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This thesis is based on the following scientific publications, which are referred to in the text by the Roman numerals

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II. Laurimaa, L., Süld, K., Davison, J., Moks, E., Valdmann, H., Saarma, U. (2016). Alien species and their zoonotic parasites in native and introduced ranges: the raccoon dog example. Veterinary Parasitology, 219, 24–33.

III. Süld, K., Saarma, U., Valdmann, U. (2017). Home ranges of raccoon dogs in managed and natural areas. PloS ONE 12(3): e0171805. doi: 10.1371/jpurnal.pone.0171805

IV. Süld, K., Tammeleht, E., Valdmann, H., Saarma, U. (2017). Severe impact of sarcoptic mange on the movements and space use for one of its most important vector species, the raccoon dog. Veterinary Parasitology, doi:10.1016/j.vetpar.2017.05.029

Personal contribution of the author to the publications referred to in this thesis is as follows:

I – main contributor in material collection, data analysis and article writing

II – participation in material collection, data analysis and article writing

III and IV – main contributor in material collection, field works, data analysis and article writing

1. INTRODUCTION

1.1 Raccoon dog as an alien species in Europe

Invasive alien species are one of the major agents of human-accelerated global change: they threaten biodiversity, alter ecosystem structure, functions and services, inflict large economic costs and cause serious problems to human health (Mazza et al., 2014). In invasion biology, mammals are among the best studied groups, because they are charismatic, more visible than most other animals, and also because they cause more harm than most other taxonomic groups (Vilà et al., 2010). Genovesi et al. (2012) have reported 117 alien mammal species in Europe, of which at least 58 are known to cause environmental or health problems, and 27 have been found to directly affect native species. One of the most successful invasive alien mammal in Europe is the raccoon dog (*Nyctereutes procyonoides*), which has a potential to affect native fauna as a predator and a competitor, and is also an important vector of zoonotic diseases (Kauhala and Kowalczyk, 2011).

The six sub-species of the raccoon dog *Nyctereutes procyonoides – N. p. albus, N. p. korensis, N. p. orestes, N. p. procyonoides, N. p. viverrinus* and *N. p. ussuriensis* – all originate from Far-East Asia, where the species natural distribution area spans much of China, north-east Indochina, Korea, Amur and Ussuri regions of eastern Siberia, Mongolia and Japan (Ward and Wurster-Hill, 1990). Motivated by the value of its fur, about 9000 individuals of the subspecies *N. p. ussuriensis* were intentionally, sometimes also accidentally as escapees from fur farms, introduced from southeast Siberia mainly to European parts of former Soviet Union between 1927 and 1957 (Lavrov, 1971; Heptner and Naumov, 1998). Characteristics including omnivorous diet, high reproductive potential and the ability to hibernate at high latitudes, have allowed the raccoon dog to successfully colonise new areas and now the species is well-established in Europe (Vila et al., 2008; Kauhala and Kowalczyk, 2011). The contemporary northern limit of the distribution area reaches as far as to 67°N in Finland (Kauhala and Saeki, 2016), whereas the southernmost point of its European range is in the Former Yugoslav Republic of Macedonia (Ćirović, 2006), and one road-kill has been reported in south-eastern Spain in 2008 (Kauhala and Kowalczyk, 2011).

The first sighting of a raccoon dog in Estonian nature was registered already in 1938 from island of Kamenka in Lake Pskov (current territory of Russia). Most probably this individual originated from raccoon dogs released in 1935 in Staraya Russa region in the current Novgorod oblast in Russia (Aul et al., 1957). There were numerous other reports of raccoon dogs from different parts of Estonia (Naaber, 1972) before the species official introduction in 1950, when 86 individuals were released in three different locations (Aul et al., 1957). At first, possibly due to the high abundance of lynx (*Lynx lynx*) and grey wolf (*Canis lupus*), population size of raccoon dogs remained low and individuals were mainly seen alongside large forest arrays and rivers. By the year 1954 there were reports of 213 raccoon dogs from different habitats from all over Estonian mainland and in 1960s the species became common also in the biggest islands Saaremaa and Hiiumaa (Naaber, 1972).

Multiple and repeated introductions as well as numerous escapees from fur farms where not the only reasons behind raccoon dog rapid spread in Europe. Adding to its inherent great migratory ability and elusiveness, raccoon dogs can hibernate during winter, which has enabled them to establish stable populations even beyond the Finnish Arctic Circle (Kauhala and Saeki, 2016). The species has also a high reproductive potential. In Finland the mean birth litter size has been estimated 8.8, varying from 2 to 16 cubs (Helle and Kauhala, 1995), while in Estonia the average litter size has been somewhat lower – 6.8 (Naaber, 1974). In addition, raccoon dogs have a monogamous breeding system, which is an important factor in terms of pup survival. During the pup rearing period there appears to be a division of labour between male and female raccoon dogs: males guard the litter in close vicinity of the den, while females forage to satisfy their increased energy requirements. There are periods when males spend even more time inside or nearby dens than females (Kauhala et al., 1998a; Drygala et al., 2008a). The same kind of behaviour also appears in Japanese subspecies *N. p. viverrinus* (Ikeda, 1983). Another important reason behind successful integration of raccoon dog into European nature is the high plasticity of the species when it comes to food and habitat requirements.

1.2 Feeding habits of the raccoon dog

Raccoon dogs are true omnivores, generalist predators characterised by an opportunistic feeding strategy, who eat almost anything they can find or catch. The diet of raccoon dogs varies between seasons and habitats, according to availability of different food items (Sidorovich et al., 2008a; Sutor et al., 2010). Geographical comparison of diet composition has revealed that throughout their distribution area raccoon dogs most often feed on insects, plants and mammals (Sutor et al., 2010). While small mammals (e.g. mice, voles, shrews) form the bulk of raccoon dog diet irrespective of season, insects, wild berries and fruits are especially important in summer and autumn (Naaber 1971; Nasimovic and Isakov, 1985; Rieg and Jedrzejewski, 1988; Kauhala et al., 1998b; Sidorovich et al., 2008a). Although, reptiles, frogs and birds also appear quite frequently in raccoon dog diet, these food items are usually consumed in a much lesser amount. In higher latitudes, where winter conditions are harsh and food sources scarce during the coldest period of the year, raccoon dogs often have to rely almost exclusively on carrion (Jedrzejewski and Jedrzejewska, 1998; Sutor et al., 2010). As a scavenger, raccoon dog is not very choosy. Selva (2004) found that their scavenging frequency was quite similar among carcass types and origin (dead, harvested, entrails, kills of other carnivores). As well, unlike other mammalian scavengers (e.g. red foxes *Vulpes vulpes*, gray wolves) raccoon dogs do not avoid feeding on carcasses of other carnivores, including other raccoon dogs (Kauhala et al, 1993; Selva et al., 2005).

As an opportunist and a carnivore the raccoon dog has been considered a potential threat to such vulnerable prey groups as ground nesting birds and amphibians (Naaber, 1971; Laanetu, 1986; Kauhala, 1996a; Neronov et al., 2008). Amphibians are an important part of raccoon dog diet in spring and summer period when they are abundant around waterbodies used for breeding (Naaber, 1974; Judin, 1977; Kauhala et al., 1993; Sutor et al., 2010) or in closed environments where other food sources are scarce. For example, frogs vanished from some small islands on the southwest coast of Finland after raccoon dogs arrived there in the 1970s (Kauhala, 1996a). As for the ground nesting birds, while some diet studies have revealed that nearby waterbodies waterfowl and their eggs can indeed constitute a major part of raccoon dog diet (Naaber, 1974; Sidorovich et al., 2008a), the predator removal studies and experiments with duck nests have shown that the negative impact of the raccoon dog to the waterfowl is almost non-existent compared to the red fox, pine marten (*Martes martes*) and American mink (*Neovison vison*) (Opermanis et al., 2001; Kauhala, 2004). Rieg and Jedrzejewski (1988) compared the diet of mammalian predators, including that of raccoon dog, in Bialowieza National Park in Poland and found that birds were almost exclusively (over 90%) eaten by red foxes. Diet studies from Finland (Kauhala et al., 1993) and Germany (Sutor et al., 2010) have shown that most of the birds consumed by raccoon dogs are passerines (*Passeriformes*), and even in the nesting season gallinaceous birds (*Galliformes*) and other ground nesting birds are rarely eaten. Kauhala and Auniola (2001) found that although in Finnish islands waterfowl, mostly eiders (*Somateria molissima*), were very frequent in raccoon dog diet (frequency of occurrence FO=66%), most of them were eaten as carcasses. Moreover, as pointed out by authors, raccoon dogs could have killed only 1.2–3.5% of female eiders in each study year. Another study, conducted few years earlier, revealed that in Finnish mainland (Kauhala et al., 1998b) the waterfowl comprised less than 5% of diet composition of the raccoon dogs. Also, according to Judin (1977), in its natural distribution area in the Far East the proportion of gallinaceous birds and waterfowl in raccoon dog diet does not exceed 4%. The findings from different localities of raccoon dog distribution area indicate that the species may be harmful to some populations of waterfowl, but pose a little danger to other birds (Kauhala et al., 1993; Sidorovich et al., 2008a; Sutor et al., 2010). Raccoon dogs as hunters are quite clumsy and have difficulties catching healthy adult birds (Naaber, 1974; Kauhala et al., 1993).

There have also been speculations that raccoon dog as a competitor could harm indigenous species with similar ecological requirements. Indeed, due to similar food objects and occupied habitats, exploitative competition between raccoon dog, European badgers *Meles meles* and red fox is possible (Holmala, 2009). Sidorovich et al. (2008b) found that after introduction of raccoon dog and American mink to Belarus, abundance of ten native species, including badgers and foxes, started to decrease. Remains of badger cubs have been found in raccoon dog scats (Jedrzejewska and Jedrzejewski, 1998), but at the same time, killing of red fox and raccoon dog cubs by badgers have also been observed (Kowalczyk et al., 2008). In Finland, the food niches of raccoon dogs and badgers seem to overlap more with each other than with that of foxes. However, their diets differ to some extent, which may help to avoid competition: red fox is the most carnivorous, raccoon dog the most omnivorous, while badger depends more on plants. Furthermore, the badger and the raccoon dog are dormant during winter, when food is scarcest, which may help them to coexist without severe competition (Kauhala et al., 1998b). As well, in its native range in the Far East raccoon dogs are sympatric with foxes, badgers and wolves, and thus may have been pre-adapted to coexistence, which reduces interspecific competion (Kauhala, 1996b; Zhang et al., 2009).

