Comparison of physical condition and parasite burdens in rural, suburban and urban hedgehogs *Erinaceus europaeus*: Implications for conservation

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Table of contents

Abstract

1. From an epidemiological point of view, it is assumed that parasitism is closely linked to host density and, therefore, to opportunities to infest a host population. Hedgehog rescue centers have recently expressed concern about an apparent increase of parasite burdens in hedgehogs. In the same time it was recognized that hedgehog populations might reach high densities in urban areas.

2. In this study, we attempted to relate the abundance and diversity of eleven hedgehog parasite species to hedgehog population densities in rural, suburban and urban habitats in the agglomeration of Bern, Switzerland.

3. Hedgehog population densities were higher in urban than in rural and suburban zones; this was mainly due to a proportionally higher number of juveniles in the former habitat. Hedgehog urban populations may hence function as source in a metapopulation system. The health status of hedgehogs was similar in all three habitats.

4. 97% of the wild hedgehogs we examined (n = 135) were infected with one or more of the eleven parasite species. *Ixodes hexagonus, Crenosoma striatum, Capillaria aerophila* and *Capillaria sp.* showed a high prevalence, but generally lower than that reported from samples brought to rescue centers. The diversity of parasite species was higher in urban than in rural areas.

5. The prevalence of the ectoparasite *Ixodes hexagonus* increased from rural through suburban to urban areas, with higher intensities in urban compared to rural habitats. Urban hedgehogs were more heavily infested with *Crenosoma striatum* compared to hedgehogs of suburban and rural areas.

6. The intensity of *Ixodes hexagonus* was negatively correlated with the haematocrit value.

7. Overall, prevalence and intensities of most parasite species correlated positively with host density, with urban hedgehogs more affected than suburban and rural ones.

8. Given high prevalences and intensities of most parasite species in thriving dense urban hedgehog populations, blood characteristics may reflect detrimental, but natural density – dependent effects.

Zusammenfassung

1. Aus epidemiologischer Ansicht wird angenommen, dass Parasitismus stark mit der Wirtsdichte und folglich der Möglichkeit eine Wirtspopulation zu befallen verbunden ist. Kürzlich äusserten Igelzenter Bedenken über einen offensichtlichen Anstieg der Parasitenbelastung von Igeln. Gleichzeitig wurde erkannt, dass Igelpopulationen in urbanem Gebiet hohe Dichten erreichen könnten.

2. In dieser Studie versuchten wir die Abundanz und Diversität von elf Igelparasitenarten mit den Dichten von Igelpopulationen aus ruralen, suburbanen und urbanen Habitaten der Agglomeration Bern, Schweiz zu verbinden.

3. Die Igelpopulationsdichten waren höher in urbanen als in ruralen und suburbanen Gebieten; hauptsächlich dank des proportional höheren Jungenanteils im erst erwähnten Habitat. Urbane Igelpopulationen könnten folglich als Quelle in einem Metapopulationssystem funktionieren. Der Gesundheitszustand der Igel war in allen drei Habitaten gleich.

4. 97% der untersuchten wilden Igeln (n = 135) waren mit einer oder mehreren der elf untersuchten Ekto- und Endoparasitenarten befallen. *Ixodes hexagonus, Crenosoma striatum, Capillaria aerophila* und *Capillaria sp.* zeigten hohe Prävalenzen, jedoch generell niedrigerer als aus Berichten von Igelnzentren bekannt. Die Parasitenartendiversität erreichte höhere Werte in urbanen als in ländlichen Gebieten.

5. Die Prävalenz des Ektoparasites *Ixodes hexagonus* vergrössert sich von ruralen zu suburbanen bis zu urbanen Gebieten, wobei die Intensität in urbanen Habitaten stärker war als in ruralen. Urbane Igel waren viel stärker mit *C. striatum* befallen als Igel aus ruralen und suburbanen Gebieten.

6. Die Intensität von *I. hexagonus* korreliert negativ mit dem Hämatokritwert.

7. Insgesamt korrelieren die Prävalenz und die Intensität von fast allen Parasitenarten positiv mit der Wirtsdichte, während urbane Igle stärker betroffen sind als suburbane und rurale.

8. In Anbetracht der hohen Prävalenz und Intensität der meisten Parasitenarten in gedeihenden dichten urbanen Igelpopulationen, kann angenommen werden, dass Blutbilder nachteilige, jedoch natürliche dichteabhängige Effekte reflektieren.

1. Introduction

A special characteristic of parasites is their occurrence in a habitat, the host, which is itself an autonomous living entity (Rohde 1993). Hosts grow, reproduce and actively react to parasites, having their own habitat requirements. Habitat selection by hosts may thus have important sanitary consequences with hosts living in habitats that differ ecologically, therefore facing different infestation risks (Begon et al. 1996). Host population density is assigned a central role in epidemiological models, for instance by positively affecting the probability that a parasite transmission stage contacts hosts (Anderson & May 1978). In turn, host infestation can affect host survival, reproduction and population dynamics (Begon et al. 1996), therefore modifying its conservation status. Recent reports by hedgehog rescue centers about increasing parasite burdens in the species have raised conservation concern. Does this trend merely reflect positive demographic developments in host populations, or does it result from a general degradation in host physical and immunological condition? The aim of this work was to approach this question by comparing hedgehog physical condition, population density and parasitism along a urbanization gradient.

Hedgehog original habitat (semi-open, mosaic-rich landscape; Bontadina et al. 1993) started to get destroyed 50 years ago by expanding urbanization and intensification of agricultural practices. Yet, hedgehogs had still suitable refuges in human settlements where they can reach high densities (Reeve 1994).

Hedgehogs harbour a wide range of ecto- and endoparasites (Smith 1968); they are particularly affected by endoparasites. The hedgehog parasite fauna is described in several reviews: Barutzki et al. (1984), Carlson (1980; 1990), Isenbügel (1975), Löwenstein et al. (1991), Mehlhorn et al. (1993), Morris (1983), Reeve (1994), Robinson and Routh (1999), Saupe and Poduschka (1998), Schütze (1979) and Smith (1968).

The most common ectoparasite found on hedgehogs is the hedgehog flea (*Archaeopsylla erinacei*). More occasional fleas reported are the rat flea (*Nosopsyllus fasciatus*), the dog flea (*Ctenocephalides canis*) and the cat flea (*Ctenocephalides felis)*. Another ectoparasite is the hedgehog tick (*Ixodes hexagonus)* that may occur at high intensity. Additionally, the sheep tick (*Ixodes ricinus*) has been recorded. Endoparasites include *Hymenolepis erinacei, Brachylaemus erinacei, Capillaria*

erinacei, Capillaria sp, Capillaria aerophila and *Crenosoma striatum. H. erinacei* is the only, albeit scarcely found cestode in hedgehogs. *B. erinacei* is comparatively more frequent, invading the intestinal and occasionally also the bile duct. Prevalent nematodes are the *C. erinacei* and *C. sp.*, whose adults infest the gut, and *C. aerophila*, of which adults reside in the bronchioles. *C. striatum* is an abundant, species-specific endoparasite of hedgehogs, reaching prevalence of up to 100%; adult worms live in their lungs.

This study consists of 3 parts. First, we assessed hedgehog population densities along an urbanization gradient (rural, suburban and urban habitats). Second, we studied hedgehog physical condition with respect to these three urbanization levels. Third, we investigated parasite species diversity, prevalence and intensities in the three habitat categories. This enabled us to unravel the relationships between parasite infestations, host population densities and host individual physical status. Through this approach it might be possible to judge whether the increasing infestation of hedgehogs by parasites is of conservation concern.

2. Methods

2.1. Study area

The study was conducted within and around the agglomeration of Bern (46°57'N, 7°26'E, 540 m altitude), which lies in the Swiss midlands between the Jura mountains and the Alps. Bern belongs to the largest cities of the country with 128'000 inhabitants over an area of 51.6 km^2. The Aare river meanders throughout the region, offering a diversified mosaic landscape. Suburban settlements have invaded the nearby, formerly isolated villages, whereas the rural landscape has kept its traditional structure with isolated villages interspersed among farmland and woodland (Appendix 1).

