feed on isopods, the intermediate hosts, more often than adult hedgehogs. Prior to our work on hedgehogs, this relationship was unknown.

This is also the first study which describes and compares most of the macroparasite fauna of *E. erinaceus* from New Zealand with native populations from Europe. The results conform to the parasite release hypothesis, which explains the success of an introduced species within its new range by the loss of parasites during the process of invasion. Almost half of the parasite species found in hedgehogs from Europe, such as *I. ricinus*, *I. hexagonus*, *A. erinacei* and *B. erinacei*, could not be detected in hedgehogs from New Zealand. Additionally, prevalences, abundances and intensities of the detected parasites were significantly lower in the new range compared to the native one. I was also able to detect occasional infections with the cat flea *C. felis felis*, the cattle tick *H. longicornis*, an undetermined species of trematode, and this study is the first to describe *P. cylindraceus* infections from hedgehogs from New Zealand.

Measuring the influence of parasites on the fitness related parameters of dead, wild animals is always difficult because many variables like pre-infection condition, intraspecific and individual variability in organ sizes over time, environmental factors, diet changes and stress levels etc, which can have significant effects on the condition of an animal, are generally unknown to the investigator. Additionally, the animals are not anatomically and physically stable over time. All of these factors can mask the influence of parasites on their hosts, so that the detection of existing effects might difficult or not possible.

In my study, I found no steady pattern of a relationship between the criterion variables (organ weights, gonad weights, condition factor) and parasite infections in juvenile hedgehogs from any investigation area. Immature animals face different physiological and morphological constraints than full-grown animals. A parasite infection in young hedgehogs might result in

compensatory growth which represents a modulation of parasite effects. A parasite infection results, therefore, not unconditionally in a reduction in body condition (measured as a relationship between size and weight), because the body weight might be similar to uninfected animals, but the body composition is likely to change.

Capillaria spp. infection showed a significant negative correlation with the body condition of adult hedgehogs. This suggests that these parasites have a major effect on morbidity and also, potentially, on the survival of their hedgehog hosts, especially in times of increased stress or energy demand like rut or hibernation. Additionally, the significant positive correlation between body condition and gonad size suggests that particularly hedgehogs with a good body condition have the possibility to invest more resources into their gonads and, therefore, into their reproductive ability. As increasing *Capillaria* spp. numbers reduce the condition of a hedgehog, this also indirectly decreases gonad size and therefore reproductive success. Additionally *Capillaria* spp. might, by reallocation of energy resources to defence responses of the hosts and reproduction and development of the parasite itself, reduce sperm production and pregnancy success, as well as success in raising offspring. This would also influence the hedgehog's reproductive ability negatively.

Such effects might be strengthened by confounding abiotic and biotic factors. The ongoing habitat fragmentation induced by humans could lead to increased numbers of *Capillaria* spp. in a habitat, an increased infection risk and also stress due to competition for available food resources, sexual partners and shelter. *Capillaria* spp. have the potential to regulate wild hedgehog populations, and must therefore, from the perspective of conservation biology, be taken into consideration when it comes to investigating factors which might lead to a decline in hedgehog populations, especially at times when hedgehogs are forced to change their behaviours due to human interference, leading to higher stress and therefore the possibility of higher infection risks.

V. Conclusions and perspectives

The main goal of my work was to investigate the influence of parasites on morbidity and the potential reproductive success of the European hedgehog. This is based on the characteristic ability of parasites to impose energetic costs on their hosts, leading to a reallocation of energy from processes like growth, fat storage or reproduction to processes which maintain the basic bodily functions. These influences can lead to a diminished reproductive ability and potential to survive in an individual. By extrapolating this to wild hedgehog populations, parasites might also affect their host's population dynamics resulting in a decline in the population density in a given area.

To achieve the aims of my project I approached it from two different perspectives. First at a specific level by measuring the influence of one ectoparasite group, ticks, on the blood physiology of hedgehogs from a semi-natural population, and second at a general level, representing a more natural situation, by investigating the influence of the whole macroparasite community on the condition factor and organ sizes of dissected animals with different infection statuses.

The results from the first part revealed that tick-induced blood loss leads to a regenerative anaemia, which represents a loss of energy that cannot be invested into important processes like growth, fat storage or immunological reactions. This increases morbidity and can also potentially lead to an enhanced mortality, especially when abiotic or biotic factors act as co-stressors. The impact of co-stressors was shown in the hedgehogs from the experimental population. Although female and male hedgehogs showed increased cortisol concentrations under equivalent conditions (high population density, external disturbance), the changes in the relationship between cortisol and tick infestation rates were triggered differently for the two sexes. This demonstrates the complexity of host-parasite relationships and how different factors can influence these relationships and also facilitate infection with parasites. Such factors, which increase the risk of hedgehogs becoming infected with parasites and pathogens, are also likely to increase parasite-induced morbidity and perhaps even mortality. Climate changes could influence the behaviour of hedgehogs and, as a result, also their risk of infection. This risk can be additionally increased by anthropogenic factors like toxins, which lower the overall condition of an animal, and/or habitat destruction or fragmentation. Habitat fragmentation leads to an aggregation of hedgehogs in small patches, which supports the transmission of directly transmitted pathogens and parasites, as well as ectoparasites, fungi and *Capillaria* spp..

In the second part of my study, I detected the negative effect of *Capillaria* spp., measured as their influence on condition factor, on the morbidity of hedgehogs. Body condition correlated positively with the weight of the sexual organs, indicating a potential indirect negative effect of the intensity of *Capillaria* spp. infection on the reproductive success of the animals.

Therefore, I was able to show, both at a specific as well as at a general level, that parasites increase morbidity in hedgehogs as well as, in all likelihood, indirectly reducing reproductive ability.

Both from the perspective of ecological parasitology and conservation biology, this provides basic insights into the host-parasite relationships of hedgehogs and the potential of parasites to influence hedgehog populations by increasing morbidity, potentially resulting in decreasing survival probability and reproductive success.

From the view point of parasite ecology my results are a further step supporting the models of ANDERSON and MAY (1978) and MAY and ANDERSON (1978), while from the point of view of conservation biology, my results provide new information for our understanding of the ecology of hedgehogs, supporting future conservation goals.

My work represents a beginning, and in the future more work must be conducted both in the laboratory as well as on wild hedgehog populations. This includes the influence of other parasite species like lungworms and fleas on physiological parameters and the behaviour of hedgehogs, the influence of various parasites on hibernation success of the animals, the influence of maternal parasitism on the growth and survival of offspring and how anthropogenic factors influence the host-parasite relationship of hedgehogs.

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Appendix I

Antiparasitic drugs

Baycox® 2.5%: active ingredient toltrazuril, Bayer Health Care, Bayer AG, Leverkusen 51368, Germany

Baytril® 2.5%: active ingredient enrofloxacin, Bayer Health Care, Bayer AG, Leverkusen 51368, Germany

Bolfo®: active ingredient propuxur, Bayer Health Care, Bayer AG, Leverkusen 51368, Germany

Cotrim®: active ingredient cotrimoxazol, Ratiopharm GmbH, Ulm 89079, Germany

Droncit®: active ingredient praziquantel, Bayer Health Care, Bayer AG, Leverkusen 51368, Germany

Duphamox®: active ingredient amoxycillin, Fort Dodge Veterinär GmbH, Würselen 52146, Germany

Flubenol® 5%: active ingredient flubendazole, Janssen-Cilag GmbH, Neuss 41457, Germany

Hexocil®: active ingredient hexedetin, Pharmacia & Upjohn GmbH, Erlangen 91058, Germany

Imaverol®: active ingredient enilconazol, Janssen-Cilag GmbH, Neuss 41457, Germany

Ivomec®: active ingredient ivermectin, Meriol GmbH, Hallbergmoos 85399, Germany

Levamisol® 10%: active ingredient levamisol, Produlab Pharma B.V.Raamsdonksveer 4941 SJ, Netherlands

Nebacetin®: active ingredients neomycin and bacitracin, Gerke Pharma GmbH, Grevenbroich 41516, Germany

Rivanol®: active ingredient ethacridinlactate, Dermapharm AG, 82031 Grünwald, Germany

Surolan®: active ingredients miconazole nitrate, polymyxin b sulphate and prednisolone acetate, Janssen-Cilag GmbH, Neuss 41457, Germany

Appendix II

Table I: Daily temperature (°C), relative humidity (%) and rainfall (mm) from February-October 2006. All data were measured by the meteorological station ID 10727, Hertzstrasse 137, 76187 Karlsruhe/Germany provided by the German Weather Service (Deutscher Wetterdienst DWD).