1.3 Habitat requirements and population density of the raccoon dog

Information about population density and habitat use of invasive species is essential to better aim actions to reduce or prevent their negative impact to native ecosystems (Melis et al., 2015). Raccoon dogs typically prefer wet habitats, especially in spring and summer, when they often move around nearby shores of lakes, rivers and other waterbodies (Nasimovic and Isakov, 1985; Kauhala, 1996b). During autumn they are more or less dependent on fruits and berries, abundance of which also strongly affects their habitat selection (Sidorovich et al., 2008a; Kauhala and Saeki, 2016). In its natural distribution area in the Russian Far East raccoon dogs prefer open landscapes, especially damp meadows and agricultural land, but avoid dark forests (Judin, 1977). In the introduced range raccoon dogs also favour moist meadows and other habitats with abundant undergrowth, but unlike in its native range prefer to stay in the safety of forests. Still, depending on the availability of different habitats, raccoon dogs can, though in a low density, also live in barren pine forests, where they often feed on crowberries (*Empetrum nigrum*) or choose to stay in agricultural areas or nearby human settlements with gardens (Kauhala and Auniola, 2001).

In case of territorial monogamous canids such as raccoon dogs, population density can be estimated from home range size as these parameters tend to be negatively correlated (Kauhala and Kowalczyk, 2011). As home ranges of female and male raccoon dogs overlap substantially, the maximum density is then two adults in each home range (Kauhala et al. 1993; Drygala et al., 2008a). According to studies performed in Finland, Poland and Germany, raccoon dog home range size varies from 50 ha to 1000 ha (Jedrzejewski and Jedrzejewska, 1998; Drygala et al., 2008a; Kauhala and Auttila, 2010; Sutor and Schwarz, 2012). Raccoon dogs tend to have significantly smaller home ranges in areas where the landscape is mosaic, providing both natural as well as managed habitat patches (e.g. gardens, fields), opposed to areas dominated by large monocultural fields or forest arrays (Drygala et al., 2008b; Holmala and Kauhala, 2009; Kauhala and Auttila, 2010; Kauhala et al., 2010; Sutor and Schwarz, 2012; Drygala and Zoller, 2013). Home ranges are the largest in autumn, when raccoon dogs move around a lot to accumulate fat reserves before winter when food sources become scarce (Drygala et al., 2008a; Sutor et al., 2010). Hence, depending on season, availability of different habitats and food sources, landscape structure and management regime, the population density of raccoon dogs can vary from less than 0.8 individuals per square kilometre in poorer (often monocultural) forest habitats (Jedrzejewski and Jedrzejewska, 1998; Kauhala et al., 2010) to as high as 4.9 individuals per square kilometre in mosaic landscapes during summer and early autumn, until the juveniles disperse (Sutor and Schwarz, 2012). In its natural range in the Far East the population density varies from 0.1 individuals per square kilometre in broadleaved forest in winter to 2.0 individuals per square kilometre in agricultural areas in summer. In the northern distribution area the population density also depends on climatic factors such as the length of growing season (summer) and duration of the snow cover (Nasimovic and Isakov, 1985; Helle and Kauhala, 1995).

1.4 An important vector of zoonotic parasites and diseases

Alien species can become a threat to native fauna and human health by bringing new zoonotic pathogens to their introduced ranges and by facilitating the spread of existing ones. Zoonotic diseases, which can be transmitted from animals to humans and *vice versa*, can be fatal to victims and have economic significance. In Europe the raccoon dog is known to be an important vector of multiple zoonotic parasites, of which some, e.g. the rabies virus, fox tapeworm *Echinococcus multilocularis* and *Trichinella* spp., are highly hazardous to human health (Kauhala and Kowalczyk, 2011). Although successive oral vaccination campaigns have substantially reduced the number of rabies cases in Europe, sporadic detection of the lineage originating from Russia, underlines the risk of reintroduction via westward spread from bordering countries (Robardet et al., 2016). In Estonia the anti-rabies vaccination campaign was initiated in 2005 and in 2013 country was declared to be rabies free (Pärtel, 2013). In parallel, shortly after initiation of oral vaccination campaign the numbers of raccoon dogs quickly started to increase (the hunting bag size grew from approximately 4,000 to more than 12,000 individuals during 2005–2012) (Veeroja and Männil, 2016). Epidemiological studies describing the endoparasite fauna of the raccoon dog in Europe have been conducted in several countries, e.g. Belarus (Shimalov and Shimalov, 2002), Lithuania (Bružinskaite-Schmidhalter et al., 2012), Denmark (Al-Sabi et al., 2013) and Germany (Thiess et al., 2001). A number of smaller studies targeting the parasites that infect humans have also been conducted in Europe, e.g. on *E. multilocularis* and nematodes from the genus *Trichinella* (Machnicka-Rowinska et al., 2002; Oivanen et al., 2002; Pannwitz et al., 2010; Schwarz et al., 2011). The only parasitological study of the subspecies *N. p. ussuriensis* in its native range originates from the 1970s (Judin, 1977), where a total of 26 endoparasite species were reported, many of which, including *E. multilocularis,* are of considerable zoonotic potential (Knapp et al., 2015). For comparison, the first case of *E. multilocularis* infection in raccoon dogs in Europe was reported only in 2001 (Thiess et al., 2001).

Besides high population density, the fact that raccoon dogs rarely dig burrows or dens, but frequently cohabit the setts of badgers, might contribute into spill over and spread of diseases. Badger burrows provide protection against cold and predators, especially at the time of pup rearing. Kowalczyk et al. (2008) found that all 15 setts permanently occupied by badgers were used by raccoon dogs for wintering and five of these for reproduction, while red foxes used one and three setts for respective purposes. That kind of shared use of setts increases the contact rate among different species of carnivores and creates circumstances favourable for transmission of diseases like sarcoptic mange and rabies, and can also promote exchange of helminths (Holmala and Kauhala 2006; Kauhala and Holmala, 2006). As the raccoon dog population is still growing and spreading, its role as a vector of zoonotic diseases may further increase in Europe (Kauhala and Kowalczyk, 2011; Sutor et al., 2014).

2. OBJECTIVES OF THE STUDY

Information about spatial requirements of a species is central to understand its role in ecosystems. In case of invasive species this kind of information is crucial for addressing actions to reduce their negative impact, as the pattern of habitat use may provide guidance for where and when to aim management efforts. It is especially important in case of species for which we have only relative abundance estimates. Quite often these estimates are based on hunting bag size, which is not always a reliable method, as it strongly depends on the motivation of hunters (e.g. the current value of fur). That also applies to the raccoon dog, which is considered among the most invasive alien species in Europe (Vila et al., 2008), having the potential to cause loss of native biodiversity. The species also acts as a vector of zoonotic diseases, which may raise both economic and health problems (Keller et al., 2011). Although raccoon dog has been present in European nature for decades, information about its impact to local ecosystems as an alien species is still scarce. The most comprehensive studies covering the introduced species' diet, space use and parasite fauna have been focusing on Finnish, German and Polish populations (e.g. Jedrzejewska and Jedrzejewski, 1998; Holmala and Kauhala, 2009; Kauhala et al., 2010; Mustonen et al., 2012; Sutor and Schwarz, 2012; Drygala and Zoller, 2013). Information about the raccoon dog from other parts of its introduced or invaded areas, including Estonia, have so far addressed only one or two aspects of its ecology.

Up until mid-2000s, three studies about raccoon dog diet had been conducted in Estonia. The earliest and most comprehensive study was carried out in 1960s by Naaber (1971), the next one in 1982/83 by Laanetu (1986) and the latest in 2003/05 by Rätsepp (2005). Many environmental aspects, mainly related with natural but also human induced forest and game management, have changed since these studies were conducted. For example, while in 1960s in autumn and winter periods raccoon dogs mostly relied on small mammals and natural plant material (e.g. wild berries) as a food source, by the mid-2000s the proportion of rodents and shrews had declined remarkably and had been replaced by carrion and anthropogenic plant material such as cereals, potatoes and fruits. The latter food items can be found in supplementary feeding sites which were not as abundant in past decades (http://pub.stat.ee/px-web.2001/Dialog/Saveshow.asp). Also the abundance of Estonian raccoon dogs based on the hunting statistics (Veeroja and Männil, 2016) has increased considerably even compared to mid-2000s (Rätsepp, 2005). Until 2004 the population size was perceptibly controlled by outbreaks of rabies and sarcoptic mange, and the hunting bag size, which unfortunately has been the only means for assessing abundance of raccoon dog in Estonia, remained under 5000 hunted animals per year. In autumn 2005 yearly oral vaccination campaign against rabies in Estonian wildlife was launched. Since then the population size of raccoon dog started to increase abruptly, peaking in 2012 when the hunting bag size was over 13000 individuals (Veeroja and Männil, 2016). The same kind of trend occurred simultaneously in the population of sympatric red fox. This was followed by an extensive outbreak of sarcoptic mange, which as a counterbalance has somewhat started to limit population size of raccoon dog and also that of red fox (Veeroja ja Männil, 2016). As raccoon dogs along with red foxes are the main vectors of the disease and infection of *Sarcoptes scabiei* can affect the population size considerably, it is of great interest to study the relationship between sarcoptic mange and different aspects of raccoon dog ecology, e.g. feeding habits, parasite fauna and space use.

High population density, as well as diet composition (many infections are acquired orally), are a major contributing factors to epizootics and spread of also other zoonotic agents besides sarcoptic mange. Few years before the oral anti-rabies vaccination campaign was launched and population size was still relatively low, Moks (2004) already identified that Estonian raccoon dogs were infected at least with six different endoparasites, three of which (*Alaria alata, Uncinaria stenocephala, Trichinella* spp.) could also infect and harm humans. Considering the small sample size (n=21) and the fact that the same study identified 12 more parasite species in sympatric red foxes, out of which for example *E. multilocularis* had also been detected in raccoon dogs elsewhere in Europe (Theiss et al., 2001), the actual number of parasites was most probably much higher (Moks, 2004).