These three habitats (urban, suburban and rural) are distinguishable based on their distance to the city and land use, with the resulting amount of sealed vs non–sealed area (Appendix 2). From an architectural viewpoint, the rural zone consists of self-contained villages with homesteads and family houses occurring at low density. Here non-sealed area is predominant. The suburban zone is characterised by human-made structures such as buildings occurring in higher proportion than non-sealed areas. The village centre is densely built and harbours shopping facilities. Schools, graveyards and other public institution parks compose the green space. Farmland is almost absent. The urban zone corresponds to the city. Industrial zones are almost entirely sealed. Non-sealed areas occur around residential buildings, in parks, graveyards and parks.

Our study system consisted of 9 sampling plots of 100 ha each, spread across the agglomeration, with 3 plots in each main habitat type (rural, suburban, urban) (Table 1, Fig.1, Appendix 1).

2.2. Sampling design

Fieldwork was carried out between 14.05.2003 – 02.10.2003. Each plot was visited during 3 consecutive nights per season (spring, summer, autumn), resulting in 9 sampling nights per plot. The temporal sequence of visits to a given plot was randomly chosen within a season. A visit consisted of 6 h of hedgehog searching by foot, with the aid of a powerful torchlight. It lasted from dusk to dawn. Censuses were restricted to weather conditions (Esser 1984). Hedgehogs were caught by hand and,

after inspection, released at capture side. Hedgehogs were handled and individually marked under licence from the office of nature conservation of the Canton of Bern (14.05.2003).

2.3. Estimation of hedgehog population densities

Hedgehog population sizes were estimated in two ways. First, the total number of individuals encountered during the entire filed study was used. Second, population densities were evaluated using Pollock's robust design (Pollock et al. 1990) implemented in MARK (Kendall 2002). In order to enable individual recognition, six colour-coded shrinking tubes were glued each to a distinct spine. Individual capture-recapture histories were drawn from the nine censusing sessions per plot. For within–seasons censuses (n = 3 per plot), population was assumed to be closed, whereas it was assumed to be open as regards among season capture-recapture histories (n = 3).

2.4. Sex and age

Male hedgehogs were recognised by the conspicuous penis sheath opening well forward on the belly, whereas the vulva of the females is very close to the anus (Reeve 1994). Two age classes were distinguished on basis of body size: juveniles (yearlings prior to hibernation) and subadults / adults (older than juveniles).

2.5. Physical condition

As a proxy of physical condition we used first body mass (taken to the nearest 25 g with a Pesola balance). Signs of sickness were recorded: 0 = no sign, 1 = some looseness, 2 = distinct breathing noises, and 3 = looseness and breathing noises.

Second, a blood cell count was performed in individuals captured in autumn. For blood sampling the hedgehog was placed in dorsal position with a hind leg extended. Blood samples was taken from the medial saphenous vein with a 25G x $^{5}/_{8}$", 0.5 x 16 mm needle (Neolus, Terumo) attached to a 1 ml syringe (Omnifix-F; Braun). Approximately 0.5 ml of blood were collected and immediately placed into a tube treated with ethylenediaminetetraacetic acid (Sarstedt AG, Sevelen, Lewis 2002). The tubes were slowly tilted to keep the blood on the move and prevent it from

coagulating. Transport action to the lab was undertaken without delay as blood analysis had to be accomplished within two hours. Blood counts were carried out both manually and with an automated analyser. For the manual count a blood smear was prepared; blood cell type assignment was accomplished twice per smear from at least 100 blood cells (Kraft 1999). The blood counting machine used (Cell Dyn 3500, Abbott Laboratories) sucks a standard amount of blood through a narrow tubing and counts with a light detector the number of cells passing through, identifying the cell type by separating the multi-angle polarized scatter. Total haemoglobin, red blood cell count (RBC), haematocrit (HCT), mean corpuscular volume (MCV), mean corpuscular haemoglobin (MCH), mean corpuscular haemoglobin concentration (MCHC), total white blood cell count (WBC), neutrophil count, lymphocyte count, monocyte count, eosinophil count, basophil count and platelet count were recorded for each animal (Kraft 1999). These manipulations were performed under licence from the Swiss federal veterinary service (License NR. 134 / 2003).

2.6. Parasite loads

Recorded ectoparasites were *Archaeopsylla erinacei*, *Nosopsyllus fasciatus*, *Ctenocephalides felis* and *C. canis*, *Ixodes hexagonus* and *I. ricinus*. To estimate ectoparasite loads, the hedgehogs were narcotised with 1–2 ml Isofluran (Robinson & Routh 1999), applied on an inhalation swab. The procedure was learned in the Zootierklinik Zürich and needed to avoid rolling up of the hedgehog during examination (Isenbügel 1975). The pelt as well as the spines were scanned for fleas and ticks. The intensity of the infestation was assigned to one of the following levels: 0-5, 6-10, 11-20, 21-50, 51-100, 101-200, >200 parasites. In addition, a representative sample was taken for later species determination. The use of a biological insecticide (BioKill) was necessary to immobilize the fleas when numerous (Rommel et al. 2000). In this case the animal was covered with a tissue, head excluded, and fumigated. After some minutes it was softly shaken over a white tissue (Van Vuren 1996), which collected the fleas. Sealed in a plastic bag, the tissue was placed in the deep freezer for killing the fleas and storage. Ticks were collected with tweezers and preserved in a solution of 70% ethanol and 2-5% glycerine (Rommel et al. 2000) in wide-necked glass flasks. External parasites were identified using the reference guides by Weidner (1998) and Mehlhorn et al. (1993), and a binocular

(Leica MZ95) if necessary. For a given individual hedgehog, we estimated 1) the number of parasite species found (species richness) as well as an index of their diversity (Shannon-Wiener; (Begon et al. 1996); 2) the intensity of each of the various species present. The prevalence of a given parasite species corresponded to the proportion of hosts harbouring it in a given study plot.

The six endoparasites quantified were *Hymenolepis erinacei*, *Brachylaemus erinacei*, *Crenosoma striatum*, *Capillaria aerophila* and *C. sp.* (including *C. erinacei*). They were investigated from faecal samples collected from hedgehogs kept in an plastic box (25 x 50 x 25 cm) with a wire cover for up to two hours until a sufficient amount was defecated (Esser 1984). In the box food and shelter were provided. A 1 g dropping subsample was taken and stored in a 10 ml Sodium acetate-Acetic acid-Formaldehyde solution for later analyses. Eggs of *B. erinacei*, *C. aerophila* and *C. sp.* were detected with the SAF-concentration technique (Marti & Escher 1990). The rest of the faecal sample was used to assign *C. striatum* larvae with the Baermann funnel technique (Rommel et al. 2000). After 24 h, 1 ml was drained and searched for larvae under a microscope (Olympus BH-2). Species determination was achieved with the help of Mehlhorn et al. (1993). Endoparasite loads were evaluated in the same way as for ectoparasites.

2.7. Statistical analyses

Discrete and continuous variables were tested for normality and variance homogeneity prior to running Anovas. Welch Anova was used to account for unequal variance. In some cases non parametric Anova procedures were chosen (Wilcoxon, Kruskal-Wallis). Post hoc pairwise comparisons between categories were conducted using Tukey's algorithm (Zar 1999). A stepwise backward elimination procedure was performed to drop out insignificant factors where needed. Tests involving parasite infestations requested a log transformation of variables.

For statistical tests involving nominal and ordinal descriptors we used logistic regression, with the Wald statistics (Zar 1999). Linear regression models (Zar 1999) were also applied. JMP4 (SAS Institute Inc. 2001, Cary, NY, USA) was used for all analyses. Throughout this study, a single individual was only investigated once in order to avoid pseudoreplication.

3. Results

3.1. Population density estimates

All together we recorded 323 encounters with hedgehogs; they concerned 213 different individuals. Sex ratio was well balanced with 50.7% of females; 59.2% of individuals were adults and 40.8% juveniles (Table 2).

Population age structure (adults vs. juveniles) varied significantly with respect to habitat and season (Stepwise backward logistic regression, factor plot nested within habitat, both factors with $P < 0.001$). The proportion of juveniles was always greater in urban habitat; overall it increased over seasons (Fig. 2). Sex ratios showed no variation in relation to habitat and season (logistic regression).