Date	Temperature °C	Relative humidity (%)	Rainfall (mm)	Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)
01.02.06	-4.5	96	0.4	01.07.06	22.8	60	0
02.02.06	-5.4	97	0.1	02.07.06	23.2	51	0
03.02.06	-5.9	93	0	03.07.06	23.8	57	0
04.02.06	-3	82	0	04.07.06	26.2	55	0
05.02.06	-0.6	81	0	05.07.06	25.7	63	13
06.02.06	1.2	83	0	06.07.06	22.6	76	0.1
07.02.06	2.8	89	0	07.07.06	20.4	87	76.5
08.02.06	3	89	4.7	08.07.06	21.9	79	1.1
09.02.06	2.2	82	0.3	09.07.06	22.8	74	11
10.02.06	1.7	83	0.1	10.07.06	24.8	64	0
11.02.06	0.5	82	0	11.07.06	26	62	0
12.02.06	-0.3	74	0	12.07.06	25.4	72	0
13.02.06	-0.4	75	0	13.07.06	25.4	72	4.7
14.02.06	2.9	82	0.6	14.07.06	23.6	69	0
15.02.06	5.6	92	15.4	15.07.06	22.3	51	0
16.02.06	7.7	91	7.1	16.07.06	22.9	48	0
17.02.06	6.1	83	4	17.07.06	23.6	45	0
18.02.06	7	78	4.3	18.07.06	25	49	0
19.02.06	7.1	71	1.7	19.07.06	26.9	45	0
20.02.06	6.4	85	4.3	20.07.06	28	52	0
21.02.06	5.4	90	0.1	21.07.06	28.4	56	0
22.02.06	3.4	76	0	22.07.06	25.6	66	3.3
23.02.06	1.5	76	0	23.07.06	24.9	74	6.4
24.02.06	3.3	66	0	24.07.06	26.5	67	0
25.02.06	1.6	61	0	25.07.06	28.3	56	0
26.02.06	-1.8	80	0	26.07.06	27.4	60	0
27.02.06	-0.2	69	0	27.07.06	27.4	60	4.5
28.02.06	0.8	81	1.1	28.07.06	23.8	75	9.2
01.03.06	0.4	74	0.2	29.07.06	22.7	80	1.9
02.03.06	-0.8	86	4.8	30.07.06	25.4	65	0
03.03.06	0.3	95	18.5	31.07.06	23.7	65	0
04.03.06	-0.3	96	0.9	01.08.06	19.4	82	2.7
05.03.06	0.3	85	0.1	02.08.06	19.3	64	0
06.03.06	0.9	83	0	03.08.06	16.8	75	1.6
07.03.06	1.5	73	0	04.08.06	18.3	75	34.4
08.03.06	1.7	87	14.3	05.08.06	18.9	79	12.9
09.03.06	8.5	92	3.8	06.08.06	18.6	88	3.4
10.03.06	5.5	83	0.6	07.08.06	21.1	66	0
11.03.06	2.6	88	6	08.08.06	17.8	78	3.1
12.03.06	-2.6	71	0	09.08.06	19.2	65	0.4
13.03.06	-2	67	0	10.08.06	16.5	78	6.1
14.03.06	-0.5	65	0	11.08.06	14.3	88	9.4
15.03.06	0.8	70	0	12.08.06	14.9	81	0.9
16.03.06	1.6	66	0	13.08.06	14.9	84	1
17.03.06	3	66	0	14.08.06	15.5	85	8.9
18.03.06	4.3	65	0	15.08.06	17.6	80	0.3
19.03.06	4.8	65	0	16.08.06	17.7	85	5.7

Date	Temperature °C	Relative humidity (%)	Rainfall (mm)	Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)
20.03.06	5.6	63	1.4	17.08.06	20.5	78	4.9
21.03.06	3.8	87	9.2	18.08.06	20	74	0.8
22.03.06	3.5	85	0	19.08.06	18.9	78	2.2
23.03.06	5.4	63	0	20.08.06	18.6	76	0.1
24.03.06	6.3	86	2.5	21.08.06	28.4	74	3.9
25.03.06	12.2	86	6.2	22.08.06	16.9	83	0
26.03.06	14.2	83	1.1	23.08.06	18.5	71	0
27.03.06	14	79	5.9	24.08.06	17.3	79	3.7
28.03.06	11	78	1.5	25.08.06	14.7	93	8.4
29.03.06	9.5	79	1.9	26.08.06	17.6	80	1.7
30.03.06	11.3	84	5	27.08.06	16.7	89	9.4
31.03.06	13.6	69	1.5	28.08.06	14.3	97	21.4
01.04.06	13.4	66	0.1	29.08.06	12.6	91	9.3
02.04.06	11.2	82	5.8	30.08.06	13.8	85	0.1
03.04.06	8.9	82	2.5	31.08.06	16	75	0
04.04.06	7.7	72	0	01.09.06	17.9	72	0
05.04.06	4.6	76	1.3	02.09.06	20.6	73	0.1
06.04.06	5.3	61	0	03.09.06	21.3	77	0
07.04.06	7.1	56	0	04.09.06	23.6	73	0
08.04.06	10.5	51	0	05.09.06	21.2	75	0
09.04.06	9.9	65	1.9	06.09.06	20.8	77	0
10.04.06	5.9	89	7.2	07.09.06	21.1	78	0
11.04.06	6.8	59	0.2	08.09.06	16	67	0
12.04.06	6.4	82	0.7	09.09.06	16.6	63	0
13.04.06	8.2	82	0.1	10.09.06	18.7	68	0
14.04.06	10.8	83	0	11.09.06	21.6	75	0
15.04.06	10.8	84	1	12.09.06	21.3	73	0
16.04.06	12.1	83	1.8	13.09.06	21.5	72	0
17.04.06	12.4	77	0	14.09.06	19.9	73	0
18.04.06	12.3	67	0	15.09.06	18.7	78	0.2
19.04.06	12.8	59	0	16.09.06	17.9	88	0.2
20.04.06	13.4	60	0	17.09.06	17.6	96	1.2
21.04.06	15.6	59	0	18.09.06	17.2	94	3.8
22.04.06	15.1	64	0.5	19.09.06	17.5	86	0.8
23.04.06	13.3	57	0	20.09.06	17.9	81	0
24.04.06	14.7	54	0.4	21.09.06	18.7	76	0
25.04.06	16.7	70	0	22.09.06	18.8	79	0
26.04.06	14.5	88	8.2	23.09.06	19.6	79	0
27.04.06	13.5	90	1.7	24.09.06	19.5	79	0
28.04.06	13.7	57	0.1	25.09.06	17.6	88	18.7
29.04.06	8.7	55	0	26.09.06	16.3	92	1.3
30.04.06	8.9	59	0.2	27.09.06	16.7	85	0
01.05.06	11.5	68	0.7	28.09.06	15.4	89	0
02.05.06	15.6	64	0	29.09.06	17.1	84	0
03.05.06	18.1	57	0	30.09.06	18.4	84	0.5
04.05.06	19.6	51	0	01.10.06	18.1	89	12.4
05.05.06	18.5	49	0	02.10.06	15.2	95	33.9
06.05.06	17.8	45	0	03.10.06	14.1	99	37.5
07.05.06	17.4	45	0	04.10.06	13	87	0.4
08.05.06	16.1	61	0	05.10.06	13	82	0.3
09.05.06	11.5	84	0.1	06.10.06	15	79	5
10.05.06	13.9	74	0	07.10.06	13.6	87	0.1
11.05.06	16.8	58	0	08.10.06	11.7	81	0
12.05.06	18.3	55	0.9	09.10.06	12.5	84	0
13.05.06	16.8	75	0.1	10.10.06	13.8	88	0