Considering the limited information about the role of the introduced raccoon dog in local ecosystems, the main objectives of this thesis were:

1) To analyse feeding habits of the raccoon dog in Estonia and evaluate temporal changes since 1960s to assess potential impact of the species on various prey categories, incl. birds (**I**).
2) To investigate parasite fauna of raccoon dogs in Estonia in order to evaluate its zoonotic potential (**II**).
3) To study space use of the raccoon dog in Estonia, by assessing the home range size and habitat use in areas with different management regimes: in an intensively managed area with anthropogenic influence and in a protected natural area (**III**).
4) To study the impact of sarcoptic mange on raccoon dog food habits (**I**), movements, habitat use and home range size, especially in the later phase of the disease (**IV**).

3. MATERIALS AND METHODS

3.1 Diet and parasites of raccoon dogs

Sample collection and treatment of study materials

Carcasses of 255 raccoon dogs were collected between autumn 2010 and spring 2012 from different parts of Estonia, covering 9 of 15 counties (**I**, Figure S1). Of these, 252 samples were collected from animals legally harvested by hunters for purposes other than this project. Three animals were obtained as roadkills. All carcasses were weighed and sexed (**I, II**). All animals collected with fur (n=227) were examined for sores and thick crusts as signs of sarcoptic mange; all skinned raccoon dogs were considered to be free of mange since hunters only retain skins without symptoms of the disease. After weighing the carcasses, intestinal organs were removed and kept at –80 ºC for at least 5 days before parasitological examination as a safety precaution (Eckert et al., 2001), since this kills the highly dangerous tapeworms *E. multilocularis* and *E. granulosus* which had been previously recorded in Estonia (Moks et al., 2005, 2006, 2008; Laurimaa et al., 2015a, 2015b). For diet analysis, stomachs were opened and the contents washed through a sieve (1 mm mesh size). For parasitological study, internal organs such as lungs, gall bladder and urinary bladder were studied by using washing and sieving techniques for helminth detection (Parre, 1985). The small and large intestines were separated and examined by the sedimentation and counting technique (Hofer et al., 2000). Up to 200 specimens were counted per helminth species. Parasites were stored in 95% ethanol. Due to decomposition or severe carcass damage six samples were excluded from the analyses.

Analysis of stomach contents

We calculated the frequency of occurrence of each food type (FO=number of stomachs containing a specific food item/total number of stomachs) and also measured the volume (ml) of each component by water displacement (Sato et al., 2000), to calculate food niche breadth and to quantify diet composition. In total, 223 stomach contents contained some food items, while 26 were empty. Identifiable material was sorted into nine food categories: small mammals (*Rodentia*, *Insectivora*), carrion (*Cervidae*, *Suidae*, *Carnivora*), birds, amphibians, fish, invertebrates, anthropogenic plants (cereals, fruits, vegetables), natural plants (wild berries, grass, etc.), garbage (peelings of vegetables, sausage skins, etc.). Mammal and bird remains were identified to the lowest taxon possible. For identification of mammals we analysed hair cuticular scale pattern, medulla and cross-section according to Teerink (1991) and our own hair reference collection. Teeth were identified according to Kaal (1981). It is important to consider the possibility that conspecific hair in diet studies could be due to grooming (Remonti et al., 2005). With this in mind, we included raccoon dog hairs as a dietary component only when the volume of hairs in a stomach was >20 ml, which we considered unlikely to result from grooming. Reference materials were also used for identification of bird feathers. To examine seasonal differences in diet composition the data was grouped into two temporal categories: 1) autumn (August–November), a period of intensive foraging and fat accumulation; and 2) winter (December–March), the period when raccoon dog activity is reduced due to cold weather. We also compared our data with the results of earlier diet studies performed in Estonia by Rätsepp (2005) and Naaber (1971) (**I**, Figure S2; Information S1).

Of all analysed stomach contents, 33 belonged to raccoon dogs exhibiting symptoms of sarcoptic mange. Differences in diet composition between sexes and seasons and in relation to sarcoptic mange infection were tested using PERMANOVA (with Bray-Curtis distance; function adonis in R package vegan) and visualised using non-metric multidimensional scaling (function metaMDS in R package vegan) (Oksanen et al., 2012). Individual food items that varied in relation to infection, sex or season were identified using chi-square-tests. To determine the potential impact of infected individuals on our results, detailed analysis of season and sex differences was carried out on two datasets: 1) 'total' (uninfected plus infected individuals, n=223); and 2) only 'uninfected' individuals (n=190).

To assess the co-occurrence of food categories in raccoon dog diet, we calculated the C-score (Stone and Roberts, 1990) for all pairs of food types. To generate a distribution of C-scores that could be expected if food types were distributed randomly with respect to one another, we generated 999 random matrices with fixed row and column occurrences, and recalculated all pairwise C-scores for each matrix. Observed C-scores were standardised by subtracting the mean of the randomised C-scores and dividing by the standard deviation of the randomised values. The significance of effects was estimated from the number of randomised C-scores more extreme than the observed value and corrected using the false discovery rate approach (Benjamini and Hochberg, 1995). Analyses were carried out on the full data set and separately for autumn and winter samples.

Identification of parasites and data analysis

Trematodes, cestodes and nematodes were identified according to their morphology after Kozlov (1977). Cestodes from genera *Echinococcus, Taenia* and *Mesocestoides* were further identified after Abuladze (1964), Loos-Frank (2000) and Hrčkova et al. (2011), respectively. For the genetic identification of *Taenia* species, genomic DNA was extracted using the High Pure PCR Template Preparation Kit (Roche) according to the manufacturer´s instructions. Samples were purified and sequenced as in Saarma et al. (2009), with sequencing performed using the same primers as in the primary PCR.

For statistical analysis, data from collected animals were divided into two seasons reflecting the availability of natural food resources: 1) autumn

(August–October), 2) winter and early spring (November–April). As few animals originated from the summer period, these were omitted from the statistical analysis. We used the Mann-Whitney U test to reveal significant associations between the season and number of identified helminth species. We also tested whether infestation with some helminth species depended on the host sex (Mann-Whitney U test); and if the number of parasite specimens (<200 or >200) depended on animal weight (Logistic regression); whether animals infected with different number of helminth species consumed some food items significantly more than others (ANOVA). Statistical tests were performed using software STATISTICA 7.

To assess the co-occurrence of parasite species and food categories, we calculated the C-score (Stone and Roberts, 1990) for all pairs of parasite species, and for parasite species and food types (data originating from I). To generate a distribution of C-scores that could be expected if parasites were distributed randomly with respect to one another, we generated 999 random matrices and recalculated all pairwise C-scores for each matrix. Analyses were carried out using software R (package vegan) on parasite species that were represented in at least 10 animals.

3.2 Telemetry studies

Study area

Telemetry studies were carried out in a protected natural area in Soomaa National Park in central Estonia (0.78 km^2; 58°25´N, 25°1´E), and in an intensively managed area in southern Estonia nearby Ilmatsalu borough (1.03 km^2; 58°24´N, 26°32´E). Both study areas are regularly flooded in springtime and in case of high precipitation, flooding also appears in autumn. There are numerous abandoned households scattered throughout the Soomaa study area and only one functional messuage (dwellings with adjacent buildings and lands) in the centre of the area. Regular grass mowing and grazing by highland cattle in small patches of meadows are the only practiced agricultural management form. Altogether 81.4% of Soomaa study area is covered with forests, 10.2% with scrubs and woodland shrubs, 4.6% with managed meadows and 3.8% with wetlands and water bodies (reed beds, rivers, drainages ditches, ponds) (**III**, Fig 1). Ilmatsalu study area with the population density of 22 residents per square kilometre is characterized by extensive anthropogenic activities: messuages and small farmsteads cover about 2.1% of the area and altogether 32.9% of the area is in agricultural use. The remaining area is covered with forests (38.8%) and transitional woodlands (scrubs and woodland shrubs; 19.7%) (**III**, Fig1). The area is also part of a local hunting ground. The only types of water bodies in the area are drainage ditches and commercial fish ponds (6.6%). The average annual temperature during the study period was 5.9 °C in Soomaa and 5.3 °C in Ilmatsalu area, with total annual precipitation of 835.5 mm and 771.5 mm, respectively (The Estonian Environment Information

Centre). Both study areas are inhabited by a diverse community of carnivores: in addition to the raccoon dog also by red fox, gray wolf, brown bear (*Ursus arctos*), European lynx, Eurasian badger and other mustelids (*Mustelidae*).

VHF and GPS tracking

In Soomaa study area three raccoon dogs were caught by using specially trained hounds and the radio-tracking was carried out from May to October 2009. In Ilmatsalu area from March 2012 to November 2013 nine raccoon dogs were captured with wire box traps. Captured animals were collared without drug immobilisation as raccoon dogs are easy to handle without (Kauhala et al., 2007; Drygala and Zoller, 2013). Three raccoon dogs from Soomaa and three animals from Ilmatsalu study area were suited with Telonics model 210 VHF-radio collars. Also three raccoon dogs from Ilmatsalu were suited with VHF collars in spring 2012, while the remaining six raccoon dogs from the same study area were suited with MiniTrack210 GPS-collars between autumn 2012 and autumn 2013 (LOTEK Wireless Inc.).

Raccoon dogs with VHF-collars were located with a handheld four-element Yagi-antenna (Y-4FL, Televilt, TVP) and with Telonics TR-4 receiver. For animals with GPS-collars, three-element flexible Yagi-antenna (AN-3FX 172), SIKA receiver (SIKARX4) and handheld VHF Command Unit (GPS-CMD VHF) were used. Tracking sessions were carried out (VHF-collars) or scheduled (GPS-collars) from 6 pm to 6 am when raccoon dogs are most active (Kauhala et al., 2007; Kauhala and Holmala, 2008; also our own observations). For raccoon dogs with VHF-collars, triangulation method was used to take the bearings, keeping the angle between bearings close to 90°. To avoid measurement errors due to animal movements, bearings were taken within as short time period as possible (5±2 minutes). The minimal time interval between triangulations was 25 minutes and the location error was measured to be about 100 m (103±55.8SD) by locating hidden VHF radio-collars (35 location points).

We divided the study period into three different seasons: 1) spring (March–April) as a mating season and summer (May–July) as a time of cub rearing; 2) autumn (August–October), the period of intensive foraging and fat accumulation; and 3) winter (November–January) as a period of reduced activity. Coordinates for winter locations were obtained only for two raccoon dogs (with VHF-collars) forming a pair in Ilmatsalu area, by seeking out their sleeping sites at least once a week.