The number of individuals found at each visit varied among the habitats, within the following ranges: 6-24 (rural); 20-23 (suburban) and 25-37 (urban). We tested for statistical differences in hedgehog number, with respect to habitat and season, on the two age classes separately. The number of adults depended only on factor "season" (nested Anova); it decreased significantly from, on average, 2.4 (spring), to 1.6 (summer) and 0.7 (autumn) individuals per night * plots (Tukey post hoc test, Table 3). The number of juveniles found differed between habitat and with seasonality (nested Anova, Table 3). A post-hoc Tukey-test assessed a significantly higher number of juveniles in urban (mean = 2.07 individuals per night * plot) than in rural (0.56) and suburban habitat (mean = 0.59). Their number also augmented over the season (mean spring = 0.30, summer = 1.48, autumn = 1.44) (Table 3).

The best models for history of encounters were obtained when adults and juveniles were treated as two distinct groups with 1) survival rates constant over time (0.45 ± 0.06), 2) emigration equal to immigration rates which were treated constant over time (3.83 *1011 ± 7.14 * 106), 3) different capture rates constant over time, and equal to the recapture rate (capture rate: juveniles = 0.29 ± 0.04, adults = 0.23 ± 0.03), and 4) different population densities over time (Appendix 3). The estimated population densities per age class, season and plot are shown in Appendix 4. The population density of a plot was estimated by adding the average of the population densities over the season for both adults and juveniles. As the area of suitable habitat varied among the plots (Fig. 1), an adjusted density was calculated from non-sealed areas (Appendix 4). Adjusted population densities differed significantly

between habitats (ANOVA, F = 6.57, df = 2, P = 0.031). Urban habitat harboured (average ±, se) 71 ± 18 individuals per 100 ha non-sealed area compared to 31 ± 3 and 16 ± 5 for suburban and rural habitats, respectively.

3.2. Physical condition

Body mass in juveniles was, on average, lighter (585 g ± 21.02) than in adults (1139 g ± 21.08; Anova, F = 343.33, df = 1, P < 0.0001) and further influenced by the season (F = 17.65, df = 2, P < 0.0001).

Out of 213 hedgehogs 89 (41%) showed some signs of sickness: looseness (n = 52) and breathing noises (n = 19). Both symptoms together were present in 18 individuals. The occurrence of signs of sickness was neither influenced by the factors "season", "zone", "plot nested in habitat" nor by "sex", "age" and "body mass" (nested Anova).

Blood samples were collected from 31 hedgehogs in autumn. The composition of this sample did not differ from the global captured hedgehog dataset (n = 213), neither as regards sex (Fisher's exact test, P = 0.17) or age (P = 0.70). The automated discrimination of some white cell types values did not match the manual differentiation (Welch ANOVA: monocyte count: F = 5.80, P = 0.01, df = 1, ANOVA: basophile count: F = 12.02, P < 0.001, df = 1). The output charts of the analyses showed disruption of the identification process of white cell types due to thrombocyte aggregations. Therefore we combined the percentages of the manual count together with the total white cell blood number obtained from the automated cell analysis (Appendix 5).

The manual blood counts revealed in nearly all blood samples an anisocytose associated with a polycytose. The measure of the haematocrit value showed differences between the age classes (nested Anova, Appendix 6). However, the factors "season", "habitat", "plot nested in habitat", "sex" and "body mass" had no significant influence on the haematocrit.

3.3. Occurrence of parasites

3.3.1. PREVALENCE

Sex and age composition of the hedgehog sample investigated for parasite loads (n = 135) did not differ from the global sample of animals found (n = 213) (Fisher's exact test, sex: P = 0.91; age: P = 0.37).

Only in four animals out of 135 (3%) none of the eleven searched parasite species was detected (Appendix 7). Logistic models on prevalence of all ectoparasites pooled or of all parasites pooled were tested for the factors "season", "habitat", "plots nested in habitat", "sex", "age" and "body mass", but were non-significant. Only the prevalence of endoparasites yielded a significant model, with body mass negatively affecting prevalence (heavier hedgehogs had less prevalence than lighter ones).

Overall, eight parasite species were found among the eleven species searched for (Table 4); prevalence decreased according to the following species sequence: *C. aerophila* (69.6%), *I. hexagonus (58.5%), C. striatum* (54.1%) and *C. sp. (50.4%), A. erinacei* (43.7%), *I. ricinus* (11.1%), *B. erinacei (10.4%)* and *C. felis* (0.7%, only one sample). *C. canis*, *N. fasciatus* and *H. erinacei* were totally missing.

The prevalence of *I. hexagonus* increased significantly from rural (36.8%) to suburban (55.0%) till urban (75.4%) habitats (logistic regression, $P < 0.001$, Fig. 3 and Table 4). The prevalence of *I. ricinus* decreased from spring (25.0%) to summer (3.7%) and autumn (8.9%, $P < 0.05$, Table 4). The prevalence of *C. striatum* decreased with the body mass of the hedgehogs ($P < 0.001$), whereas the prevalence of *C. aerophila* increased with body mass ($P < 0.001$) and concerned mostly males ($P < 0.05$) (Table 4).

3.3.2. INTENSITY

A total of 2173 ectoparasites (4 species) and 9477 endoparasites (4 species) were found on the 135 hedgehogs examined. Species intensities and significant models for the mean intensity of parasite species per hedgehog are shown in Table 4 (nested Anova with a stepwise backward elimination procedure). The intensity of *A. erinacei* in the rural habitat (retransformed mean = 1.07 parasite individuals per hedgehog) was significantly lower than in the suburban habitat (means = 1.95, Turkey post hoc test, $P < 0.05$, Fig. 4a). The mean intensity of *I. hexagonus* differed

significantly among rural habitats (mean = 0.84 parasites per hedgehog) and suburban (3.26), urban (4.25) habitats respectively (Tukey post hoc test, $P < 0.001$, Fig. 4b). Mean *C. striatum* increased from spring (mean = 0.88) to summer (8.33) and autumn (10.56; Tukey post hoc test, $P < 0.001$) and increased with decreasing body mass (regression: $t = -4.94$, $P < 0.001$). The mean intensity of *C. striatum* increased from rural (mean = 4.58 parasites) and suburban (3.14) to urban habitats (9.66, Tukey post hoc test, $P < 0.01$, Fig 4c). The intensity of *C. aerophila* was much higher in spring (mean = 5.12 parasites per hedgehog) compared to summer (mean = 2.07) and autumn (mean = 1.34, Tukey post hoc test, $P < 0.001$). Moreover, males (mean = 3.22) had higher loads than females (mean = 1.74, Tukey post hoc test, $P < 0.05$).

3.3.3. DIVERSITY

Variation in parasite diversity by the Shannon-Wiener indices revealed higher diversity in ectoparasite than in endoparasite species (Wilcoxon, $\chi 2 = 22.03$, $df = 1$, $P < 0.001$; Table 4). The Shannon-Wiener index of ectoparasite species diversity showed a higher value in the urban areas (mean = 0.11) compared to rural (mean = 0.05) and suburban (mean = 0.06) habitats (Kruskal-Wallis). The other factors ("plot within habitat", "season", "sex", "age", "signs of sickness", "body mass") were not significant (Table 4).

3.4. Parasite intensity vs blood cell count

To compare the intensity of parasite infestation of the animals with the blood cell count parameter, a Spearman's correlation test was conducted between the mean intensity of parasite species and the single blood parameters using their residuals of the ANOVA models performed looking for differences between all possible groups (Appendix 6). The haematocrit value correlated negatively with the intensity of *I. hexagonus* (Appendix 8).

4. Discussion

4.1. Parasite abundance

Our results confirm the massive parasite infestation often reported in hedgehogs (Barutzki et al. 1987; Degiorgis 1998; Schütze 1979). However, as high intensities as observed in hedgehog rescue centers were not found in our free-ranging hedgehogs, what supports Esser's view (1984) that rescued hedgehogs represent a biased sample consisting mostly of unhealthy individuals. Esser (1984) reported a parasite prevalence of 100% in adult hedgehogs which is even higher than our findings (97%). Yet, our prevalence values concerned both juveniles and adults, between which we could not find any difference, contrary to Esser (1984) and Berthoud (1982), who found higher prevalences in adults.

In this study ectoparasites had a prevalence of 63.2% to 84.2% according to habitat type, whereas overall endoparasite prevalence was in general around 90%. Comparably high endoparasite prevalences of 77% to 90% were reported by Barutzki et al. (1987; 1984), Esser (1984) and Laubmeier (1985).

The ectoparasite *I. hexagonus* and the endoparasites *C. aerophila*, *C.* and *C. sp.* were the most frequent parasite species in our study with prevalence ranging from 50% to 70% according to species and habitat.