Date	Temperature °C	Relative humidity (%)	Rainfall (mm)	Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)
14.05.06	16.8	69	0	11.10.06	12.4	96	0
15.05.06	17.9	66	0.2	12.10.06	15.6	88	0
16.05.06	18.6	78	3.5	13.10.06	16.2	90	0
17.05.06	19	73	0	14.10.06	14.2	83	0
18.05.06	17.3	85	2.7	15.10.06	12.2	85	0
19.05.06	15.6	67	0.2	16.10.06	10.8	82	0
20.05.06	13.5	75	5.5	17.10.06	8.8	89	0
21.05.06	15.8	66	0	18.10.06	10.5	89	0
22.05.06	14.6	81	5.3	19.10.06	13.7	91	0.2
23.05.06	14.5	57	0	20.10.06	16.1	82	2
24.05.06	13.8	58	0	21.10.06	15.8	86	0.3
25.05.06	12.6	75	7.2	22.10.06	16.2	80	2
26.05.06	15.2	94	9.5	23.10.06	15.9	96	38.2
27.05.06	17.8	85	5.4	24.10.06	15.5	74	0.2
28.05.06	17.8	70	0	25.10.06	12.4	80	0
29.05.06	11.5	86	16.7	26.10.06	13.9	84	0
30.05.06	8.7	89	5.3	27.10.06	16.4	90	1
31.05.06	9.7	80	0.9	28.10.06	16	89	2
01.06.06	9.4	83	4.5	29.10.06	15.3	82	0.1
02.06.06	11.3	75	0	30.10.06	10.1	85	0
03.06.06	12.3	76	4.4	31.10.06	10.4	86	0.4
04.06.06	13.1	73	0				
05.06.06	13.3	68	2.8				
06.06.06	13.1	64	0				
07.06.06	14.7	59	0				
08.06.06	16.5	53	0				
09.06.06	18.4	51	0				
10.06.06	20.1	54	0				
11.06.06	20.9	50	0				
12.06.06	22	49	0				
13.06.06	23.8	53	0				
14.06.06	25	56	0				
15.06.06	24.2	64	0				
16.06.06	22.1	68	0				
17.06.06	20.2	54	0				
18.06.06	24.6	53	0				
19.06.06	22.8	69	1.7				
20.06.06	21.8	81	0.8				
21.06.06	22.7	71	0				
22.06.06	19.7	67	0				
23.06.06	19.4	49	0				
24.06.06	23.1	55	0				
25.06.06	24.4	69	41.4				
26.06.06	22.2	74	0				
27.06.06	22.4	73	5.5				
28.06.06	20.2	82	4				
29.06.06	22.5	70	0.1				
30.06.06	22.6	66	0				

Table II: Daily temperature (°C), relative humidity (%) and rainfall (mm) from February-October 2007. All data were measured by the meteorological station ID 10727, Hertzstrasse 137, 76187 Karlsruhe/Germany provided by the German Weather Service (Deutscher Wetterdienst DWD).

Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)	Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)
01.02.07	4.6	95	0.5	01.07.07	20.1	75	2.9
02.02.07	6.2	94	0.6	02.07.07	18	84	6.4
03.02.07	6.2	79	0	03.07.07	16.2	84	9.5
04.02.07	6.3	78	0	04.07.07	15.2	85	2.4
05.02.07	3.5	92	1.6	05.07.07	14.4	91	2.7
06.02.07	3.3	93	3	06.07.07	16.9	78	4.1
07.02.07	3.2	96	5.8	07.07.07	18.1	67	0
08.02.07	5	89	9.2	08.07.07	19.4	76	11.7
09.02.07	6.7	80	0.4	09.07.07	17.4	77	0
10.02.07	6.8	84	0.4	10.07.07	14.8	77	0.3
11.02.07	7.3	89	17.9	11.07.07	15	83	2.1
12.02.07	8.3	87	7.2	12.07.07	18.5	73	0.7
13.02.07	7.6	83	0.7	13.07.07	22	71	0
14.02.07	5.7	89	8	14.07.07	25.1	64	0
15.02.07	8	75	0	15.07.07	27.6	59	0
16.02.07	6.9	69	0	16.07.07	27.6	53	0
17.02.07	6.2	68	0	17.07.07	23.3	63	4.5
18.02.07	4	85	0	18.07.07	23.2	77	0
19.02.07	4.8	88	0	19.07.07	21.4	79	3.8
20.02.07	2.6	95	0	20.07.07	22.4	78	0
21.02.07	6.2	89	0.3	21.07.07	19.3	78	1.4
22.02.07	9.3	76	0	22.07.07	20	66	0
23.02.07	9.7	73	0	23.07.07	18.9	77	6.5
24.02.07	7.8	85	7	24.07.07	18.1	76	0.3
25.02.07	8.8	79	6	25.07.07	19.8	65	0
26.02.07	7.3	91	2.3	26.07.07	22	63	0
27.02.07	6.9	85	3.6	27.07.07	21	67	0
28.02.07	9.8	86	13.4	28.07.07	20.8	74	0
01.03.07	8.3	90	16.3	29.07.07	18	87	7.5
02.03.07	7.1	74	4.6	30.07.07	16.4	64	0
03.03.07	9.5	78	4	31.07.07	15.7	60	0
04.03.07	10.4	67	0	01.08.07	18.6	53	0
05.03.07	9.9	69	0	02.08.07	19.9	73	5.5
06.03.07	8.7	72	5.7	03.08.07	18.8	81	0
07.03.07	9.2	85	0.4	04.08.07	20	68	0
08.03.07	6.8	82	0	05.08.07	23.2	52	0
09.03.07	8.2	75	6	06.08.07	23.7	56	2.7
10.03.07	6.8	73	0	07.08.07	19	94	13.1
11.03.07	6.9	67	0	08.08.07	16.6	92	15.8
12.03.07	8.6	63	0	09.08.07	14.8	96	19.7
13.03.07	9.6	69	0	10.08.07	14.8	97	11.2
14.03.07	8.6	76	0	11.08.07	18.9	87	0
15.03.07	9.2	69	0	12.08.07	20.3	77	23.4
16.03.07	8.4	73	0	13.08.07	20.8	78	0
17.03.07	8.3	79	0	14.08.07	22.2	74	0
18.03.07	8.5	79	8.5	15.08.07	25.2	65	4.8
19.03.07	3.5	89	4.5	16.08.07	19.2	73	0
20.03.07	4	72	0	17.08.07	17.1	69	0
21.03.07	3.9	78	1.6	18.08.07	17.7	68	0
22.03.07	1.9	97	18.3	19.08.07	18.7	71	0
23.03.07	2.1	96	7.7	20.08.07	17.9	68	0

Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)	Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)
24.03.07	2.9	97	3.4	21.08.07	17.6	70	0.6
25.03.07	8.1	74	0	22.08.07	18.6	69	0
26.03.07	12	52	0	23.08.07	20.3	62	0
27.03.07	11.3	52	0	24.08.07	20.9	64	0
28.03.07	9.9	55	1.2	25.08.07	22.2	64	0
29.03.07	10	78	0	26.08.07	22.5	65	0
30.03.07	10.5	70	0	27.08.07	20	68	0
31.03.07	6	91	1.6	28.08.07	17.9	56	0
01.04.07	10.1	73	0	29.08.07	17.5	57	0
02.04.07	12.1	62	0	30.08.07	15.9	55	0
03.04.07	10	62	0	31.08.07	16.9	66	0
04.04.07	7.8	63	0	01.09.07	17.9	66	0
05.04.07	8.2	55	0	02.09.07	17.8	71	0
06.04.07	11.6	60	0	03.09.07	14.9	84	13.2
07.04.07	10.6	65	0	04.09.07	12.7	69	1.6
08.04.07	10.7	55	0	05.09.07	12.2	68	0
09.04.07	11.9	60	0	06.09.07	11	87	1.3
10.04.07	12.1	63	0	07.09.07	14.1	89	0.2
11.04.07	13.8	64	0	08.09.07	15.9	77	0
12.04.07	16.7	60	0	09.09.07	15.5	72	0
13.04.07	18.7	56	0	10.09.07	12.6	84	2.3
14.04.07	19.6	53	0	11.09.07	13.6	81	0
15.04.07	18.7	48	0	12.09.07	14.3	76	0
16.04.07	18.4	47	0	13.09.07	14.9	71	0
17.04.07	17.5	55	0	14.09.07	16.5	73	0
18.04.07	11.5	52	0	15.09.07	16.6	63	0
19.04.07	11.3	54	0	16.09.07	15.9	71	0
20.04.07	12	58	0	17.09.07	17.5	83	11.3
21.04.07	12.9	53	0	18.09.07	13.1	86	6.8
22.04.07	14.9	52	0	19.09.07	10.9	76	0
23.04.07	28	53	0	20.09.07	12.1	71	0
24.04.07	20.2	52	0	21.09.07	13.6	73	0
25.04.07	21.2	49	0	22.09.07	15.7	74	0
26.04.07	19.1	47	0	23.09.07	17.3	72	0
27.04.07	18.7	54	0	24.09.07	17.9	79	9.4
28.04.07	20.1	60	0	25.09.07	13.7	76	0
29.04.07	19.2	56	0	26.09.07	11.6	76	2.4
30.04.07	16.1	40	0	27.09.07	10.9	92	10.4
01.05.07	15.7	39	0	28.09.07	11.4	86	0.2
02.05.07	15.3	32	0	29.09.07	14.3	69	0
03.05.07	14.8	49	0	30.09.07	13.7	68	0
04.05.07	16.6	55	0.6	01.10.07	15.3	76.8	0
05.05.07	15.5	64	0.1	02.10.07	17.4	88	1.9
06.05.07	17.2	56	0	03.10.07	17.9	89.9	0.4
07.05.07	15.4	71	3.8	04.10.07	19	84.4	0
08.05.07	15.3	83	6.8	05.10.07	16.3	76.3	0
09.05.07	13.9	90	8.8	06.10.07	12.3	73.8	0
10.05.07	19	57	0.1	07.10.07	11.5	75	0
11.05.07	16.7	57	0.3	08.10.07	10.2	79.7	0
12.05.07	16.7	62	0	09.10.07	10.7	78.7	0
13.05.07	19	63	0.1	10.10.07	12	78.3	0
14.05.07	13.7	88	22.8	11.10.07	10.5	77.4	0
15.05.07	11.4	86	2.2	12.10.07	10.5	83.7	0
16.05.07	11.9	85	12.1	13.10.07	12.1	76.5	0
17.05.07	11	96	1.4	14.10.07	10.5	68.6	0

Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)	Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)
18.05.07	13.7	77	0	15.10.07	11.2	76.7	0
19.05.07	18.2	72	0	16.10.07	13.9	78.1	0
20.05.07	21.8	58	0	17.10.07	13.8	79.6	0.1
21.05.07	23.3	61	0	18.10.07	9.1	78.9	1.4
22.05.07	23.1	63	0	19.10.07	6.7	83.4	1
23.05.07	21.4	75	9.9	20.10.07	4.5	76.4	0
24.05.07	22.7	72	0	21.10.07	4.3	87.7	1.8
25.05.07	24.7	61	0	22.10.07	4.8	74.1	0
26.05.07	22.7	67	12.2	23.10.07	6	68.3	0
27.05.07	17	83	5.8	24.10.07	7	70.6	0
28.05.07	11.1	98	17.3	25.10.07	9	72.8	0
29.05.07	10.5	95	5.3	26.10.07	9.3	71.7	0
30.05.07	13.8	64	0	27.10.07	9.3	74.9	0
31.05.07	16	71	0.4	28.10.07	7.9	78.3	0
01.06.07	14.1	96	12.7	29.10.07	8	81	0.4
02.06.07	16.8	86	5.8	30.10.07	8.9	82.6	0.6
03.06.07	18.9	76	0	31.10.07	3.8	92	0
04.06.07	20.2	74	0				
05.06.07	20.7	71	0				
06.06.07	21.7	71	0.2				
07.06.07	23.7	66	0				
08.06.07	24	66	0				
09.06.07	22	75	0				
10.06.07	22.9	67	11				
11.06.07	21	80	0				
12.06.07	21.3	75	0				
13.06.07	22	65	0				
14.06.07	22.3	73	8				
15.06.07	18.1	91	6.2				
16.06.07	17.6	74	5.2				
17.06.07	20.6	71	9.3				
18.06.07	20.7	80	10.8				
19.06.07	23.8	66	0				
20.06.07	25.2	67	9.3				
21.06.07	19.2	86	2.7				
22.06.07	16.3	86	1.5				
23.06.07	16.4	84	4.4				
24.06.07	20.3	67	0.3				
25.06.07	17.9	86	12.5				
26.06.07	14.8	78	2.6				
27.06.07	14.4	75	0.1				
28.06.07	14.9	79	5.4				
29.06.07	16.3	76	0.9				
30.06.07	17.7	79	1.1				

Table III: Daily temperature (°C), relative humidity (%) and rainfall (mm) from February-October 2008. All data were measured by the meteorological station ID 10727, Hertzstrasse 137, 76187 Karlsruhe/Germany provided by the German Weather Service (Deutscher Wetterdienst DWD).

Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)	Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)
01.02.08	5.5	83	16	01.07.08	24.7	53.1	0
02.02.08	2.6	75	0	02.07.08	27.6	48.3	0.3
03.02.08	0.7	69	0	03.07.08	19.3	84.7	10.5
04.02.08	2.4	84	0.3	04.07.08	19	60.8	0
05.02.08	6.3	76	9.3	05.07.08	20.5	53.9	0
06.02.08	8.7	79	3.5	06.07.08	19.5	73.9	1.2
07.02.08	4.5	78	0	07.07.08	18.3	63.3	0.9
08.02.08	3.7	68	0	08.07.08	17.4	64.4	1.8
09.02.08	4.8	56	0	09.07.08	19.4	61.8	0.7
10.02.08	4.9	61	0	10.07.08	24.4	50	2.2
11.02.08	5	69	0	11.07.08	21.1	70.8	9.7
12.02.08	5.3	73	0	12.07.08	19.5	65.1	0.7
13.02.08	2.4	82	0	13.07.08	17.7	67.4	0.3
14.02.08	-1.1	92	0	14.07.08	18.2	58.3	0
15.02.08	2	66	0	15.07.08	20.7	54.9	0
16.02.08	-0.1	50	0	16.07.08	21.4	59.2	3.4
17.02.08	-0.3	48	0	17.07.08	17	77.9	8.2
18.02.08	1.5	53	0	18.07.08	18.3	72.1	0
19.02.08	1.8	57	0	19.07.08	20	70	3.9
20.02.08	3.2	77	2.8	20.07.08	18.6	62.2	0
21.02.08	8.1	89	0.2	21.07.08	15	65.2	2.5
22.02.08	10.9	71	0	22.07.08	15	73	0
23.02.08	10.7	70	0	23.07.08	18	62	0
24.02.08	9.3	74	0	24.07.08	20.5	53.8	0
25.02.08	9.9	70	0	25.07.08	23.2	53.5	0
26.02.08	11	75	3.7	26.07.08	24.2	60.2	0
27.02.08	7.9	72	0	27.07.08	23	69.9	0.5
28.02.08	7.4	66	5.9	28.07.08	25.4	64.2	0
29.02.08	10.4	90	10.7	29.07.08	24.8	62.7	0
01.03.08	10.3	71	6.2	30.07.08	25.3	61.6	0
02.03.08	10	78	3	31.07.08	26.3	58	0.1
03.03.08	7.9	88	9.4	01.08.08	22.8	70.3	1
04.03.08	2	90	3.2	02.08.08	22.4	62.1	0.8
05.03.08	1.9	64	0	03.08.08	21.7	75.8	7.8
06.03.08	2.5	63	0	04.08.08	20	85.4	17.4
07.03.08	5.1	67	0.9	05.08.08	21.1	66.2	0
08.03.08	6.6	81	0	06.08.08	23.2	60.6	0
09.03.08	8.3	65	0	07.08.08	23.9	65.7	2.8
10.03.08	9.6	65	4.2	08.08.08	18.3	86	9
11.03.08	9.4	64	12.2	09.08.08	19.3	76.1	0.1
12.03.08	10.2	67	0.4	10.08.08	20.7	66.3	0.4
13.03.08	7.4	70	3.3	11.08.08	20.8	78.8	6
14.03.08	9.4	91	4.8	12.08.08	18.6	89.5	5.1
15.03.08	12.5	77	1.9	13.08.08	19.9	58.4	0
16.03.08	10.4	79	6.9	14.08.08	19.8	57.9	6.8
17.03.08	6.9	71	0.9	15.08.08	16.2	83	1.1
18.03.08	4.7	53	0.1	16.08.08	17.2	69.5	0
19.03.08	2.6	77	1.7	17.08.08	18.6	64.9	0
20.03.08	3.3	77	12.2	18.08.08	22.1	61.6	0
21.03.08	3	89	8.1	19.08.08	18.9	80.9	10.5
22.03.08	3.5	85	7.9	20.08.08	17.8	72.7	0

Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)	Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)
23.03.08	0.4	79	0.2	21.08.08	18.6	65.6	0
24.03.08	-0.2	79	0.6	22.08.08	17.1	78.5	4.8
25.03.08	2.1	75	0.2	23.08.08	16.1	81.2	4.7
26.03.08	4.9	72	0.4	24.08.08	17.3	69.3	0.7
27.03.08	6.1	78	0.8	25.08.08	19.9	70.6	0
28.03.08	9.3	57	3.7	26.08.08	19.5	72	0
29.03.08	10.3	56	0	27.08.08	20.4	69.4	0
30.03.08	12.4	46	0	28.08.08	18.2	73.7	0
31.03.08	11.1	64	0	29.08.08	18	71.1	0
01.04.08	11.6	61	0.1	30.08.08	20.5	62.7	0
02.04.08	10.3	66	0.2	31.08.08	22	64.8	13.6
03.04.08	7.5	71	1	01.09.08	20.7	77.1	0
04.04.08	8.9	65	1.5	02.09.08	20.2	66.9	0
05.04.08	7.9	83	14.5	03.09.08	17.5	82.5	22.2
06.04.08	4.7	87	8.1	04.09.08	14.3	90.6	6.1
07.04.08	2.6	77	0	05.09.08	18.5	84.2	0.7
08.04.08	5	62	1.2	06.09.08	17.9	87.5	2.9
09.04.08	6.1	89	14	07.09.08	17	72.8	0
10.04.08	6.8	90	1.8	08.09.08	17.8	71.6	0
11.04.08	8.6	92	12.7	09.09.08	17.6	71.8	0
12.04.08	9.7	69	0	10.09.08	18.7	84	0.2
13.04.08	10.6	66	3	11.09.08	19.5	86.3	0.1
14.04.08	8.9	77	6.3	12.09.08	16.7	91.1	3.6
15.04.08	6.4	91	10.4	13.09.08	13.6	92	9.2
16.04.08	5.9	81	3.9	14.09.08	11	68.8	0.2
17.04.08	6	74	0	15.09.08	9.5	81	0.3
18.04.08	11.2	57	0	16.09.08	10.5	77.2	0
19.04.08	10.5	77	1.8	17.09.08	9.1	66.7	0
20.04.08	12.6	72	0	18.09.08	10.8	63.6	0
21.04.08	11.6	79	4.2	19.09.08	12.4	60.1	0
22.04.08	10.9	87	2.6	20.09.08	11	60.6	0
23.04.08	12.9	73	0	21.09.08	12.2	68.3	0.1
24.04.08	14.6	65	0.2	22.09.08	11.1	82.3	0
25.04.08	13.5	62	0	23.09.08	11.4	78	0
26.04.08	13.5	57	0	24.09.08	13.1	75.6	0
27.04.08	15.6	47	0	25.09.08	12.8	76.3	0.2
28.04.08	14.8	69	0.3	26.09.08	12.3	64.7	0
29.04.08	13.2	61	0	27.09.08	11.4	69.9	0
30.04.08	11.2	71	2.3	28.09.08	11.1	72.3	0
01.05.08	12.4	63	0.4	29.09.08	11.8	77.7	0
02.05.08	13.9	58	0	30.09.08	11.4	79.5	3.4
03.05.08	14.8	55	0	01.10.08	12.4	85.8	11.5
04.05.08	15.4	49	0	02.10.08	11.6	78.9	0.6
05.05.08	15.2	49	0	03.10.08	9.1	82.4	7.4
06.05.08	17.4	56	0	04.10.08	8.7	80.9	0.2
07.05.08	16.9	51	0	05.10.08	11.2	61.1	2.8
08.05.08	17.4	44	0	06.10.08	14.4	79.7	4.2
09.05.08	18.6	43	0	07.10.08	16.1	82.1	0
10.05.08	19.3	42	0	08.10.08	15.7	82.1	0
11.05.08	19	39	0	09.10.08	14	81.4	0
12.05.08	18.5	42	0	10.10.08	14.4	84.1	0
13.05.08	19.2	41	0	11.10.08	13	87.4	0
14.05.08	20.5	42	0	12.10.08	12.7	88.7	0
15.05.08	19.6	56	1.3	13.10.08	14.6	85.5	0
16.05.08	19.4	62	0	14.10.08	16	80.6	0

Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)	Date	Temperature (°C)	Relative humidity (%)	Rainfall (mm)
17.05.08	16.7	74	0.8	15.10.08	15.4	80	9.8
18.05.08	14.8	81	25.1	16.10.08	11.7	95.1	9.4
19.05.08	13.9	74	0	17.10.08	14.3	85	0
20.05.08	15.5	48	0	18.10.08	15.9	79.8	0
21.05.08	14	57	0.1	19.10.08	16.4	79	0
22.05.08	14.6	67	0	20.10.08	21.8	82.1	0
23.05.08	26.6	60	0	21.10.08	20.6	85.6	19
24.05.08	26.8	71	3	22.10.08	9.2	94.7	5.4
25.05.08	20.3	67	0.1	23.10.08	12.8	79.8	0
26.05.08	21.9	63	0	24.10.08	13.9	80	0
27.05.08	23.5	65	0	25.10.08	16.7	77.6	0
28.05.08	24	55	0	26.10.08	14.7	77.5	0.4
29.05.08	23.2	67	17.1	27.10.08	12.5	87.5	11.7
30.05.08	20	83	5.1	28.10.08	9.8	95.5	7.9
31.05.08	19.3	78	0.2	29.10.08	7.6	93.7	13.1
01.06.08	20.7	71.6	0	30.10.08	5.3	92.8	2
02.06.08	22	72.6	22.3	31.10.08	0.65	91.2	1.6
03.06.08	19.2	74.3	0				
04.06.08	18.8	78.6	19.1				
05.06.08	16.6	94.4	2.5				
06.06.08	18.2	85.5	1				
07.06.08	16.4	84.2	0.4				
08.06.08	17.8	80.3	1.5				
09.06.08	19.4	71.8	0				
10.06.08	22	63.5	0				
11.06.08	19.3	61.3	0				
12.06.08	16.1	63.3	5.8				
13.06.08	13.6	66.6	0				
14.06.08	14.5	61.2	0				
15.06.08	13.4	78.8	7.2				
16.06.08	14.4	77.8	0.4				
17.06.08	14.1	85.6	1.2				
18.06.08	19.3	61.8	0				
19.06.08	20.5	57.7	0.5				
20.06.08	20	67.5	0				
21.06.08	23.2	57.6	0				
22.06.08	25.4	62.8	0				
23.06.08	24.2	63.1	0				
24.06.08	22.4	61.1	2.6				
25.06.08	22.6	76.8	7				
26.06.08	20.8	60.6	0				
27.06.08	20.8	60.2	0				
28.06.08	21.8	60.6	0				
29.06.08	23.8	58.5	0				
30.06.08	23.1	51.5	0				

Table IV: Mean monthly tick weight collected from hedgehogs from the experimental population (N = 46) during the investigation period (March-October) in 2006. Hedgehog sexes were pooled. LL = larvae, NN = nymphs, F = females, M = males, *I.h.* = *Ixodes hexagonus*, *I.r.* = *Ixodes ricinus*, N = sample number, ø = mean tick weight in gram, SD = standard deviation, R = range.