There was a severe outbreak of sarcoptic mange during our tracking period in Ilmatsalu study area. Due to the disease, one raccoon dog died soon after collaring and as very limited amount of data was gathered for that animal (**III**, M3_gps_IL in Table 1), it was excluded from further analysis.

Home range calculations and habitat analysis

Home range areas were calculated for each animal by using the fixed kernel method and minimum convex polygon method (MCP). For kernel estimations we used the least squares cross validation smoothing parameter. We considered 95% kernel home range (K95) as the total home range area since the 100% kernels tend to overestimate the actual home range size due to occasional trips outside the most frequently used area. The K95 values were not calculated when there were less than 50 location points available for the animal (Seaman and Powell, 1996). The 100% minimum convex polygons (MCP100) were calculated for the purpose of comparison with previous home range studies (e.g. Jedrzejewska and Jedrzejewski, 1998), as MCP method has been the most widely used method. Home range analysis was conducted with RANGES 8.

Compositional analysis (Aebicher at al., 1993) was used to study habitat use and selection. We obtained relative habitat use for fixes within home ranges. Availability of different habitat types was estimated by using CORINE Land Cover 2006 map. We used Jacobs' selectivity index $P_i = (U–V)/(U+V–2UV)$, where U is the proportion of habitat used and V the proportion of habitat available (Jacobs et al., 1974) to estimate habitat preferences within study areas. The P_i values can vary from –1 to +1. Values below 0 indicate preference, values over 0 indicate avoidance and values equal or close to 0 indicate that habitats are used in proportion to their availability. Programs Biotas and R package 'adehabitatHS' were used for habitat analysis.

Spatiotemporal movement dynamics during sarcoptic mange outbreak

To analyse the spatial and temporal effects of sarcoptic mange to raccoon dogs, two individuals from Ilmatsalu study area that initially had no external symptoms of *S. scabiei* infection, but developed these during the study period, where GPS-collared in a mange outbreak area. We determined alterations in their home range sizes and activity rate. Changes in the size of the area used by the raccoon dogs were calculated in 7 day intervals. Home range sizes were estimated by using MCP100. For activity rates we calculated the daily distances using *ts* and *lowess* functions in program R. We also determined if there were any differences in habitat use between periods when raccoon dogs were active (animals moved actively around) and passive (animals stayed in one place). For that we compared frequencies of location points in different habitats (arable land, forest, shrub, waterside) between active and passive periods in seven day intervals within raccoon dogs' home ranges. Distribution of location points in different habitats were determined by using CORINE Land Cover 2006 map and program Biotas.

4. RESULTS

4.1 Diet of raccoon dogs in Estonia

The most frequently consumed food items were anthropogenic plants (FO=56.1%) and carrion (FO=48.4%); small mammals, invertebrates and natural plants were recorded nearly two times less frequently (**I**, Table 1). Anthropogenic plants included cereals (rye *Secale cereale*, wheat *Triticum* spp., oat *Avena sativa*), whereas carrion consisted mainly of artiodactyls (FO=34.5%), such as wild boar and roe deer (*Capreolus capreolus*), but also carnivores (FO=17.5%). Among carnivores, the most frequently found remains belonged to raccoon dogs (FO=9.0%) (**I**, Table 2), whereas of small mammals (FO=29.6%), voles (*Microtus* spp.), and especially the bank vole (*Myodes glareolus*) and shrews (*Sorex* spp.), were most frequent in stomach contents (**I**, Tables 1 and 2). Of birds, 37.9% were identified as *Passeriformes*, and 6.9% belonged to the hazel grouse (*Tetrastes bonasia*); the remaining feathers could not be identified due to severe degradation.

Overall, individual raccoon dog stomachs contained either broadly anthropogenic (anthropogenic plants, garbage and carrion commonly co-occurred) or broadly natural (invertebrates, amphibians and natural plants co-occurred) items, but mixtures of these categories were less frequent than expected (**I**, Table 4; Table S3; Figure S3). To some extent this reflects the availability of different food items in the different seasons, but the distinction remained largely intact within each season (**I**, Table S4). Natural plants and anthropogenic plants never co-occurred in the same stomach sample (**I**, Table 4). Anthropogenic plants were found alongside small mammals significantly more often than expected by chance. Anthropogenic plants also commonly co-occurred with carrion, though this relationship did not deviate significantly from random.

Raccoon dog diet differed significantly between autumn and winter (PERMANOVA, pseudo–F=28.2, R2=11.7, P=0.001; **I**, Figure 1). The largest differences between seasons were in the consumption of amphibians and invertebrates, which were consumed significantly more in autumn, whereas small mammals, carrion, natural plants and garbage were more frequent in the winter diet. Anthropogenic plants appeared to be the only category consumed frequently in both autumn and winter (**I,** Table 1). Food niche breadth was very similar for the sexes, 2.79 for females and 2.65 for males, and food niche overlap between the sexes was very high (0.99), while the overall food niche breadth for all the raccoon dogs was 2.83.

4.2 Parasite fauna of raccoon dogs in Estonia

In total, 249 small intestines, 240 lung and 223 urinary bladder samples were examined. We identified a total of 17 helminth species (**II**, Table 1), 12 from small intestine, three from lungs, one from urinary bladder and gall bladder (**II**,

Table S1). Raccoon dogs were most often infected with *U. stenocephala* (97.6%) and *A. alata* (68.3%). Infestation with other helminth species was considerably lower (**II**, Table 1). Genetic identification of tapeworms confirmed the presence of *Taenia polyacantha*. Altogether four (1.6%) animals were found to be infected with *E. multilocularis*. In two raccoon dogs, ascarid nematodes were found in the stomach in addition to the small intestine. We also often found intestinal helminth *A. alata* metacercaria in the lungs (13.3%). Two *Mesocestoides* species (*M. litteratus* and *M. lineatus*) were present in raccoon dogs, but we were unable to determine the species in most cases due to the absence of mature proglottids. Among individuals for which all internal organs (intestines, lungs and urinary bladder) were examined (n=205), 84.9% were infected with one to four species (**II,** Table 2). Average parasite species richness was 2.86 species (95% CI 2.64 to 3.08) and only two animals had no parasites in the studied organs. The highest number of different parasite species in the internal organs of a single raccoon dog was nine.

Although all animals harbouring more than five helminth species were males (**II,** Table 2), we did not find any significant relationship between the number of helminth species and animal sex (Mann-Whitney U test: $z=-0.75$; $p=0.46$). While there was no significant difference between animal sex and weight (mean weight for males 4.81 vs 4.84 for females), heavier animals were infected with more parasite specimens than smaller individuals: there was a significant relationship between animal weight and the infection intensity (logistic regression: Chi-square =9.08, $p<0.01$).

The number of helminth species detected in raccoon dogs varied between seasons (Mann-Whitney U test: $z=-5.19$; $p<0.01$): animals sampled from the autumn period were infested with more helminth species than animals collected from winter and early spring. Moreover, there was a significant relationship between the number of helminth species and consumed food categories (ANOVA: $F(7,193)=4.99$; $p<0.01$). Animals infected with higher numbers of helminth species consumed both natural plants and invertebrates more frequently (**II**, Table 3). We also detected a significant positive relationship between infection with one of the most prevalent parasite species *A. alata* and consumption of natural plants (Mann-Whitney U test $z=-4.32$; $p<0.01$). Analysis of co-occurrence between parasite species and different food categories detected four significant relationships (**II,** Table S3): *A. alata* and invertebrates, trematodes and natural plants, trematodes and invertebrates co-occurred, while trematodes and carrion never co-occurred in studied raccoon dogs.

4.3 Home ranges and habitat use of raccoon dogs in areas with different management intensity

In summer and autumn periods, the raccoon dogs used considerably larger (~2×) areas in intensively managed Ilmatsalu study area than in Soomaa National Park where anthropogenic influence to environment is by legislative regulations kept minimal: the mean MCP100 home range sizes of all analysed individuals were 391.9ha±292.9SD and 193.3ha±37.3SD, respectively (**III,** Table 1). In both study areas the summer home ranges (MCP100) were significantly larger than autumn ranges (Soomaa: 143 ha vs 111 ha; chi-square=83.426, df=2, p<0.001; Ilmatsalu: 358 ha vs 243 ha; chi-square=991.3, df=4, p<0.001). In winter period raccoon dog pair from Ilmatsalu changed their resting sites 18 times in the area covering 599 ha (MCP100). The total home range size for that animal was 72 ha (MCP100).

Although in both study areas most of the location points could be found in forest habitat, watersides were used more often than expected from the proportion of availability (**III,** Table 2). Also, according to preference indices (P_i), in Ilmatsalu study area raccoon dogs distinctively preferred watersides (P_i=0.77) to other habitats (open area P_i=–0.34; forests P_i=–0.22; shrubs P_i=–0.2). While P_i value for watersides was also the highest (0.38) compared to other habitats in Soomaa, the preference was not as pronounced as in Ilmatsalu (shrubs P_i=0.36; open areas forests P_i=–0.2; forests P_i=–0.38). Though in autumn period raccoon dogs could be quite often located in meadows and fields (open area), in seasonal bases no significant habitat selection could be found (summer period: Λ=0.59, chi-square=0.917, p=0.296; autumn period: Λ=0.77, chi-square=0.454, p=0.558).

4.4 Impact of sarcoptic mange to raccoon dogs

Impact of sarcoptic mange on raccoon dog feeding habits and parasite fauna

Overall diet composition did not differ between raccoon dogs infected with sarcoptic mange (n=33) and uninfected individuals (n=190) (PERMANOVA, pseudo-F=0.25, R2=0.001, P=0.79; **III,** Figure 1). However, in comparison with uninfected animals, individuals with symptoms of sarcoptic mange consumed carrion significantly more frequently during the whole study period (FO=45.3 vs FO=66.7; chi-square=5.61, df=1, p=0.023), while healthy animals consumed significantly more invertebrates (FO=31.6 vs FO=12.1; chi-square=5.20, df=1, p=0.023) (**III,** Table 3). No significant differences were found in the consumption of other food categories. When infected individuals were excluded from the seasonal comparison (autumn versus winter), the only change that could be noticed was the consumption of 'birds', occurrence of which was significantly higher in winter period (chi-square=7.33, p=0.007; **III,** Table 1).