Overall species pattern of infestation varied across seasons (*C. striatum, C. aerophila* and *C. sp.)* and in relation to body mass *(C. striatum, C. aerophila*). Additionally *I. hexagonus* prevalence and intensity differed between habitats (rural, suburban, urban), whilst *C. striatum* differed only in intensity.

The overall prevalence of *I. hexagonus* in this study (58%) is smaller than that (95%) reported by Liebisch and Walter (1986). However, their sample was most certainly biased towards animals with high infestations given that pet owner, farmers and hunters participated in hedgehog collection. Our results established a dramatic increase in prevalence and intensity of *I. hexagonus* from rural to urban habitats. While in rural areas 37% of hedgehogs harbour an average of 1.5 Ixodes parasites, 55% of suburban hedgehogs are infested with, on average, 10 ticks, vs 75% with 14 ticks per individual in urban habitats.

Liebisch and Walter (1986) and Ogden (2000) also found *I. hexagonus* more frequently on hedgehogs of suburban yards and park like landscape. As this parasite

is not very host specific (at least 10 host mammal species described in Germany, predominately Mustelidae, cats and dogs, (Liebisch & Walter 1986) it could be assumed that the availability of dense host populations, including several alternative hosts, in urban areas might dictate this pattern. But note that *I. ricinus*, rare in our study, showed exactly the opposite pattern, namely a high occurrence in rural zones (Liebisch & Walter 1986), which is further supported by a study of the same tick species on Blackbirds (Gregoire et al. 2002).

Our prevalences of endoparasites do not differ much form the ranges in previous descriptions [Endoparasite species of wild hedgehogs were investigated by Barutzki et al. (1987; 1984), Esser (1984) and Laubmeier (1985).]: *C. aerophila*: 15-59%; this study 70%; *C. striatum*: 38-72%; 54%; *C. sp.*: 72–74%; 50%. Overall variation might be accounted for by different sampling methods (Bauer & Stoye 1984; Esser 1984; Majeed et al. 1989; Schütze 1979). In particular, Majeed et al. (1989) claim that the only valid technique is section. Yet, for conservation reasons a section of animals were out of though in our study.

C. striatum showed no difference in prevalence among habitats but did as concerns intensity: it occurred with a mean intensity of 104 larvae per hedgehog in urban habitat, while the intensity in suburban (10) and rural (18) hedgehogs was much smaller. Spatial variation in prevalence may be linked to habitat-dependent risks of infestation (Gregoire et al. 2002). *C. striatum* lives in the bronchi and bronchioles of hedgehogs. It is transmitted via molluscan intermediate hosts which ingest larvae excreted with faeces; the cycle is completed when hedgehogs eat slugs and snails (Saupe & Poduschka 1998). The latter are very much abundant in urban lawns, gardens and parks where hedgehogs use to scavenge food. According to Esser (1984) a high snails and slugs availability increases the risk of infection and the level of infestation.

4.2. Habitat–dependent hedgehog population density

Average, adjusted population densities of hedgehogs varied from 0.16 individuals per ha in rural habitat, 0.31 in suburban habitat and 0.67 in urban zones. This agrees with former findings of 0.22–0.83 animals per ha (Berthoud 1982; Bontadina et al. 1993; Esser 1984; Kristiansson 1990; Morris 1988; Reeve 1982; Zingg 1994). We used two approaches for estimating population densities: 1) estimation of the

minimum number of individuals encountered; 2) capture-recapture histories. As the second method accounts for spatial-temporal variation in trappability, the among-habitat discrepancies cannot stem from habitat sensitive censusing techniques only, as criticized by Esser (1984), and mirror actual populations densities. Reeve's (1994) assumption that hedgehogs thrive in suburban environments, and may even reach higher densities than in rural habitats, is clearly supported by our study. In the end, abundance is influenced positively by food availability (Boitani & Reggiani 1983), a sufficient offer of nest sites, and low predation levels (Doncaster 1992; Ward et al. 2000). All these conditions appear to be fulfilled in urban areas.

As a proxy of hedgehog physical condition we referred to body mass and blood cell counts. Yet, they did not differ among our three habitat types despite distinctive parasite loads. This may indicate no influence of habitat on physical condition or that body mass is not a good proxy. Eventually a body condition index combining body mass and body length would have yielded different results.

Another way to judge health would be to inspect faeces more carefully for coloration and consistence (Isenbügel 1975). On the other hand faeces appearance depends also on the food eaten; it remains thus unclear how reliable is this technique.

Our results suggest that although population densities vary with habitat there is no evidence for density-dependent effects on physical condition. A higher amount and proportion of juveniles in urban habitats compared to suburban and rural ones is surprising. The reasons why cities represent a optimal reproduction habitat remain ill-understood; may be a higher ambient temperature could play a role (Klausnitzer 1988). Despite an apparently high urban-specific mortality, city hedgehogs may represent source populations exporting individuals to suburban and rural habitats.

4.3. Parasite burdens vs host density

In the two parasites *I. hexagonus* and *C. striatum,* prevalence and mean intensity increased with host population density from rural through suburban to urban habitats. This probably results from an increased parasite transfer rate which is proportional to the encounter rate of infested and susceptible hedgehog hosts (Begon et al. 1996). As hedgehogs are solitary, except for short encounters during the courting season (Morris 1983; Reeve 1994), horizontal transmission of ectoparasites may take place

either after direct contact between hosts, or more probably, through active parasite dispersal and colonization (Heeb et al. 1996). Morris (1983) presumes increasing numbers of *I. hexagonus* as a result of its reproduction in the host's nest. Furthermore, the presence of several additional hosts, such as cats and dogs in urban areas, probably increases exchange opportunities. Degiorgis (1998) designates artificial feeding places, which often attract many hedgehogs, as possible source of contaminations with endoparasites like *C. striatum.*

In general, high host density is a key factor in promoting parasite species richness (Morand & Poulin 1998), since dense host populations will more readily sustain populations of adult parasites (Bell & Burt 1991). This is supported by our study, which showed a correlation between ectoparasite fauna diversity and host density. The relationships between host life history traits and parasite species richness and diversity are stronger in directly transmitted parasites than in indirectly transmitted mammalian parasites (Arneberg 2002). This may explain that a link occurred in our study as regards ectoparasites but not as concerns endoparasites, the latter being rarely transmitted directly through contact among individuals hosts.

4.4. Impact of parasitism on hedgehog conservation

Many wild hedgehogs that apparently thrive may harbour unexpectedly high amounts of parasites (Barutzki et al. 1984). This is corroborated by our finding of no apparent impact of parasites upon body condition and signs of sickness. However, blood cell counts clearly indicated an activation of the immune function. Blood samples showed abnormalities in the red cells and hematocrit values correlating negatively with the intensity of *I. hexagonus.* Mass infestations of this blood-sucking tick may hence be a source of health concern for hedgehog individuals, especially in dense urban populations (Saupe & Poduschka 1998).

But can the observed amount of parasitism really affect species population dynamics negatively (Esser 1984)? On the one hand, urban hedgehog populations thrive and reach densities not known from other habitats, on the other hand they are highly contaminated. That hedgehogs thrive in urban habitat appears as a paradox. Despite its fine-grained habitat mosaic, its wide offer of shelters and food sources, its favorable climatic conditions (Klausnitzer 1988), a town, on first glance, seems to be a nightmare for hedgehogs. Roads and fences fragment the habitat and vehicle

traffic represents a permanent challenge (Rondinini & Doncaster 2002). In the end, even gene flow might be affected by all these physical barriers (Becher & Griffiths 1998). In this context, parasitism might just be seen as one supplementary factor acting on population dynamics. The records of rescue centres about an increasing number of hedgehogs with high parasite burden may therefore simply reflect high local population densities. That juveniles represent a greater proportion of the population in urban than in suburban and rural habitat, as established in this study suggests that the high parasite loads of city hedgehogs might represent more a nuisance for the individuals affected than a serious conservation issue.