2006	March				April				May				June			
	N	ø	SD	R	N	ø	SD	R	N	ø	SD	R	N	ø	SD	R
LL *I.r.*																
NN *I.r.*	3	0.01	0.02	0.0-0.03	32	0.39	0.5	0.0-2.6	37	0.17	0.15	0.0-0.7	33	0.03	0.05	0.0-0.21
F *I.r.*	3	0.0	0.0	0.0	32	1.01	0.99	0.0-3.3	37	1.06	0.86	0.09-3.7	33	0.15	0.25	0.0-0.96
M *I.r.*																
Total *I.r.*	3	0.01	0.02	0.0-0.03	32	1.36	1.15	0.0-3.87	37	1.2	0.92	0.0-3.97	33	0.18	0.27	0.0-0.98
LL *I.h.*																
NN *I.h.*	3	0.03	0.02	0.01-0.05	32	0.06	0.07	0.0-0.27	37	0.07	0.12	0.01-0.75	33	0.27	0.35	0.02-1.42
F *I.h.*	3	0.04	0.07	0.0-0.12	32	0.21	0.27	0.0-1.14	37	0.11	0.11	0.0-0.34	33	1.21	1.19	0.0-3.95
M *I.h.*																
Total *I.h.*	3	0.07	0.07	0.01-0.15	32	0.28	0.31	0.0-1.36	37	0.18	0.18	0.01-0.89	33	1.48	1.26	0.03-4.66
Total tick weight	3	0.08	0.09	0.01-0.18	32	1.63	1.27	0.04-5.23	37	1.38	0.98	0.01-3.99	33	1.65	1.2	0.06-4.71
2006	July				August				September				October			
	N	ø	SD	R	N	ø	SD	R	N	ø	SD	R	N	ø	SD	R
LL *I.r.*	31	0.12	0.12	0.0-0.42	29	0.15	0.31	0.0-1.5								
NN *I.r.*	31	0.04	0.05	0.0-0.19	29	0.53	0.72	0.0-2.74	33	0.57	0.47	0.01-2.44	23	0.56	0.51	0.01-1.73
F *I.r.*	31	0.01	0.03	0.0-0.11	29	0.29	0.54	0.0-1.39	33	3.03	2.44	0.27-9.67	23	1.56	1.35	0.0-4.42
M *I.r.*																
Total *I.r.*	31	0.17	0.16	0.0-0.54	29	0.71	0.95	0.0-4.24	33	3.6	2.71	0.31-11.19	23	2.12	1.66	0.01-5.04
LL *I.h.*																
NN *I.h.*	31	0.1	0.12	0.0-0.5	29	0.04	0.07	0.0-0.35	33	0.1	0.16	0.0-0.71	23	0.21	0.27	0.01-1.03
F *I.h.*	31	1.67	1.94	0.0-7.45	29	1.22	1.41	0.0-5.88	33	0.95	0.95	0.0-3.42	23	0.46	0.78	0.0-03.32
M *I.h.*																
Total *I.h.*	31	0.177	2.0	0.0-7.49	29	1.27	1.43	0.0-5.92	33	1.06	1.04	0.0-3.91	23	0.67	0.9	0.01-3.83
Total tick weight	31	1.94	1.96	0.0-1.94	29	1.97	1.81	0.02-1.97	33	4.65	3.12	0.36-4.65	23	2.79	2.31	0.11-8.59

Appendix III

Table V: Mean monthly tick weight collected from hedgehogs from the experimental population (N = 36) during the investigation period (March-October) in 2007. Hedgehog sexes were pooled. LL = larvae, NN = nymphs, F = females, M = males, *I.h.* = *Ixodes hexagonus*, *I.r.* = *Ixodes ricinus*, N = sample number, ø = mean tick weight in gram, SD = standard deviation, R = range.

2007	March				April				May				June			
	N	ø	SD	R	N	ø	SD	R	N	ø	SD	R	N	ø	SD	R
LL *I.r.*	22	0.01	0.01	0.0-0.0	26	0.01	0.01	0.0-0.03	31	0.02	0.02	0.0-0.09	32	0.04	0.05	0.0-0.25
NN *I.r.*	22	0.2	0.23	0.01-0.98	26	0.14	0.15	0.0-0.74	31	0.09	0.09	0.0-0.36	32	0.01	0.01	0.0-0.07
F *I.r.*	22	1.14	0.9	0.0-3.31	26	0.66	0.61	0.0-2.07	31	0.74	0.64	0.0-2.54	32	0.25	0.37	0.0-1.62
M *I.r.*	22	0.0	0.0	0.0-0.01	26	0.0	0.0	0.0-0.1	31	0.0	0.0	0.0-0.01	32	0.0	0.0	
Total *I.r.*	22	1.35	1.07	0.08-3.65	26	0.75	0.73	0.0-2.85	31	0.85	0.71	0.0-2.96	32	0.31	0.38	0.0-1.7
LL *I.h.*	22	0.01	0.02	0.0-0.11	26	0.01	0.01	0.0-0.05	31	0.01	0.01	0.0-0.05	32	0.01	0.02	0.0-0.09
NN *I.h.*	22	0.03	0.06	0.0-0.28	26	0.01	0.01	0.0-0.05	31	0.05	0.06	0.0-0.2	32	0.06	0.09	0.0-0.45
F *I.h.*	22	0.44	0.94	0.0-4.3	26	0.04	0.08	0.0-0.35	31	0.15	0.24	0.0-0.93	32	0.45	0.86	0.0-4.47
M *I.h.*	22	0.0	0.0		26	0.0	0.0	0.0-0.01	31	0.0	0.0		32	0.0	0.0	0.0-0.01
Total *I.h.*	22	0.48	0.98	0.0-4.4	26	0.05	0.09	0.0-0.35	31	0.21	0.27	0.0-1.01	32	0.53	0.91	0.0-4.77
Total tick weight	22	1.83	1.46	0.1-5.0	26	0.8	0.78	0.0-2.94	31	1.0	0.8	0.0-3.1	32	0.78	0.95	0.0-4.91
2007	July				August				September				October			
	N	ø	SD	R	N	ø	SD	R	N	ø	SD	R	N	ø	SD	R
LL *I.r.*	30	0.08	0.07	0.01-0.25	26	0.1	0.07	0.0-0.27	22	0.03	0.03	0.01-0.12	18	0.01	0.01	0.0-0.03
NN *I.r.*	30	0.04	0.03	0.01-0.15	26	0.01	0.1	0.0-0.46	22	0.18	0.15	0.02-0.57	18	0.25	0.3	0.0-1.24
F *I.r.*	30	0.04	0.09	0.0-0.36	26	0.71	0.67	0.0-2.47	22	0.69	0.57	0.0-2.32	18	0.54	0.54	0.0-1.92
M *I.r.*	30	0.0	0.0		26	0.0	0.0	0.0-0.1	22	0.0	0.0	0.0-0.1	18	0.0	0.0	0.0-0.01
Total *I.r.*	30	0.15	0.12	0.02-0.43	26	0.89	0.73	0.02-2.71	22	0.87	0.62	0.0-2.53	18	0.73	0.66	0.0-2.54
LL *I.h.*	30	0.01	0.03	0.0-0.15	26	0.0	0.0	0.0-0.02	22	0.0	0.01	0.0-0.02	18	0.01	0.01	0.0-0.03
NN *I.h.*	30	0.11	0.14	0.0-0.58	26	0.03	0.03	0.0-0.1	22	0.01	0.01	0.0-0.05	18	0.02	0.02	0.0-0.07
F *I.h.*	30	0.27	0.29	0.0-0.13	26	0.55	0.54	0.0-1.82	22	0.21	0.26	0.0-0.86	18	0.13	0.18	0.0-0.61
M *I.h.*	30	0.0	0.0		26	0.0	0.0	0.0-0.01	22	0.0	0.0	0.0-0.01	18	0.0	0.0	
Total *I.h.*	30	0.39	0.38	0.01-1.53	26	0.58	0.56	0.01-1.87	22	0.21	0.26	0.0-0.9	18	0.14	0.18	0.0-0.63
Total tick weight	30	0.55	0.42	0.12-1.85	26	1.48	0.99	0.02-3.5	22	1.08	0.78	0.0-3.43	18	0.86	0.74	0.0-2.84

Table VI: Mean monthly tick weight collected from hedgehogs from the experimental population (N =27) during the investigation period (March-October) in 2008. Hedgehog sexes were pooled. LL = larvae, NN = nymphs, F = females, M = males, *I.h.* = *Ixodes hexagonus*, *I.r.* = *Ixodes ricinus*, N = sample number, ø = mean tick weight in gram, SD = standard deviation, R = range.