Impact of sarcoptic mange on the movements and space use of raccoon dogs

During the outbreak of sarcoptic mange in Ilmatsalu study area, we were able to follow the movements of one female and one male raccoon dog who were asymptomatic at the time of collaring but got infected with the disease and died shortly after. The female animal could be radio tracked only for five weeks (32 days) and male animal for nine weeks (59 days) before their death. Both carcasses had severe symptoms of sarcoptic mange – extensive skin crusting and alopecia all over the body. The home range sizes for both animals declined noticeably in a certain time period before their death. For the male raccoon dog, the abrupt decrease in home range size – more than 200x (from 81.0 ha to 0.35 ha) – took place during its last week alive (**IV**, Table 1, Fig 1b and 1c). As for the female raccoon dog, the same kind of abrupt decline in home range size started about a month before its death. On the fifth tracking week the female moved around in the area covering 301.0 ha, while in the sixth week the home range size was 2.1 ha and by the week prior to its death the area had diminished to 0.3 ha, reducing thus about 1000x during the study period (**IV**, Table 1, Fig 1e and 1f).

The daily distances covered by raccoon dogs also shortened considerably. The abrupt decline of the average distance covered in 24 h started six days before the male raccoon dog's death, being 2986 m/day before the 26th tracking day and 276 m/day after (**IV**, Fig 1a). For the female raccoon dog, the most notable decline in movement activity took place 25 days before its death and was on average 3406 m/day before the 31st tracking day and 283 m/day after (**IV**, Fig 1d). Thus, both the male and female reduced their daily movements more than 10-fold.

There was also a significant difference between the use of habitats in active and passive periods for both raccoon dogs (female raccoon dog: chi-square=454.57, df=7, p<0.0001; male raccoon dog chi-square=747.55, df=7, p<0.0001). In active periods neither of the raccoon dogs showed any preference towards certain habitat, as there were less than 40% of location points in each habitat during each tracking week. However, in passive periods female raccoon dog spent most of its time in forest habitat (53% of the location points) and male raccoon dog most often resided in shrubs (83% of the location points).

5. DISCUSSION

5.1 Diet of raccoon dogs in Estonia

It has been suggested that the introduced raccoon dog may pose a threat to populations of ground nesting birds and amphibians, especially during their respective breeding seasons (Naaber, 1974; Laanetu, 1986; Kauhala, 1996a; Neronov et al., 2008). However, comparison of our study results with those of Naaber (1971) and Rätsepp (2005) support the idea of the raccoon dog as a species with opportunistic feeding strategy (e.g. Sutor et al., 2010), whose diet largely depends on the availability and phenology of different food items. For example, amphibians and birds are easiest to catch in their respective breeding seasons, whereas in other periods their availability generally remains low. Moreover, as most of the bird remains in the analysed samples belonged to passerines, raccoon dogs as poor hunters most probably fed on carcasses rather than killed the birds themselves. In our study the phenological effect is also evident in the consumption of invertebrates, which formed an important part of raccoon dog diet in autumn (FO=53.7%), but were rarely consumed in winter due to their low availability (**I**, Table 1).

Comparison of our results with dietary studies conducted in Estonia in 1960s (Naaber, 1971) and early 2000s (Rätsepp, 2005), revealed some significant trends in raccoon dog feeding habits. While the consumption of birds in autumn and winter period has remained roughly the same, small mammals are consumed much less frequently than other mammals. The reduced importance of rodents and insectivores in raccoon dog diet found in this study probably reflects the increased availability of alternative supplementary food (**I**, Information S1, Figure S2). Our results showed that in autumn and winter periods from 2010 to 2012 the most important food sources for the raccoon dogs were anthropogenic plants (FO=56.1%) and carrion (FO=48.4%), which were far less frequent in the diet in 1960s and early 2000s (Naaber, 1971; Rätsepp 2005). The fact that both food categories often co-occurred (**I**, Table 4), strongly suggests that both food groups were consumed at supplementary feeding sites created for wild boars, which were numerous at the time of our study. The number of feeding sites, which are regularly provisioned with cereals, vegetables and fruit, had increased substantially, from approximately 2000 to 4000 since the early 1990s by the time of our study. Alongside anthropogenic plant material, also remains of hunted animals are often left at or nearby feeding sites. The frequent consumption of ungulate carcasses (FO=34.5%) could also be attributed to the high mortality of ungulates during harsh winters in 2010–2012 (The Estonian Environment Information Centre). Although Selva et al. (2005) have shown that unlike other scavengers raccoon dogs do not avoid carnivore carcasses as a food source, still the frequency of occurrence of carnivore remains as high as 17.5% in our study (**I**) was somewhat surprising. Moreover, our results showed that raccoon dogs do not scorn carcasses of conspecifics, as hairs of raccoon dogs were found in 9% of the stomachs, which once more indicates that the species indeed is an opportunist when it comes to food and feeding.

5.2 Parasite fauna of raccoon dogs in Estonia

Altogether 17 endoparasite species were identified in Estonian raccoon dogs (**II**; Table 1). In addition, we also detected ectoparasite *S. scabiei*, an agent for sarcoptic mange, infection in 13.3% of the animals. We could not identify any difference in infection intensity and in weight between male and female raccoon dogs. This can be explained by the notion that raccoon dogs are monogamous and pairs tend to den and forage together most of the time (Kauhala et al., 1993; Drygala et al., 2008a).

We found that animals sampled in autumn (August–October) were infested with more helminth species than those from winter and early spring (November–April) (Mann-Whitney U test $z=-5.19$; $p<0.01$). Also animals originating from autumn period were infected with higher number of parasite species (logistic regression: chi-square=9.08, $p<0.01$). These findings are consistent with changes in the seasonal food habits of raccoon dogs. Namely, in autumn, raccoon dogs forage intensively and widely in order to accumulate subcutaneous fat to survive the cold winter (Drygala et al., 2008a), and therefore encounter a wide variety of parasites. However, in winter, especially when the snow cover exceeds 35 cm as it did in winters 2010/2011 and 2011/2012 in Estonia (Estonian Weather Service, 2012–2013), it becomes difficult for raccoon dogs to forage (Kauhala et al., 2007), which leads to reduced feeding opportunities and fewer contacts with parasites. If the temperature drops far below zero, as in the winters during this study (Estonian Weather Service, 2012–2013), raccoon dogs tend to stay in their dens for several days or even weeks without feeding.

Co-occurrence analysis of different food items and parasites showed that raccoon dogs infected with trematodes fed significantly more on natural plants and avoided eating carrion (**II**, Table S3). The mesocercariae of one of the most frequent trematode parasites detected in this study – *A. alata*, have been increasingly detected in wild boar tissues during official *Trichinella* inspections (Riehn et al., 2010; Portier et al., 2011). Moreover, wild boar remains constituted the largest share (FO=18%) among the carrion consumed by raccoon dogs (**I**). On one hand this fact appears to be in discord with the avoidance of carrion identified by the co-occurrence analysis; however, raccoon dogs that were already infected with a high burden of *Alaria* flukes (>200 specimens) might be expected to feed more on natural plants and avoid eating carrion. Indeed, we found significant relation between the number of *Alaria* flukes and consumption of natural plants (Mann-Whitney U test $z=-4.32$; $p<0.01$). Different grasses (e.g. *Poaceae*) and decayed plant material, though in small quantities, constituted the majority (53%) of natural plants (**I**). Intentional consumption of grass has been documented among many carnivore species, e.g.

dogs, wolves and civets (*Viverricula indica*), and it has been hypothesised that plant consumption occurs more often in animals exhibiting signs of illness (Stahler et al., 2006; Sueda et al., 2008; Su et al., 2013). Furthermore, we found that animals that harboured more helminth species fed significantly more on natural plants (**II**; Table 3). Given this, we suggest self-medicating behaviour among Estonian raccoon dogs.

5.3 The raccoon dog as a vector of zoonotic endoparasites

Out of 17 endoparasites detected in this study, nine are of zoonotic importance. Among these, the fox tapeworm *E. multilocularis* can be considered the most dangerous to humans, as it can cause severe organ damage (predominantly liver), which could lead to death with the mortality rate ~90% if left untreated (Eckert et al., 2001). This study was the first detecting the fox tapeworm in raccoon dogs in Estonia, making it the sixth country in Europe after Germany, Poland, Latvia, Slovakia and Lithuania (Thiess et al., 2001; Machnicka-Rowinska et al., 2002; Bagrade et al., 2008; Hurnikova et al., 2009; Bružinskaite-Schmidhalter et al., 2012; Marcinkute et al., 2015), where *E. multilocularis*-infected raccoon dogs have been reported. Although the tapeworm was detected in only four carcasses out of 249, the relatively high numbers of raccoon dogs in Estonia (Veeroja and Männil, 2016) suggests that the actual number of infected animals could be rather high. Thus the importance of raccoon dog as a vector and cause of environmental contamination with *E. multilocularis* and other zoonotic parasites cannot be underestimated.

The most prevalent parasite species, which can occasionally infect humans and cause serious health problems, were *U. stenocephala* (97.6%) and *A. alata* (68.3%). Therefore, both species can be considered to have very high zoonotic potential. *Uncinaria stenocephala* larvae can pass through a human skin and migrate subcutaneously, causing a painful itchy rash called cutaneous larva migrans (Tamminga et al., 2009), while *A. alata* can damage organs (e.g. eyes) or muscle tissue (Wasiluk, 2009). Infectivity to humans and dogs, and the observed high prevalence rates in Estonia as well as in Denmark and Lithuania (Bružinskaite-Schmidhalter et al., 2012; Al-Sabi et al., 2013) make *U. stenocephala* and *A. alata* pathogens that represent a considerable public health risk.

The comparison of raccoon dog parasite fauna in introduced areas in Europe with the subspecies native distribution area in Far East Russia, revealed that all three zoonotic agents, along with *Metorchis bilis*, *Mesocestoides* spp., *Crenosoma vulpis*, *Toxascaris leonina* and *Toxocara canis* were present in both areas (**II**; Table 4). Taking into account that the animals used for translocation were most probably free of parasites, as they were regularly treated with anthelmintics (Skomodorov, 1939), the parasites must have been acquired *in situ* after introduction. In addition, raccoon dogs have acquired five more zoonotic endoparasites, which originally were absent in their native range, indicating that raccoon dogs can be highly susceptible to new zoonotic agents.