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Table 1. The nine study plots, their habitat allocation, distance to the city centre (km) and amount of sealed area (ha); means (+ sd) for habitats are given in italics

Plot	Habitat	Local term	Coordinates	Distance	Sealed area
R1	rural	Oberbottigen	46°56'N, 7°21'E	7.44	31
R2	rural	Richigen	46°55'N, 7°35'E	11.36	28
R3	rural	Gasel	46°54'N, 7°24'E	5.64	29
Average (sd) rural habitat				*8.15 (2.93)*	*29.48 (1.06)*
S1	suburban	Bolligen, Ittigen	46°59'N, 7°30'E	5.58	60
S2	suburban	Ostermundigen	46°58'N, 7°29'E	3.34	55
S3	suburban	Zollikofen	47°00'N, 7°27'E	5.69	47
Average (sd) suburban habitat				*4.87 (1.33)*	*53.92 (6.77)*
U1	urban	Holligen (Bern)	46°57'N, 7°25'E	2.14	58
U2	urban	Breitfeld, Breitenrain (Bern)	46°58'N, 7°27'E	1.96	75
U3	urban	Bethlehem, Bümpliz (Bern)	46°57'N, 7°23'E	4.24	64
Average (sd) urbran habitat				*2.78 (1.27)*	*65.77 (8.55)*

Table 2. Number (percentage) of individuals found (n = 213), with recaptures (n = 110), at the nine plots in the three habitats.

Plot	Adults			Juveniles			Total	Total
Habitat	Female	Male	Total	Female	Male	Total	individuals	recaptures
R1	8 (33.3)	8 (33.3)	16	4 (16.7)	4 (16.7)	8	24	9
R2	8 (38.1)	9 (42.9)	17	4 (19.0)	0 (0.00)	4	21	7
R3	2 (33.3)	1 (16.7)	3	3 (50.0)	0 (0.0)	3	6	3
R	*18 (35.3)*	*18 (35.3)*	*36*	*11 (21.6)*	*4 (7.8)*	*15*	*51*	*19*
S1	7 (30.4)	9 (39.1)	16	3 (13.0)	4 (17.4)	7	23	10
S2	12 (60.0)	5 (25.0)	17	0 (0.0)	3 (15.0)	3	20	5
S3	5 (21.7)	12 (52.2)	17	2 (8.7)	4 (17.4)	6	23	9
S	*24 (36.4)*	*26 (39.4)*	*50*	*5 (7.6)*	*11 (16.7)*	*16*	*66*	*24*
U1	10 (27.0)	5 (13.5)	15	8 (21.6)	14 (37.8)	22	37	31
U2	8 (23.5)	9 (26.5)	17	9 (26.5)	8 (23.5)	17	34	28
U3	7 (28.0)	1 (4.0)	8	6 (24.0)	11 (44.0)	17	25	8
U	*25 (26.0)*	*15 (15.6)*	*40*	*23 (23.9)*	*33 (34.4)*	*56*	*96*	*67*
Total	67	59	126	39	48	87	213	110

Table 3. The number of adults and juveniles found per night (n = 81) with the effects of the factors "season", "habitat" and "plot [habitat]" (nested ANOVA, df = degree of freedom, P = probability). Results of pairwise comparisons (Post hoc Tukey test) are shown in Fig.2.

Source of variation	Sum of squares	df	Variance	F ratio	P
Number of adults found					
Season	37.56	2	18.78	11.33	**<0.0001**
Habitat	3.85	2	1.93	1.16	0.3188
Plot [habitat]	18.59	6	3.10	1.87	0.0982
Error	116.00	70	1.66		
Number of juveniles found					
Season	24.52	2	12.26	12.23	**<0.0001**
Habitat	40.52	2	20.26	20.22	**<0.0001**
Plot [habitat]	4.37	6	0.73	0.73	0.6294
Error	70.15	70	1.00		

Table 4. Prevalence (ordinal logistic regression, mean ± CI), intensity (nested ANOVA, mean ± se) and diversity (Kruskal-Wallis, mean ±se) of the single parasites species, ecto-, endo- and all parasite species pooled tested on the factors "season", "habitat", "plot [habitat]", "age", "sex", "body mass" and "signs of sickness". Only significant factors are shown. (df = degree of freedom, P = probability; * = Wald χ^2)

Parasites	Prevalence				Intensity				Diversity			
Source of variation	**χ^2**	**df**	**P**	**Mean (± CI)**	**F ratio**	**df**	**P**	**Mean (± se)**	**χ^2**	**df**	**P**	**Mean (± se)**
Archaeopsylla erinacei	23.97	8	**0.0023**	43.7 *(35.2 - 52.5)*	2.72	16	**0.0010**	6.5 (± 1.6)				
Habitat					3.94	2	**0.0220**					
Plot[habitat]	15.52*	6	**0.0166**		5.77	6	**<0.0001**					
Ctenocephalides felis	4.08	8	0.8499	0.7 *(0.0 - 4.06)*	0.62	16	0.8661	0.0 (± 0.0)				
Ctenocepalides canis				0.0 *(0.0 - 2.7)*								
Nosopsyllus fasciatus				0.0 *(0.0 - 2.7)*								
Ixodes hexagonus	15.89	2	**0.0004**	58.5 *(49.7 - 66.9)*	2.040	16	**0.016**	9.0 (± 1.9)				
Habitat	14.48*	2	**0.0007**		10.76	2	**<0.0001**					
Ixodes ricinus	9.48	2	**0.0087**	11.1 *(6.4 - 17.7)*	1.19	16	0.2822	0.5 (± 0.3)				
Season	8.14*	2	**0.0149**									
Ectoparasite species	16.89	16	**0.3924**	76.3 *(68.2 - 83.2)*				4.0 (± 0.6)	8.14	2	**0.0171**	0.1 (± *0.12*)
Hymenolepis erinacei				0.0 *(0.0 - 2.7)*								
Brachylaemus erinacei	13.67	16	0.6231	10.4 *(5.8 - 16.8)*	1.04	16	0.4254	1.4 (± 0.8)				
Crenosoma striatum	11.03	1	**0.0009**	54.1 *(45.3 - 62.7)*	4.95	16	**<0.0001**	35.6 (± 7.7)				
Body mass	10.08*	1	**0.0015**		8.00	1	**0.0054**					
Habitat					5.42	2	**0.0055**					
Season					13.17	2	**<0.0001**					
Capillaria aerophila	16.45	2	**0.0003**	69.6 *(61.1 - 77.2)*	2.20	16	**0.0084**	7.4 (± 1.6)				
Sex	8.45*	1	**0.0037**		6.22	1	**0.0139**					
Body mass	9.67*	1	**0.0019**									
Season					8.54	2	**0.0003**					
Capillaria sp.	20.91	16	0.1819	50.4 *(41.6 - 59.1)*	1.67	16	0.0613	9.4 (± 3.9)				
Endoparasite species	7.49	1	0.0620	90.4 *(84.1 - 94.8)*				13.4 (± 2.3)	2.51	2	0.2851	0.1 (± *0.52*)
Body mass	6.10*	1	**0.0135**									
Parasite species	19.52	16	0.2428	97.0 *(92.6 - 99.2)*				8.7 (± 1.2)	5.34	2	0.0692	0.3 (± *0.17*)

Figure captions

Fig. 1. Characteristics of the three habitat types sampled: a) distance (m) of study plots form the city centre (mean ± se); b) percentage of sealed area (mean ± se). Error bars depict among plots (n = 3 per habitat) variation. Anova with Tukey post hoc pairwise comparisons, *: $P < 0.05$; **: $P < 0.01$.

Fig. 2. Changes in the proportion of juveniles (mean of plots ± se) in rural, suburban and urban habitats (total n = 213) according to season. Ordinal logistic regression, $P < 0.001$ for both factors.

Fig. 3. Prevalence of I. hexagonus in relation to habitat (mean ± 95% CI, the latter showing among plot variation) in 135 hedgehogs. Ordinal logistic regression, $P < 0.001$.

Fig. 4. Parasite intensity in relation to habitat (retransformed means ± se, the latter showing among individual variation): a) A. erinacei, b) I. hexagonus and c) C. striatum (n = 135). Anova with Tukey post hoc pairwise comparisons, *: $P < 0.05$; **: $P < 0.01$, ***: $P < 0.001$.