2008	March				April				May				June			
	N	ø	SD	R	N	ø	SD		N	ø	SD	R	N	ø	SD	R
LL *I.r.*	10	0.01	0.01	0.0-0.02	21	0.03	0.03	0.0-0.15	20	0.05	0.05	0.0-0.17	23	0.05	0.08	0.0-0.4
NN *I.r.*	10	0.52	0.47	0.02-1.45	21	1.15	1.22	0.0-4.62	20	0.56	1.51	0.0-1.72	23	0.13	0.16	0.0-0.69
F *I.r.*	10	0.19	2.14	0.0-6.42	21	1.72	1.84	0.0-5.7	20	1.68	1.51	0.0-6.88	23	0.73	0.89	0.0-3.61
M *I.r.*	10	0.01	0.01	0.0-0.02	21	0.01	0.01	0.0-0.07	20	0.0	0.0	0.0-0.01	23	0.01	0.04	0.0-0.17
Total *I.r.*	10	2.46	2.2	0.05-6.79	21	2.9	2.9	0.0-9.12	20	2.29	1.72	0.0-7.38	23	0.92	0.92	0.0-3.71
LL *I.h.*	10	0.0	0.0		21	0.0	0.01	0.0-0.04	20	0.01	0.02	0.0-0.08	23	0.01	0.01	0.0-0.05
NN *I.h.*	10	0.02	0.02	0.0-0.07	21	0.01	0.02	0.0-0.06	20	0.04	0.07	0.0-0.24	23	0.05	0.08	0.0-0.32
F *I.h.*	10	0.07	0.14	0.0-0.44	21	0.06	0.13	0.0-0.55	20	0.24	0.37	0.0-1.58	23	0.41	0.41	0.0-1.37
M *I.h.*	10	0.0	0.0		21	0.0	0.0		20	0.0	0.0		23	0.0	0.0	
Total *I.h.*	10	0.09	0.16	0.0-0.48	21	0.08	0.14	0.0-0.6	20	0.3	0.42	0.0-1.75	23	0.46	0.45	0.0-1.42
Total tick weight	10	2.54	2.26	0.1-6.8	21	2.98	2.95	0.0-9.31	20	2.58	1.83	0.0-7.55	23	1.39	1.06	0.0-3.84
2008	July				August				September				October			
	N	ø	SD	R	N	ø	SD	R	N	ø	SD	R	N	ø	SD	R
LL *I.r.*	21	0.3	0.26	0.0-0.82	13	0.2	0.16	0.0-0.41	10	0.02	0.02	0.0-0.07	9	0.03	0.03	0.0-0.07
NN *I.r.*	21	0.1	0.19	0.0-0.82	13	0.17	0.16	0.0-0.62	10	0.16	0.15	0.0-0.39	9	0.48	0.52	0.0-1.58
F *I.r.*	21	0.14	0.29	0.0-1.07	13	1.36	1.34	0.0-4.44	10	1.86	1.34	0.34-4.6	9	1.79	2.02	0.0-6.49
M *I.r.*	21	0.0	0.0		13	0.01	0.01	0.0-0.04	10	0.0	0.0	0.0-0.1	9	0.0	0.0	0.0-0.01
Total *I.r.*	21	0.55	0.49	0.0-1.65	13	1.73	1.4	0.0-4.58	10	2.04	1.27	0.36-4.62	9	2.29	2.3	0.0-7.54
LL *I.h.*	21	0.02	0.04	0.0-0.18	13	0.03	0.05	0.0-0.2	10	0.0	0.0	0.0-0.01	9	0.0	0.0	0.0-0.01
NN *I.h.*	21	0.04	0.06	0.0-0.27	13	0.09	0.12	0.0-0.37	10	0.03	0.05	0.0-0.15	9	0.02	0.02	0.0-0.06
F *I.h.*	21	0.59	0.73	0.0-2.92	13	0.48	0.48	0.0-1.57	10	0.22	0.18	0.0-0.48	9	0.06	0.09	0.0-0.2
M *I.h.*	21	0.0	0.01	0.0-0.02	13	0.0	0.0		10	0.0	0.0		9	0.0	0.0	
Total *I.h.*	21	0.64	0.77	0.0-3.03	13	0.6	0.57	0.0-1.78	10	0.25	0.19	0.0-0.48	9	0.08	0.09	0.0-0.22
Total tick weight	21	1.19	1.05	0.0-3.55	13	2.33	1.49	0.0-4.61	10	2.29	1.23	0.36-4.63	9	2.37	2.33	0.0-7.69

Appendix IV

Table VII: Pairwise comparison of blood parameters of the R-group (N = 5) for the different sampling dates. Blood samples were taken on 14.4.2009 (1), 12.5.2009 (2) and 26.5.2009 (3). After the first sampling all hedgehogs were kept tick-free for the rest of the experiment. The probability p was estimated with a Bonferroni correction as a post-hoc test. Only not significant parameters are shown. For significant values see table 37.

Parameter	(I) sample date	(J) sample date	Mean difference (I-J)	p	95% Confidence interval for difference	
					Lower bound	Upper bound
Leucocytes (/nl)	1	2	0.64	1	-5.96	7.24
		3	0.22	1	-5.32	5.76
	2	1	-0.64	1	-7.24	5.96
		3	-0.42	0.785	-1.69	0.85
	3	1	-0.22	1	-5.76	5.32
		2	0.42	0.785	-0.85	1.69
Thrombocytes (/nl)	1	2	129.2	0.4	-142.99	401.39
		3	133.6	0.384	-142.56	409.76
	2	1	-129.2	0.4	-401.39	142.99
		3	4.4	1	-15.39	24.19
	3	1	-133.6	0.384	-409.76	142.56
		2	-4.4	1	-24.19	15.39
Neutrophils (%)	1	2	8.5	1	-46.25	63.25
		3	13.0	0.85	-35.61	61.61
	2	1	-8.5	1	-63.25	46.25
		3	4.5	0.219	-3.55	12.55
	3	1	-13.0	0.85	-61.61	35.61
		2	-8.5	0.219	-12.55	3.55
Eosinophils (%)	1	2	-1.25	1	-15.32	12.82
		3	-3.0	1	-18.1	12.1
	2	1	1.25	1	-12.82	15.32
		3	-1.75	1	-9.52	6.02
	3	1	3.0	1	-12.1	18.1
		2	1.75	1	-6.02	9.52
Basophils (%)	1	2	1.33	0.551	-3.77	6.43
		3	0.33	1	-8.86	9.53
	2	1	-1.33	0.551	-6.43	3.77
		3	-1.0	1	-12.68	10.68
	3	1	-0.33	1	-9.53	8.86
		2	1.0	1	-10.68	12.68
Monocytes (%)	1	2	3.25	0.153	-1.76	8.26
		3	-2.0	1	-18.82	14.82
	2	1	-3.25	0.153	-8.26	1.76
		3	-5.25	0.447	-18.46	7.96
	3	1	2.0	1	-14.82	18.82
		2	5.25	0.447	-7.96	18.46

Parameter	(I) sample date	(J) sample date	Mean difference (I-J)	p	95% Confidence interval for difference	
					Lower bound	Upper bound
Lymphocytes (%)	1	2	-10.75	0.978	-55.32	33.82
		3	-9.75	1	-61.88	42.38
	2	1	10.75	0.978	-33.82	55.32
		3	1.0	1	-10.04	12.04
	3	1	9.75	1	-42.38	61.88
		2	-1	1	-12.04	10.04
Reticulocytes (‰)	1	2	88.22	0.101	-21.87	198.31
		3	89.12	0.101	-21.88	200.12
	2	1	-88.22	0.101	-198.31	21.87
		3	0.9	1	-4.23	6.03
	3	1	-89.12	0.101	-200.12	21.88
		2	-0.9	1	-6.03	4.23
Reticulocytes (/nl)	1	2	309.28	0.819	-655.32	1273.88
		3	306.68	0.873	-692.62	1305.98
	2	1	-309.28	0.819	-1273.88	655.32
		3	-2.6	1	-57.95	52.75
	3	1	-306.68	0.873	-1305.98	692.62
		2	2.6	1	-52.75	57.95

Table VIII: Pairwise comparison of blood parameters of the C-group (N = 4) for the different sampling dates. Blood samples were taken on 14.4.2009 (1), 12.5.2009 (2) and 26.5.2009 (3). Hedgehogs were kept tick-free before and during the whole experiment. The probability p was estimated with Bonferroni correction as a post-hoc test. Only not significant parameters are shown. For significant values see table 38.