Considering the relatively high number of zoonotic parasites identified in raccoon dogs so far, the species should be regarded in Europe as an important source of environmental contamination with zoonotic agents.

5.4 Spatial requirements of raccoon dog: home ranges and habitat use

Although based on a relatively small sample size, our study results indicate that home ranges of raccoon dogs could be considerably smaller in forest-dominated areas, where the human impact to natural environment is minimal, compared to intensively managed areas (**III**). We expected the opposite, as studies conducted elsewhere in Europe have shown that home ranges of raccoon dogs are generally smaller in landscapes where majority of the land is in agricultural use and intensively managed, compared to areas were human activity is low (Drygala et al., 2008a; Kauhala and Holmala, 2008; Sutor and Schwarz, 2012; Drygala and Zoller, 2013). However, studies from Finland and Germany have also demonstrated that size of the area used by a raccoon dog depends on habitat richness: raccoon dogs tend to have smaller home ranges in areas with a variety of small habitat patches (Drygala et al., 2008a; Kauhala and Auttila, 2010; Kauhala et al., 2010; Drygala and Zoller, 2013). For example, Kauhala et al. (2010) have shown that in Finland in areas dominated by monocultural spruce forest, home ranges of raccoon dogs were twice the size compared to the areas comprised of meadows, mixed forests and gardens. The same kind of trend was identified by Drygala et al. (2008a) in northeastern Germany, while Sutor and Schwarz (2012) demonstrated the opposite. Although both investigations took place in landscapes dominated by agricultural practices, home ranges were considerably smaller in the study of Sutor and Schwarz (2012), which had higher diversity of habitat types – forests with abandoned badger dens, hedges, and grasslands – compared to the former, which was characterised by vast homogenous crop fields (Drygala et al., 2008b; Sutor and Schwarz, 2012). Similar pattern to that observed by Sutor and Schwarz (2012) was also characteristic to our study, as the range of different habitat patches was more diverse in Soomaa than in Ilmatsalu. The habitat type 'forest' consisted of deciduous, coniferous and mixed forests in Soomaa, while only of mixed forest in the Ilmatsalu study area. In addition, while the drainage ditches were the only type of water bodies represented within the home ranges of the raccoon dogs in Ilmatsalu, two rivers flowing through the Soomaa study area provided additional habitats such as reed beds and meadows. Therefore, it is possible, that at a smaller scale the habitat composition in Soomaa was more suitable for raccoon dogs than in Ilmatsalu. Therefore, it is also possible that for an opportunistic omnivore like raccoon dog natural protected areas provide a bigger variety of food objects and hiding places than an intensively managed landscapes, where the anthropogenic food sources are plentiful, but only periodically.

However, we cannot overlook the impact of diseases and hunting pressure when comparing Soomaa and Ilmatsalu study areas. During the study period there was an outbreak of sarcoptic mange in Ilmatsalu area, which kept the population density low, probably enabling the healthy raccoon dogs to broaden their home ranges. Moreover, the hunting pressure during our study (**III**) period was high in Ilmatsalu area (over 50 kills per 12 square kilometres; personal communications with local hunters). Hence it is likely that the population density of the raccoon dogs was considerably higher in Soomaa study area, where the game management was forbidden and no evidence of the spread of sarcoptic mange could be noticed during the study period (personal communication with Soomaa National Park managers; our own observations).

It is common for raccoon dogs to broaden their home ranges in autumn compared to summer, as the cub rearing period has ended and raccoon dogs start to accumulate fat reserves for the coming winter period (Kauhala et al., 1993; Drygala et al., 2008b; Sutor and Schwarz, 2012). It is interesting to note that in Ilmatsalu area, the raccoon dog pair radio-tracked through both seasons extended their movement area in autumn, whereas two animals from Soomaa reduced their home ranges by half during the same period (**III**, Table 1). This seemingly contradictory behaviour could be explained by the changes in the water level in Soomaa. Just like in spring, the flooding occurred also in autumn, restricting movements of raccoon dogs on the overflown water meadows surrounding the rivers. The other reason for smaller autumn home ranges could be an increased availability of anthropogenic food in this period. One of the raccoon dogs shifted its range to the vicinity of the Soomaa National Park Centre where ripe fruits and food waste from the compost heap were available. The other raccoon dog visited repeatedly at least two old orchards (relicts of the abandoned messuages) where apples were available. Though households with orchards existed also within and nearby the home range of the raccoon dog pair from Ilmatsalu, those were fenced and guarded by dogs, making the potential food sources inaccessible. The latter might have also affected the home range size, forcing the raccoon dog pair to forage in larger areas.

As for the habitat use in the summer period, raccoon dogs in both study sites most often roamed in forest areas (**III**, Table 2), which provide safe environment (burrows, as well as food) for the period of pup rearing. Still, throughout the study period, raccoon dogs used forest habitats in proportion to their availability and showed clear preference only towards watersides, which is in accordance with previous findings (e.g. Nasimovic and Isakov, 1985; Kauhala, 1996a). In autumn, the raccoon dogs visited more frequently meadows, shrubs and reed beds at riversides. This kind of seasonal shift in habitat selection could be explained by phenological changes in food availability, e.g. the amphibians gather nearby the watersides during their mass migrations, making themselves easily accessible prey for the opportunistic raccoon dog. Indeed, in Estonia the frequency of occurrence of different kind of plant material (FO=89.9%) and also amphibians (FO=14.4%) in raccoon dog diet was rather high in autumn period (**I**). Also, after pups become independent and start to disperse, adult raccoon dogs expand their home ranges to forage more intensively and accumulate fat reserves before winter. Compared to early spring, raccoon dogs double their body weight by the end of autumn (4.3 kg *vs* 8.6 kg; Mustonen et al., 2007).

We also studied movements of the raccoon dog pair in Ilmatsalu area from November 2012 to January 2013. The pair stayed together for the whole study period and moved around extensively, covering the area of 599 ha. As this result is based on only 18 resting sites it is possible that the area where the raccoon dogs moved around could have been even larger. Our results are similar to the winter home range reported in eastern Finland (586 ha) (Mustonen et al., 2012) (**III**, Fig 2, Table B in S1 File). In Poland (Jedrzejewska and Jedrzejewski, 1998), the movements at this period ranged from 50–400 ha. In Germany, where weather conditions are milder in winter, home ranges size have reached up 669 ha (Drygala et al., 2008a) (**III**, Fig 2, Table B in S1 File). Larger home range sizes in winter period could be explained by the need to cover long distances between suitable resting and feeding sites. In our study area, most of the resting sites were situated in reed beds and around the commercial fish ponds, which were drained for the winter period. The preference of open areas in winter period has also been demonstrated by Mustonen et al. (2012).

Kauhala et al. (2007) have shown that raccoon dogs stay dormant in their dens when air temperature is below -10 °C and snow depth is over 35 cm. In the Ilmatsalu study area, Oja (2010) has registered the absence of raccoon dogs at supplementary feeding sites at temperatures below -6 °C. The frequent changes of the resting sites observed in Ilmatsalu area were probably due to mild weather conditions: during the study period the snow depth did not exceed 16 cm, and the short periods when temperature dropped below -10 °C quickly alternated with the thaw (Estonian Weather Service). Kauhala et al. (2007) and Mustonen et al. (2012) have pointed out that frequent movements of raccoon dogs during their usual winter lethargy could facilitate the spread of diseases. Like mentioned before, there was an outbreak of sarcoptic mange in the Ilmatsalu study area during our tracking period. Therefore, it is highly likely that sarcoptic mange was also the cause of death of the raccoon dog pair in March 2013, although both animals were in good condition when observed in January.

5.5 Impact of sarcoptic mange to raccoon dog

The drastic changes in movements and space use of two raccoon dogs during the outbreak of sarcoptic mange demonstrated how severe and rapid could the course of the disease be (**IV**). Both animals had no visible evidence of infestation at the time of collaring, which means that at this point they were either uninfected or infection was so recent that external symptoms (skin crusting) had not yet appeared. Just few weeks after collaring – 32 days for the female and 59 days for the male raccoon dog – the mange had progressed so intensively that both animals died. Kido et al. (2011) have shown in their study that raccoon dogs infested with *S. scabiei* developed malnutrition and severe dehydration due to appetite loss, as well as sepsis and insufficient renal perfusion if the mange infestation was untreated. Abrupt decline in home range size and in daily covered distances indicates that at some stage the impact of mange started to affect the physiological state of infected animals so forcefully that made them almost immobile, which was probably caused by severe sepsis leading to organ failure. In the study of Nakagawa et al. (2009) the predominant causes of death in 43 studied raccoon dogs with mange were sepsis and pneumonia. This could, at least in part, explain why both raccoon dogs during their active period did not favour one habitat type over others. While raccoon dogs are known to usually spend most of their time in wet open habitats (e.g. damp meadows, marshlands, river valleys) that are rich in various food objects (Kauhala and Kowalczyk, 2011; **III**), the diseased individuals in our study (**IV**) obviously had not enough energy to spend most of their time searching for food as healthy animals do. It has been shown in wombats *Vombatus ursinus* that individuals with severe mange spend only a fraction of time walking, which may result from an attempt to reduce energy expenditure associated with movements as a trade off against fighting infection (Simpson et al., 2016). The development of severe sepsis leading to organ failure could also explain why in the passive period raccoon dogs spent most of their time either in forest or in shrubs that probably provided suitable hiding and resting places to avoid contact with predators. There were also several messuages in the study area, most with domestic dogs, which from time to time were able to stray around freely, creating favourable conditions to indirect or direct contact with infected raccoon dogs. In fact, one of the dogs that lived in a household visited by collared raccoon dogs, got mange infection and had to be allocated to medical treatment, supporting the concept of mange spillover between wild canids and dogs (Matsuyama et al., 2015). Results of the diet study (**I**) also suggest that sarcoptic mange may influence raccoon dog foraging decisions or the ability to locate or catch live prey. Diet comparison of infected and uninfected raccoon dogs revealed that infected individuals consumed significantly less invertebrates (FO: 12.1% vs. 31.6%), but more carrion (FO: 66.7% vs 45.3%). At least some of the carrion consumed by the raccoon dogs examined in our diet study (**I**) originated from supplementary feeding sites, as remains of ungulates/carnivores and anthropogenic plants co-occurred in stomach contents more often than could be expected by chance (**I**; Table 4). As shown by Oja (2012), infected raccoon dogs visit supplementary feeding sites more often than healthy individuals. At least in autumn and winter time it is far less energy consuming for nutritionally impoverished animals to rely on food sources available at feeding sites than to spend time searching for invertebrates. Also findings of Saito and Sonoda (2017) indicate that raccoon dogs with mange infection occur more often in human-modified landscapes than asymptomatic animals.