Figures

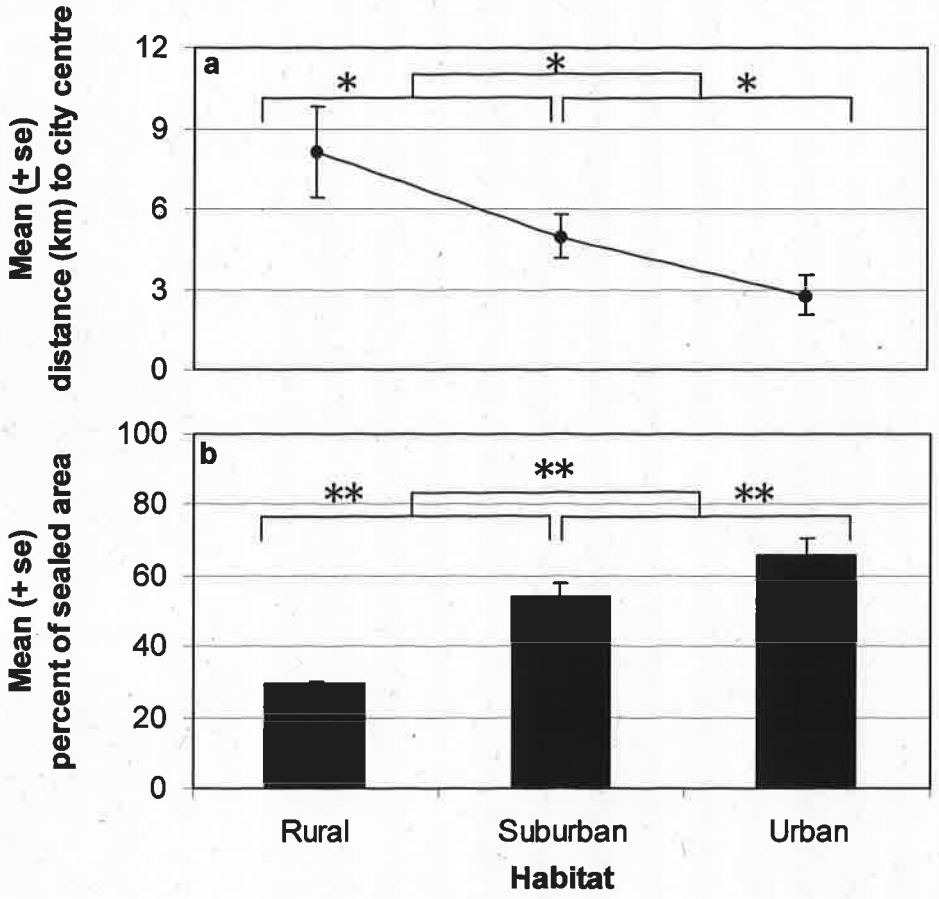


Fig. 1

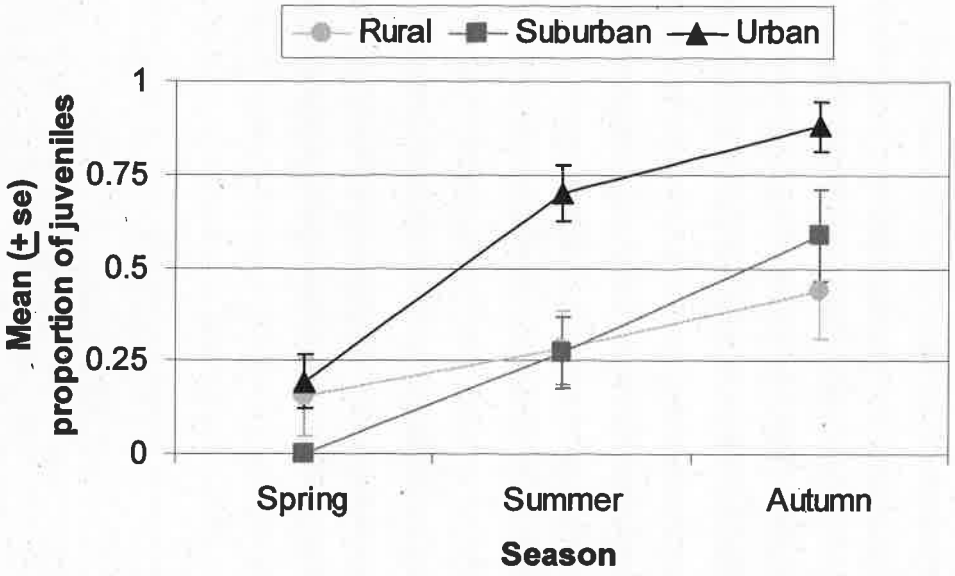

Rural
Suburban
Urban
1
0.75
0.5
0.25
0
Mean (± se) proportion of juveniles
Spring
Summer
Autumn
Season