Parameter	(I) sample date	(J) sample date	Mean difference (I-J)	p	95% Confidence interval of difference	
					Lower bound	Upper bound
Leucocytes (/nl)	1	2	2.23	0.558	-4.1	8.55
		3	2.3	0.340	-2.74	7.34
	2	1	-2.23	0.558	-8.55	4.1
		3	0.08	1	-2.66	2.81
	3	1	-2.3	0.340	-7.34	2.74
		2	-0.08	1	-2.81	2.67
MCV (fl)	1	2	-1.58	1	-10.38	7.23
		3	-1.4	1	-10.69	7.89
	2	1	1.58	1	-7.23	10.38
		3	0.18	1	-1.96	2.31
	3	1	1.4	1	-7.89	10.69
		2	-0.18	1	-2.31	1.96
MCH (pg)	1	2	-0.58	0.693	-2.44	1.29
		3	-0.55	0.960	-2.8	1.7
	2	1	0.58	0.693	-1.29	2.44
		3	-0.03	1	-0.78	0.83
	3	1	0.55	0.960	-1.7	2.8
		2	-0.03	1	-0.83	0.78
MCHC (g/dl)	1	2	-0.25	1	-2.98	2.45
		3	-0.20	1	-2.32	1.92
	2	1	0.25	1	-2.48	2.98
		3	0.05	1	-1.23	1.33
	3	1	0.20	1	-1.92	2.32
		2	-0.05	1	-1.33	1.23
Thrombocytes (/nl)	1	2	39.50	0.949	-120.36	199.36
		3	41.75	1	-149.41	232.91
	2	1	-39.50	0.949	-199.36	120.36
		3	2.25	1	-97.53	102.03
	3	1	-41.75	1	-232.91	149.41
		2	-2.25	1	-102.03	97.53
Neutrophils (%)	1	2	-3.0	0.207	-8.25	2.25
		3	-4.5	1	-27.15	18.15
	2	1	3.0	0.207	-2.25	8.25
		3	-1.5	1	-21.77	18.77
	3	1	4.5	1	-18.15	27.15
		2	1.5	1	-18.77	21.77

Parameter	(I) sample date	(J) sample date	Mean difference (I-J)	p	95% Confidence interval of difference	
					Lower bound	Upper bound
Monocytes (%)	1	2	0.0	1	-24.59	24.59
		3	-8.67	0.259	-29.54	12.2
	2	1	0.0	1	-24.59	24.59
		3	-8.67	0.843	-53.99	36.66
	3	1	8.67	0.259	-12.2	29.54
		2	8.67	0.843	-36.66	53.99

Appendix V

Table IX: Pearson correlation between the cortisol concentration and blood parameters responsible for the immune response of female hedgehogs for the investigation period (2007-2008). Months are pooled, years are examined separately. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups in cortisol concentrations in 2007 (calculated with an ANOVA and a Tukey test) these groups were treated separately. No haematological values were analyzed in 2006.

Blood parameter/ Year (period)	N	r	p
Leucocytes (/nl)/ 2007 (May-October)	55	0.007	0.959
Leucocytes (/nl)/ 2007 (April-July, September-October)	53	-0.03	0.829
Leucocytes (/nl)/ 2007 (March-April)	8	0.397	0.33
Leucocytes (/nl)/ 2008	46	-0.217	0.147
Neutrophils (%)/ 2007 (May-October)	52	0.044	0.759
Neutrophils (%)/ 2007 (April-July, September-October)	50	-0.012	0.932
Neutrophils (%)/ 2007 (March-April)	8	-0.446	0.268
Neutrophils (%)/ 2008	45	-0.06	0.695
Eosinophils (%)/ 2007 (May-October)	52	-0.257	0.066
Eosinophils (%)/ 2007 (April-July, September-October)	50	-0.007	0.961
Eosinophils (%)/ 2007 (March-April)	8	0.645	0.084
Eosinophils (%)/ 2008	43	0.119	0.446
Basophils (%)/ 2007 (May-October)	39	-0.072	0.664
Basophils (%)/ 2007 (April-July, September-October)	42	-0.06	0.708
Basophils (%)/ 2007 (March-April)	8	0.626	0.097
Basophils (%)/ 2008	36	-0.128	0.457
Monocytes (%)/ 2007 (May-October)	51	0.009	0.95
Monocytes (%)/ 2007 (April-July, September-October)	50	-0.078	0.59
Monocytes (%)/ 2007 (March-April)	5	-0.151	0.721
Monocytes (%)/ 2008	42	-0.058	0.716
Lymphocytes (%)/ 2007 (May-October)	53	0.003	0.982
Lymphocytes (%)/ 2007 (April-July, September-October)	51	0.011	0.937
Lymphocytes (%)/ 2007 (March-April)	8	0.031	0.942
Lymphocytes (%)/ 2008	46	0.003	0.983

Table X: Pearson correlation between the cortisol concentration and blood parameters responsible for the immune response of male hedgehogs for the investigation period (2007-2008). Months are pooled, years are examined separately. N = number of samples, r = correlation coefficient, p = probability, significant p-values are in bold. Note: According to different homogenous groups in cortisol concentrations in 2007 (calculated with an ANOVA and a Tukey test) these groups were treated separately. No haematological values were analyzed in 2006.

Blood parameter/ Year (period)	N	r	p
Leucocytes (/nl)/ 2007 (May-October)	84	0.024	0.831
Leucocytes (/nl)/ 2007 (April-June, September-October)	65	-0.057	0.651
Leucocytes (/nl)/ 2007 (March)	7	0.952	**0.001**
Leucocytes (/nl)/ 2008	65	-0.082	0.515
Neutrophils (%)/ 2007 (May-October)	83	-0.089	0.424
Neutrophils (%)/ 2007 (April-June, September-October)	64	-0.126	0.321
Neutrophils (%)/ 2007 (March)	7	-0.643	0.120
Neutrophils (%)/ 2008	63	0.162	0.204
Eosinophils (%)/ 2007 (May-October)	77	0.075	0.516
Eosinophils (%)/ 2007 (April-June, September-October)	58	0.207	0.119
Eosinophils (%)/ 2007 (March)	7	-0.312	0.496
Eosinophils (%)/ 2008	62	0.143	0.268
Basophils (%)/ 2007 (May-October)	63	0.058	0.652
Basophils (%)/ 2007 (April-June, September-October)	47	0.066	0.661
Basophils (%)/ 2007 (March)	6	0.487	0.328
Basophils (%)/ 2008	55	-0.234	0.086
Monocytes (%)/ 2007 (May-October)	80	0.086	0.45
Monocytes (%)/ 2007 (April-June, September-October)	62	0.115	0.375
Monocytes (%)/ 2007 (March)	7	-0.527	0.224
Monocytes (%)/ 2008	62	0.068	0.601
Lymphocytes (%)/ 2007 (May-October)	82	0.04	0.72
Lymphocytes (%)/ 2007 (April-June, September-October)	63	-0.08	0.534
Lymphocytes (%)/ 2007 (March)	7	0.85	**0.015**
Lymphocytes (%)/ 2008	63	-0.163	0.201

Appendix VI

Table XI: Pearson correlation between the testosterone concentration and blood parameters responsible for the immune response of male hedgehogs for the investigation period (2007-2008). Months are pooled, years are examined separately. N = number of samples, r = coefficient factor, p = probability, significant p-values are in bold. Note: According to different homogenous groups in testosterone concentrations (calculated with an ANOVA and a Tukey test) these groups were treated separately. No haematological values were analysed in 2006.

Blood parameter/year (period)	N	r	p
Leucocytes (/nl)/ 2007 (March-July)	57	0.047	0.727
Leucocytes (/nl)/ 2007 (August-October)	43	-0.157	0.316
Leucocytes (/nl)/ 2008 (March-July)	43	-0.024	0.881
Leucocytes (/nl)/ 2008 (August-October)	18	-0.110	0.665
Neutrophils (%)/ 2007 (March-July)	57	-0.178	0.186
Neutrophils (%)/ 2007 (August-October)	42	-0.158	0.317
Neutrophils (%)/ 2008 (March-July)	41	-0.029	0.855
Neutrophils (%)/ 2008 (August-October)	18	-0.327	0.186
Eosinophils (%)/ 2007 (March-July)	54	0.029	0.834
Eosinophils (%)/ 2007 (August-October)	39	-0.267	0.1
Eosinophils (%)/ 2008 (March-July)	41	-0.002	0.99
Eosinophils (%)/ 2008 (August-October)	17	-0.102	0.689
Basophils (%)/ 2007 (March-July)	46	-0.089	0.557
Basophils (%)/ 2007 (August-October)	32	-0.09	0.624
Basophils (%)/ 2008 (March-July)	37	0.162	0.339
Basophils (%)/ 2008 (August-October)	14	-0.074	0.802
Monocytes (%)/ 2007 (March-July)	56	0.09	0.508
Monocytes (%)/ 2007 (August-October)	40	-0.056	0.734
Monocytes (%)/ 2008 (March-July)	41	0.046	0.777
Monocytes (%)/ 2008 (August-October)	17	0.343	0.177
Lymphocytes (%)/ 2007 (March-July)	57	0.131	0.331
Lymphocytes (%)/ 2007 (August-October)	41	0.127	0.427
Lymphocytes (%)/ 2008 (March-July)	41	-0.113	0.481
Lymphocytes (%)/ 2008 (August-October)	18	0.107	0.673