5.6 The role of raccoon dog in introduced ecosystems

Based on our results (**I**) and on those conducted elsewhere in Europe in the last decades (e.g. Drygala, 2009; Sutor et al., 2010), raccoon dog behaves like a true opportunist choosing habitats and food items according to their availability. However, its skills as a predator seem to be rather modest. Small-scale applied studies with trail cameras from Estonia have demonstrated that the impact of raccoon dogs in nest depredation is minimal. Out of 91 artificial ground nests in forest habitat (Veeroja, 2015) and out of 38 artificial ground nests in coastal meadows (Laos and Männil, 2017), only one was depredated by raccoon dog. In a pilot study conducted in a framework of our telemetrical study in Ilmatsalu, out of 11 artificial groundnests none were depredated by raccoon dogs. In all of these studies most of the nests were depredated by either martens or red foxes although raccoon dogs were recorded several times passing by the nests. These results are in accordance with those of Opermanis et al. (2001) and Kauhala (2004), who also identified red foxes and martens but also American mink as main nest predators, and suggested that raccoon dogs pose a minimal threat to ground nesting birds in the presence of other carnivores. These results indicate that the overall impact of raccoon dogs to native fauna is probably low. Nevertheless, based on several dietary studies (Naaber, 1971; Laanetu, 1984; Kauhala, 1996a), ground nesting birds and their eggs, but also amphibians can periodically form a major part of raccoon dog diet. Thus, the species could seasonally and locally be harmful to some prey groups and additional dietary studies are needed in areas where threats to native fauna could possibly appear, especially in isolated populations (e.g. small islands). Moreover, evidence of possible harm to waterfowl in autumn period from Estonia date back to 1960s (Naaber. 1971) and 1980s (Laanetu 1984), and based on our study results (**I**), it is possible that due to numerous supplementary feeding sites which provide easily attainable food sources, the predation pressure on waterfowl outside their breeding season has probably decreased substantially. It has been suggested by Sidorovich et al. (2008a) that raccoon dogs do not always choose protein-rich food, such as birds, which are difficult to capture, but rather consume energetically less valuable food, which occur in big quantities and in Estonia that kind of food source is easily obtainable at supplementary feeding sites.

From the standpoint of conservation, the high number of supplementary feeding sites might have been beneficial to such vulnerable vertebrate groups as ground nesting birds and amphibians. At the same time wild boar feeding sites concentrate many other non-target species like rodents and red foxes besides raccoon dogs (Oja, 2012), creating favourable conditions for spread of diseases and parasites through interspecific as well as intraspecific contact. Also in our dietary study (**I**) we identified that rodents and carrion were often consumed at or nearby feeding sites, as these food categories often co-occurred with cereals and fruits. We recorded that Estonian raccoon dogs harbour at least 17 helminth species (**II**), most of which are also common for red foxes (Laurimaa, et al., 2016) and for many of which the infection source are rodents. This data but also that of Oja et al. (2017) suggests that supplementary feeding sites are considerable source for spill over of parasites and play an important role in preserving them in nature. Most of the parasites recorded from Estonian raccoon dogs (**II**) but also from red foxes (Laurimaa et al., 2016) are of zoonotic importance, which means that supplementary feeding sites, though indirectly, also pose a threat to human health. The problem is even more relevant, considering that among other helminth species we also recorded the fox tapeworm *E. multilocularis* in Estonian raccoon dogs for the first time (**II**; Laurimaa et al., 2015c). *E. multilocularis* is an agent of alveolar echinococcosis, which is typically asymptomatic for the definitive host, but causes severe illness with high mortality rate in its intermediate hosts, including humans. While about 30% of red foxes in Estonia are infected with *E. multilocularis* (Moks et al., 2005; Laurimaa et al., 2016), the parasite has been found also in an urban area. Recently, two red fox fecal samples infected with *E. multilocularis* were recorded in Tartu, Estonia (Laurimaa et al., 2015a). Although, unlike red foxes, raccoon dogs are rarely met in European urban environments, as a vector the species could be the initial source of the infection through interspecific contacts.

Another zoonotic disease spread by raccoon dogs is the sarcoptic mange, which is a highly contagious mite infection caused by *S. scabiei* burrowing in the skin of domestic and wild animals, but also humans (Pence and Ueckermann, 2002; Micali et al., 2016). Sarcoptic mange can be transferred indirectly by visiting or sharing dens and passage sites (Kraabøl et al., 2015). This kind of disease transmission is common in the populations of European red foxes and raccoon dogs. Both species have been shown to be amongst the main reservoirs and carriers of the sarcoptic mange in European wildlife (Kauhala and Kowalczyk, 2011; Kolodziej-Sobocinska et al., 2014). Like elsewhere in Europe (Kauhala et al., 1998b; Kowalczyk et al., 2008), raccoon dogs have been recorded to use badger setts also in Estonia. Jõgisalu (2012) reported that out of 365 badger setts (with over 4000 burrow openings) raccoon dogs' activity was identified in 16%. Moreover, in 13% of setts or burrows co-existence of badgers, foxes and raccoon dogs were reported. That kind of shared use of setts increases the interspecific contact rate among different species of carnivores and creates circumstances favourable for the transmission of diseases like sarcoptic mange, but also rabies and alveolar echinococcosis (Holmala and Kauhala, 2006; Kauhala et al., 2006). Actively used badger setts and red foxes were also present in our study areas in Soomaa and Ilmatsalu (**III, IV**). During our telemetry study (**III**) there was a severe outbreak of sarcoptic mange in Ilmatsalu study area, which was also a part of a local hunting ground with several supplementary feeding sites existed. At the same time there is no information of an outbreak of similar extent from the study area situated in Soomaa National Park, where game management is not allowed. This once more suggests that supplementary feeding sites facilitate the spread of diseases. Moreover, Oja (2012) found that in winter time when natural food sources are scarce, raccoon dogs visiting feeding sites had often symptoms of sarcoptic mange, which indicates that anthropogenic food is essential for the survival of infected animals. Like elsewhere in Europe, also in Estonia raccoon dog has the status of an alien species that can potentially harm local ecosystems. Therefore, the species is treated as a pest and hunting is allowed all through the year, with some exceptions, e.g. in small islands from 1. October to 30. April (Hunting Act 2016, RT I, 13.01.2016, 7). Due to the high reproductive potential, promoted by monogamous social system with bi-parental care, the raccoon dog population is difficult to control. Based on the age structure of hunted raccoon dogs, the mortality rate is highest among juveniles – about 90% of hunted individuals are less than 2 years old (Veeroja and Männil, 2015). This suggests very high proportion of juveniles in the raccoon dog population, which aside of intrinsically high reproduction of the species, might indirectly be a consequence of high hunting pressure. When the population density is lower than it would be without control, there is more food per female, and females may therefore have larger litters, which in turn keeps the population density high in spite of high hunting pressure (Helle and Kauhala, 1995; Drygala, 2009). Therefore, in Estonia where the species is already intensively hunted, keeping the number of supplementary feeding sites low seems the most efficient game management practice that could help to prevent further damages by raccoon dogs on their prey, particularly amphibians and birds, and the spread of pathogens harboured by raccoon dogs.

SUMMARY

Invasive alien species are one of the major agents of human-accelerated global change: they threaten biodiversity, alter ecosystem structure and functions, inflict large economic costs and can cause serious problems to human health. In invasion biology mammals are among the best studied groups, because they are charismatic, more visible than other animals and can cause more harm than most other animal groups. One of the most successful invasive alien mammals in Europe is the raccoon dog (*Nyctereutes procyonoides*). Motivated by the value of its fur, about 9000 individuals of the subspecies *N. p. ussuriensis* were intentionally, and sometimes accidentally as escapees from fur farms, introduced from south-east Siberia mainly to European parts of the former Soviet Union between 1927 to 1957. Characteristics including omnivorous diet, high reproductive potential and the ability to hibernate at high latitudes during winter have allowed the raccoon dog to successfully colonise new areas. The species is currently well-established in Europe and continues to extend its range. Studies from different parts of Europe have revealed that raccoon dog has a potential to damage native fauna as a predator and is also an important vector of zoonotic diseases.

The main objectives of this thesis were to investigate the feeding habits of the raccoon dog in Estonia to determine if there have been any temporal changes in the food habits compared with studies conducted decades ago, and to assess potential impact of the species on various vulnerable prey categories, incl. birds (**I**). Also, we aimed to analyse parasite fauna of raccoon dogs in order to evaluate the species zoonotic potential (**II**), and to assess the impact of sarcoptic mange on raccoon dog feeding habits (**I**), movements, habitat use and home range size (**IV**). In addition, we aimed to study space requirements of raccoon dogs in Estonia, to assess their home range size and habitat use in areas with different management regimes (**III**).

Our diet study (**I**) revealed that in autumn and winter period the most important food sources for Estonian raccoon dogs are anthropogenic plants (e.g. cereals, vegetables, fruit) (FO=56.1%) and carrion (FO=48.4%). Compared with 1960s and early 2000s the consumption of birds has remained roughly the same (12% in 1960s, 9% in 2000s and 13% in our study), while small mammals are consumed much less frequently (46% in 1960s vs 29.6% in our study) than other mammals. The reduced importance of rodents and insectivores in raccoon dog diet probably reflects the increased availability of alternative food sources, such as anthropogenic plants but also leftovers of hunted game animals, easily obtainable at supplementary feeding sites created for wild boars (*Sus scrofa*), which were numerous at the time of our diet study (**I**). The feeding sites also concentrate many other non-target species, like rodents and red foxes (*Vulpes vulpes*), creating favourable conditions for the spread of diseases and parasites through interspecific, as well as intraspecific contacts. We also recorded that Estonian raccoon dogs harbour at least 17 helminth species (**II**), most of which

are also common in red foxes and for many the infection source is rodents. This data suggests that supplementary feeding sites have the potential to be a considerable source for parasite spillover and could play an important role in propagating parasites in nature. Nine parasites recorded from Estonian raccoon dogs (**II**), but also from red foxes, are of zoonotic importance, which means that supplementary feeding sites indirectly also pose a threat to human health and their number should be strictly controlled.