Fig. 2

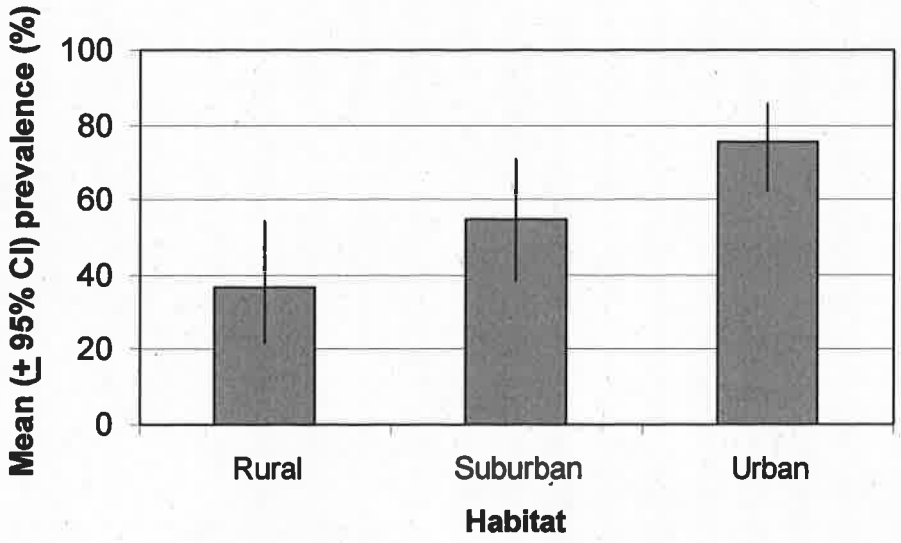

Mean (± 95% CI) prevalence (%)
100
80
60
40
20
0
Rural
Suburban
Urban
Habitat

Fig. 3

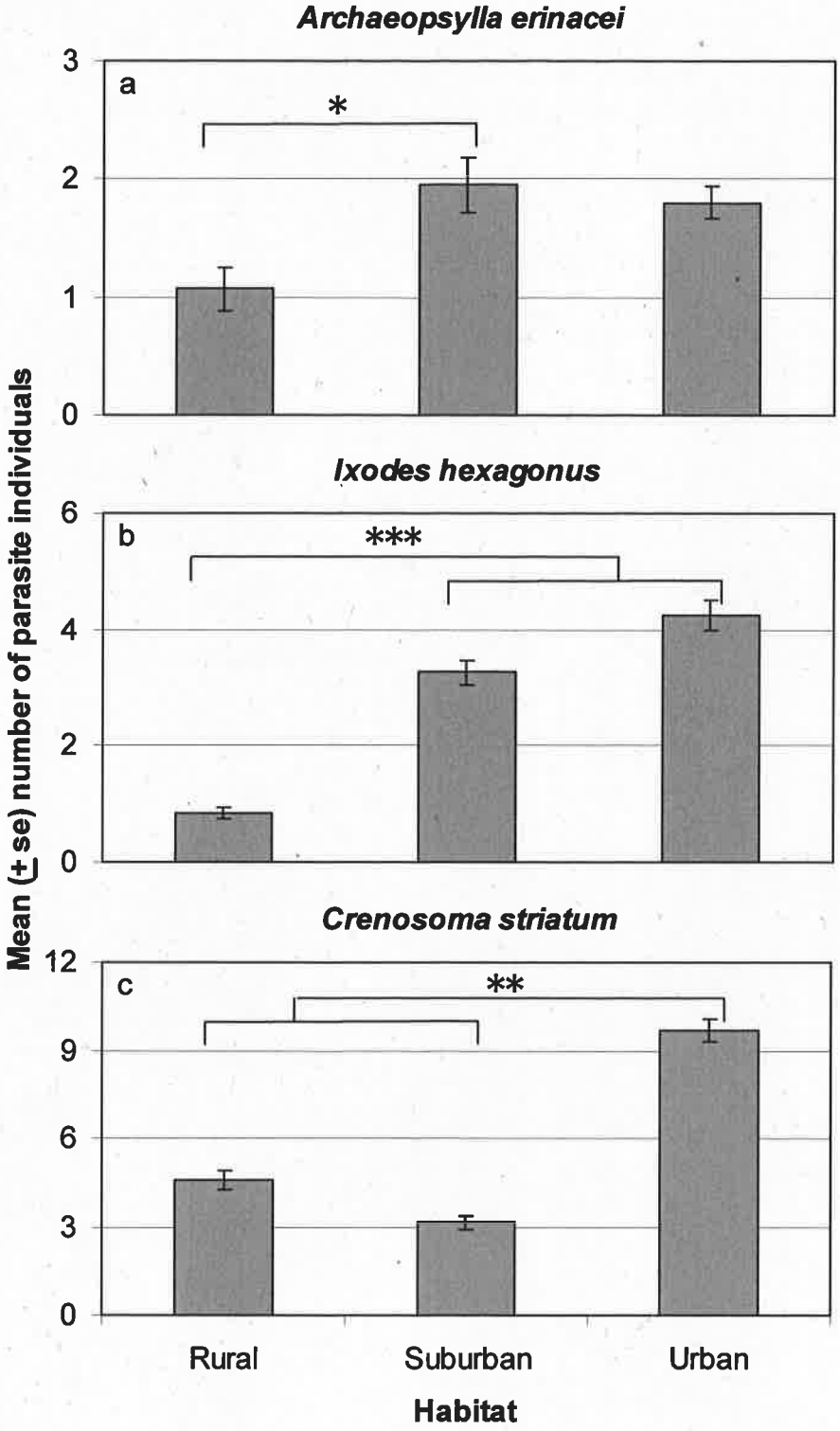
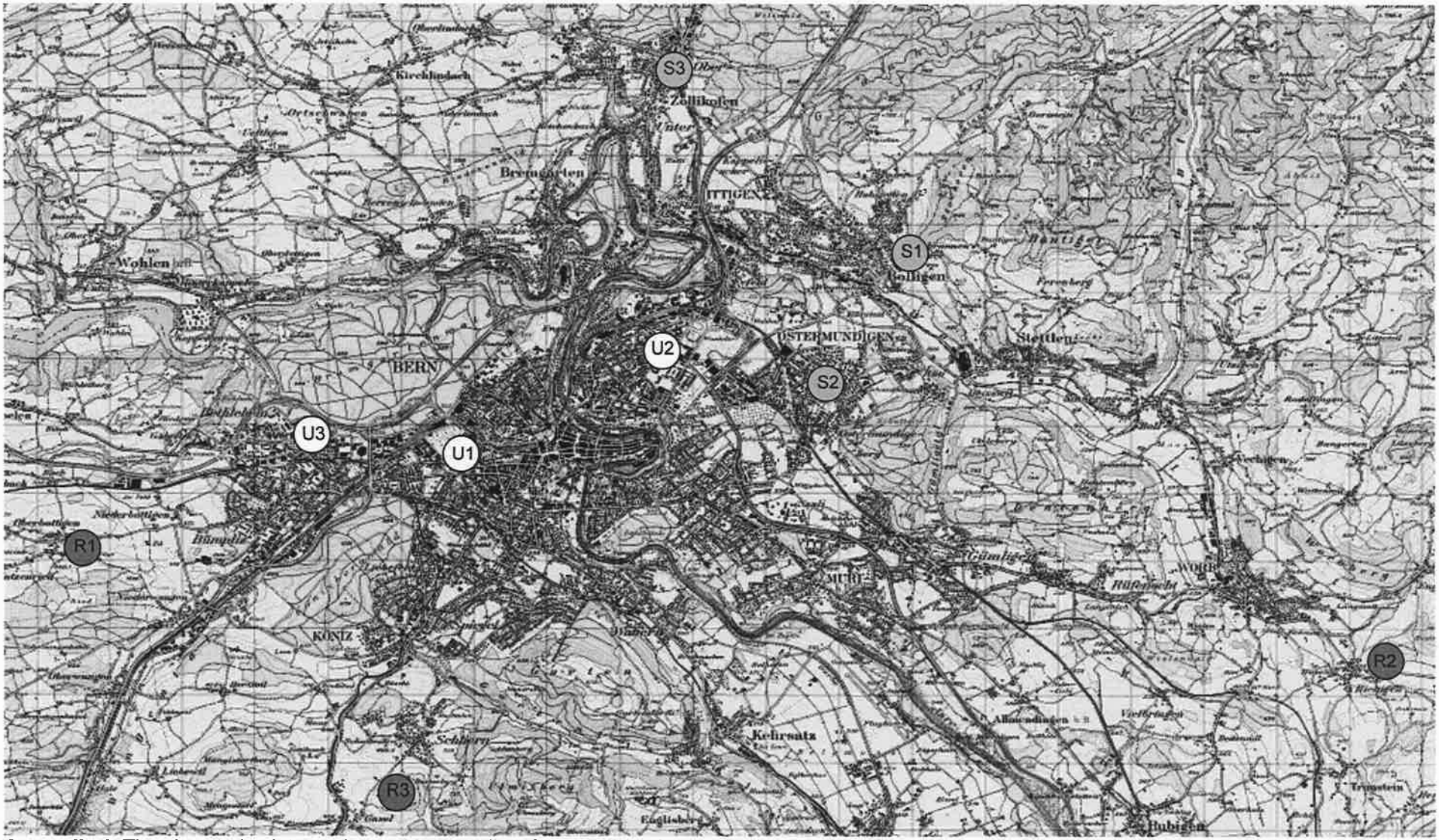

Archaeopsylla erinacei
a
*
3
2
1
0
Ixodes hexagonus
b
***
6
4
2
0
Crenosoma striatum
c
**
12
9
6
3
0
Mean (± se) number of parasite individuals
Rural
Suburban
Urban
Habitat

Fig. 4



Appendix 1. The nine study plots are located in a gradient from rural (dark grey dots) to suburban (light grey dots) and urban (white dots) areas (city of Bern).

Appendix 2. Land use types (according to UNA – Atelier für Naturschutz und Umweltfragen 1993) with an estimation of the proportion of non- sealed (e.g. yards, parks,...) vs sealed (buildings, streets,...) areas

Planar type		Non - sealed area	Sealed area
Old town buildings			
A1	Buildings in lines	0.1	0.9
City residential buildings			
B1	Block edge buildings	0.2	0.8
B2	Buildings in lines, streets oriented	0.2	0.8
Apartment buildings			
C1	Buildings in lines, free space oriented	0.55	0.45
C2	Multistory buildings	0.55	0.45
Houses			
D1	Villas	0.9	0.1
D2	One- or two-family houses	0.65	0.35
D3	Terraced houses	0.5	0.5
D4	Homesteads	0.4	0.6
Institutions			
E1	Schools	0.3	0.7
E2	Hospitals, homes, churches	0.55	0.45
Industry and trade			
F1	Normal type	0.1	0.9
F2	Mixed types	0.3	0.7
Green space with special use			
G1	Sports facilities	0.7	0.3
G2	Garden areas	0.95	0.05
G3	Graveyards	0.95	0.05
Green space without special use			
H1	Parcs	0.95	0.05
H2	Nature oriented greenspace	0.95	0.05
Other greenspace			
H3	Agricultural used space	0.8	0.2
H4	Forests	0.8	0.2
Miscellaneous			
X	Streets, rails,...	0	1

Appendix 3. Models tested for population estimations and their evaluation, S = survival, Gamma = emigration = immigration, p = capture rate, c = recapture rate and N = population size.

Model	AICc	Number of parameters	Deviance
{S(.), gamma(.), p(age), N(session*age}	631.8143	9	308.91212
{S(.), gamma(.), p(age), N(age}	632.1604	5	317.64405
{S(.), gamma(.), p(age), N(plots*age}	638.4432	17	298.10955
{S(.), gamma(.), p(age), N(session}	649.2864	7	330.60371
{S(.), gamma(.), p(age), N(.)}	649.6854	5	335.169
{S(.), gamma(.), p(age), N(plots}	650.9311	12	321.59756
{S(.), gamma(.), p(age)}	689.1437	48	271.64867
{S(.), gamma(.)}	693.8601	58	247.60877
{S(.), gamma(age)}	696.8461	59	247.59886
{S(.), gamma(.), p(plots)}	698.615	56	258.28788
{S(.), gamma(.), p(.)}	698.9795	51	273.08046
{S(.), gamma(plots)}	709.1855	65	241.47323
{S(.}	733.1995	74	236.11433
{S(age}	739.1467	76	235.24238
{S(plots}	752.4596	81	231.01217
{S(g)p=c, Gamma=Gamma}	859.9156	108	229.56975
{S(g)p=c}	949.1631	126	229.55021
{Start}	1747.2226	216	126.51815

Appendix 4. Plots and habitats with estimated hedgehog population densities per age class and season (Pollock's robust design, averages for a given plot are in italics, non-adjusted population density (n/100 ha) and adjusted population density (n/100 ha of non-sealed area). See text for more details.

	Season	R1	R2	R3	R	S1	S2	S3	S	U1	U2	U3	U
Adultes	Spring	12.34	8.66	1.27	7.42	10.50	17.85	19.68	16.01	17.85	23.36	4.98	15.40
	Summer	10.50	12.34	4.98	9.27	14.18	8.66	12.34	11.73	12.34	19.68	6.82	12.95
	Autumn	10.50	17.85	0.00	9.45	8.66	4.98	6.82	6.82	6.82	4.98	6.82	6.21
	Average	*11.11*	*12.95*	*2.08*	*8.72*	*11.11*	*10.50*	*12.95*	*11.52*	*12.34*	*16.01*	*6.21*	*11.52*
Juveniles	Spring	1.00	0.00	1.00	0.67	0.00	0.00	0.00	0.00	0.00	4.18	4.18	2.79
	Summer	4.18	2.60	2.60	3.12	2.60	1.00	4.18	2.59	15.20	18.35	15.20	16.25
	Autumn	5.76	2.60	1.00	3.12	8.91	2.60	4.18	5.23	26.20	8.91	10.48	15.20
	Average	*3.65*	*1.73*	*1.53*	*2.30*	*3.84*	*1.20*	*2.79*	*2.61*	*13.80*	*10.48*	*9.96*	*11.41*
Non-adjusted population		14.76	14.68	3.62	11.02	14.95	11.70	15.74	14.13	26.14	26.49	16.17	22.93
Non-sealed area		69.41	71.52	70.65	70.53	40.06	44.77	53.41	46.08	41.54	24.83	36.30	34.22
Population density		21.27	20.53	5.12	15.64	37.32	26.13	29.46	30.97	62.93	106.68	44.54	71.38

Appendix 5. Mean (± SD) and range for the haematology data from 31 hedgehogs.

Parameter	Mean	Range
Total WBC[1] count (x 10^9/l)	7.50 (± 2.03)	4.40 - 11.60
Neutrophil count (x 10^9/l)	2.90 (± 1.64)	0.46 - 8.35
Lymphocyte count (x 10^9/l)	3.35 (± 1.41)	1.21 - 7.31
Monocyte count (x 10^9/l)	0.31 (± 0.20)	0.05 - 1.05
Eosinophil count (x 10^9/l)	0.65 (± 0.39)	0.17 - 1.63
Basophil count (x 10^9/l)	0.21 (± 0.13)	0.00 - 0.55
RBC[2] count (x 10^{12}/l)	6.89 (± 0.82)	5.60 - 8.96
Hb[3] (mmol /l)	6.94 (± 0.78)	5.30 - 8.63
HCT[4] (l/ l)	0.35 (± 0.04)	0.26 - 0.43
MCV[5] (fl)	51.25 (± 3.93)	43.30 - 61.20
MCH[6] (fmol)	1.01 (± 0.09)	0.84 - 1.22
MCHC[7] (mmol/ l)	19.72 (± 0.51)	18.51 - 20.80
RDW[8]	21.67 (± 1.29)	19.40 26.10
Platelet count (x 10^9/l)	162.86 (± 111.75)	5.71 - 390.00

[1] WBC = Whit blood cells

[2] RBC = Red blood cells

[3] HB = Haemoglobin

[4] HCT = Haematocrit

[5] MCV = Mean cellular volume

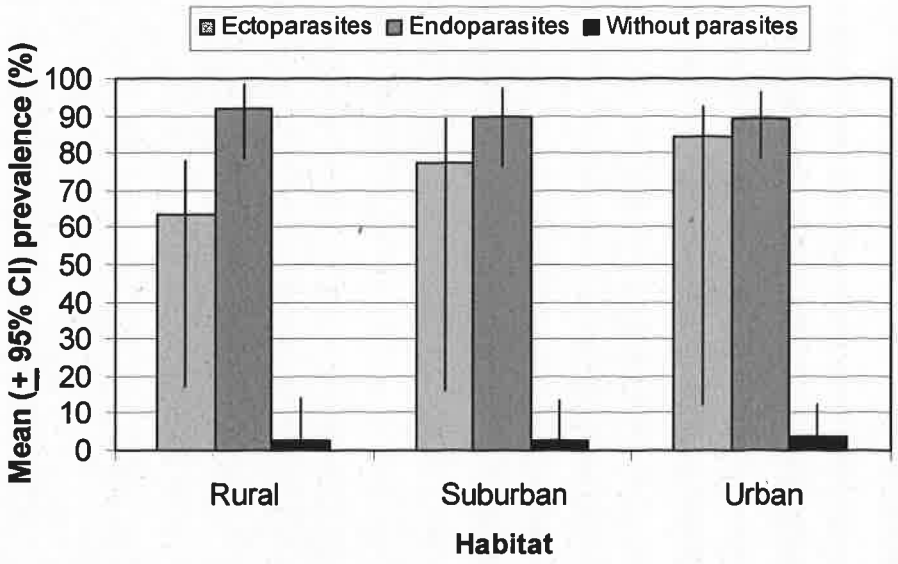
[6] MCH = Mean cellular haemoglobulin

[7] MCHC = Mean cellular haemoglobulin concentration

[8] RDW = Red blood cell distribution width

Appendix 6. Effects of the factors "season", "habitat", "plot [habitat]", "sex", "age" and "body weight" on blood characteristics (nested backward stepwise ANOVA). Df = degree of freedom, P = probability. Significant values are written in bold

Source of variation	Sum of squares	df	Variance	F ratio	P
Total WBC count					
Model	53.61	16	3.350625	0.67	0.7786
Neutrophil count					
Model	36.12	16	2.2575	0.70	0.7516
Lymphocyte count					
Model	34.14	16	2.13375	1.19	0.376
Monocyte count					
Model	0.49	16	0.030625	0.60	0.837
Eosinophil count					
Model	1.22	16	0.07625	0.31	0.99
Basophil count					
Model	0.30	16	0.0185625	1.05	0.4697
RBC count					
Model	14.84	16	0.9275	2.44	0.0504
Hb					
Age	4.19	1	4.19	8.61	**0.0065**
Error	14.10	29	0.49		
HCT					
Age	0.00	1	0.00	4.89	**0.0349**
Error	0.04	29	0.00		
MCV					
Age	187.32	1	187.32	19.60	**0.0001**
Error	277.16	29	9.56		
MCH					
Age	0.11	1	0.11	31.31	**< 0.0001**
Sex	0.02	1	0.02	4.84	**0.0363**
Error	0.09	28	0.00		
MCHC					
Age	0.92	1	0.92	5.21	**0.0312**
Sex	0.87	1	0.87	4.93	**0.0356**
Signs of sickness	1.89	3	0.63	3.55	**0.0287**
Error	4.42	25	0.18		
RDW					
Model	20.91	16	1.31	0.63	0.8127
Platelet count					
Model	215132.79	16	13445.80	1.18	0.3811



Appendix 7. Mean (± 95% CI) parasite prevalence: proportion of ecto-, endoparasitized and not parasitized hedgehogs according to habitat

Appendix 8. Spearman ς rank correlation coefficients (P = probability) between four parasite intensities (*I. hexagonus, C. aerophila, I. ricinus and B. erinacei*) and some of the blood cell count parameters. Only significant coefficients are listed.

Source of variation	Spearman Rho	P
Ixodes hexagonus		
Residuals RBC	-0.44	0.0144
Residuals Hb	-0.40	0.0268
Residuals HCT	-0.43	0.0155
Residuals eosinophil count	-0.38	0.0374
Ixodes ricinus		
Residuals MCHC	-0.45	0.0115
Residuals WBC	-0.37	0.0412
Residuals monocytes count	-0.36	0.0496
Capillaria aerophila		
Residuals MCV	-0.52	0.0025
Residuals MCH	-0.48	0.0059
Residuals platlet count	0.36	0.0449
Brachylaemuns erinacei		
Residuals neutrophil count	0.37	0.0415