Among the parasites of zoonotic importance found in raccoon dogs, the fox tapeworm (*Echinococcus multilocularis*) can be considered the most dangerous to humans. The fox tapeworm causes disease named alveolar echinococcosis, which can severely damage internal organ that could lead to death (estimated mortality rate is ~90% if left untreated). The parasite was found in 1.6% of investigated animals, and this was also the first time the fox tapeworm was detected in Estonian raccoon dogs. The most prevalent parasite species, which can also occasionally infect humans and cause serious health problems, were *Uncinaria stenocephala* (97.6%) and *Alaria alata* (68.3%). Therefore, both species can be considered to have high zoonotic potential. In addition, we also detected ectoparasite *Sarcoptes scabiei*, an agent for sarcoptic mange, in 13.3% of the animals. As revealed by the diet study (**I**) sarcoptic mange may influence raccoon dog's food habits. Diet comparison of infected and uninfected raccoon dogs revealed that infected individuals consumed significantly less invertebrates (FO: 12.1% vs. 31.6%), but more carrion (FO: 66.7% vs 45.3%). Scabied raccoon dogs, but also red foxes, often forage for food around human settlements, which poses health risks for humans and domestic animals, especially for domestic dogs.

We equipped 12 raccoon dogs with radio-collars to study their home range and habitat use in two areas with different management regimes in Estonia: in a protected natural area and in an intensively managed area (**III**). From May to October raccoon dogs inhabiting the natural area had considerably smaller home ranges compared to the managed area: 193.3ha±37.3SD and 391.9ha±292.9SD, respectively. This result contradicts earlier findings from other parts of Europe, where the home range sizes in natural areas in summer and autumn period have been larger compared to managed areas. In both study areas raccoon dogs preferred watersides, where amphibians and other semi-aquatic prey are abundant, to other habitats available in their home ranges.

During the space use study (**III**) there was an outbreak of sarcoptic mange in the intensively managed area. This provided us a rare opportunity to study the course of mange on two radio-collared raccoon dogs, which initially had no external symptoms of *S. scabiei* infection, but developed these during the study period (**IV**). Both raccoon dogs spent most of their time in the safety of forest patches or shrubs, which provided them with suitable place for resting and hiding to avoid contact with predators. One of the raccoon dogs died just after 32 and the other after 52 days of collaring. During a relatively short period before their death, there was an abrupt and drastic decline in their home range size and daily covered distances. These results indicate that at the later stages of sarcoptosis, possibly septicaemia affected the physiological state of the diseased animals so forcefully that made them almost immobile. Our results show for the first time how rapid and severe could the impact of sarcoptic mange be in one of its most important reservoir and vector species.

In conclusion, raccoon dog seems to act as a true opportunist in terms of habitat use and feeding habits. Raccoon dogs prefer to live in wet habitats, which means that as a predator the species could potentially harm also vulnerable prey groups such as waterfowl and frogs. However, that kind of negative impact is strongly dependent on season and mostly applies to isolated populations, which means that in general raccoon dogs do not pose a threat to local native fauna. Moreover, raccoon dog is a vector of severe zoonotic pathogens, spread of which is directly correlated with the raccoon dog population density. Therefore, it is important to reduce and control the number of wild boar supplementary feeding sites that provide additional food for raccoon dog, promote their reproduction, but also concentrate other non-target species and therefore facilitate the spread of pathogens, including zoonotic.

SUMMARY IN ESTONIAN

Kährikkoer (*Nyctereutes procyonoides*) Eesti looduses zoonooside levitaja ja kiskjana toitumis-, parasitoloogiliste- ning telemeetriauuringute põhjal

Invasiivsed võõrliigid võivad uude keskkonda sattudes rikkuda kohalike ökosüsteemide tasakaalu ja vähendada looduslikku mitmekesisust. Päritolualadelt võivad nad kaasa tuua uusi haigustekitajaid või osutuda uuteks vektorliikideks juba olemasolevatele patogeenidele, põhjustades kahju nii inimese kui loomade tervisele ja majandusele. Üheks edukaimaks võõrliigiks Euroopas on kährikkoer (*Nyctereutes procyonoides*), kes seoses karusnaha kõrge hinnaga introdutseeriti ajavahemikul 1927–1957 Kagu-Siberist mitmetesse Ida-Euroopa riikidesse. Kõrge sigimispotentsiaali, laia toiduspektri ning koerlaste seas ainulaadse omaduse tõttu jääda karmides talveoludes taliuinakusse, levis kährikkoer kiirelt pea üle kogu Euroopa. Viimastel kümnenditel läbi viidud uuringud on näidanud, et kährikkoer võib kiskjana olla ohuks kohalikule faunale ning on samas ka mitmete loomadelt inimestele kanduvate haiguste ehk zoonooside levitaja.

Saamaks ülevaadet muutustest kährikkoera toitumises Eestis võrreldes möödunud aastakümnetega ning kisklussurvest tundlikumatele saakliikidele (näiteks maaspesitsevatele lindudele ja kahepaiksetele) analüüsisime maosisude põhjal kährikkoerte toitumist. Uurisime ka kärntõve mõju toitumisele, võrreldes toitumiserinevusi nakatunud ja mittenakatunud isendite vahel (**I**). Hindamaks liigi zoonootilist potentsiaali, uurisime ka kährikkoera parasitofaunat (**II**). Ühtlasi viisime läbi telemeetrilised uuringud, hindamaks kährikkoerte kodupiirkonna suurust ning elupaigakasutust erineva maakasutuse intensiivsusega piirkondades (**III**) ja kärntõve mõju kährikkoerte ruumikasutusele (**IV**).

Toitumisuuringu tulemustest selgus (**I**), et sügis- ja talveperioodil toituvad kährikkoerad peamiselt raipest, mille esinemissagedus (ES) oli 48,4% ning antropogeenset päritolu taimsest materjalist (nt. teravili, aedvili; ES=56,1%). Võrreldes 1960. ja 2000. aastatel teostatud uuringutega on lindude esinemissagedus kährikkoera toidus püsinud stabiilselt madalana (vastavalt 12%, 9% ja 13%), seevastu näriliste ja selgrootute loomade osakaal on oluliselt vähenenud. Viimati nimetatud toiduobjektid on suuresti asendunud antropogeense taimse materjaliga, mis on seoses metssigade (*Sus scrofa*) lisasöötmiseks mõeldud söödaplatside hulga kasvuga muutunud järjest kättesaadavamaks. Ka raipe suur osakaal toidus näib olevat seotud söödaplatsidega, kuna enamasti esines see toidukategooria magudes koos teravilja või aedvilja jäänustega. Lisaks kährikkoerale käivad söödaplatsidelt looduslikule toidule lisa otsimas ka punarebased (*Vulpes vulpes*) ning närilised, mis aitab liikidevaheliste kaudsete ja otseste kontaktide kaudu kaasa erinevate haiguste, sealhulgas ka inimesele ohtlike, levikule. Seitsmeteistkümnest eesti kährikkoertel leitud parasiidiliigist üheksa põhjustavad zoonootilisi haigusi ning enamik neist on varasemalt kindlaks tehtud ka punarebastel. Seejuures on mõlema koerlase puhul peamiseks nakkusallikaks sageli närilised. Et söödaplatside rohkus võib kaudselt ohustada ka inimese tervist, siis peaks taolisele jahimajanduspraktikale seadma selged piirangud.

Parasitoloogilise uuringu (**II**) käigus tuvastati kährikkoertel Eestis esmakordselt ka inimesele eluohtliku alveokokk-paelussi (*Echinococcus multilocularis*) nakkus – 1,6% isenditest olid nakatunud. Samas kõrgeima esinemissagedusega zoonootilisteks parasiidiliikideks olid inimesel nahakahjustusi tekitav *Uncinaria stenocephala* (97,6%) ja silmade ning lihaskoe kahjustusi põhjustav *Alaria alata* (68,3%). Lisaks tuvastasime 13,3% uuritud kährikkoertel sarkoptoosi ehk kärntõbe tekitava süüdiklesta (*Sarcoptes scabiei*) nakkuse, mis võib nakatada ka inimesi ja koduloomi. Toitumisuuringu tulemused viitavad (**I**), et kärntõbi võib oluliselt mõjutada kährikkoerte toitumist, eelkõige võimet püüda elusaid saakloomi. Nimelt näitas tervete ja nakatunud loomade võrdlus, et kärntõbised loomad toitusid oluliselt harvem selgrootutest loomadest (ES: 12,1% *vs.* 31,6%) ning tarbisid sagedamini hoopis raipeid (ES: 66,7% *vs.* 45,3%). Kärntõves kährikkoerad, aga ka punarebased, liiguvad toiduotsingutel sageli asulate läheduses, mistõttu toovad ulatuslikumad kärntõve puhangud metsloomade hulgas reeglina kaasa ka nakkusjuhtude sagenemise koduloomadel, eelkõige koertel. Kui inimese puhul ei vaja kärntõve infektsioon meditsiinilist sekkumist, siis koduloomadel võib ravi hilinemine põhjustada tõsiseid ja sageli eluaegseid terviseprobleeme.

Raadiotelemeetrilise uuringu tulemused näitasid, et vastupidiselt mujal Euroopas elutsevatele kährikkoertele on siinsete loomade kodupiirkonnad loodusmaastikus pea poole väiksemad võrreldes intensiivselt majandatavate aladega (vastavalt 193,3ha±37,3SD ja 391,9ha±292,9SD) (**III**). Mõlemal uurimisalal eelistasid kährikkoerad viibida veekogude läheduses, kus sageli leidub poolveelise eluviisiga loomi (nt kahepaikseid). Lisaks oli meil intensiivselt majandataval uurimisalal aset leidnud ulatusliku kärntõve puhangu tõttu esmakordne võimalus uurida haiguse mõju kahele isendile, kel kaelustamise hetkel haigussümptomid puudusid (**IV**). Kärntõve kulg oli kiire – üks kährikkoertest hukkus juba 32 ning teine 52 päeva peale raadiokaelusega varustamist. Selle aja jooksul vähenes mõlema isendi kodupiirkonna suurus ning päevateekonna pikkus oluliselt ning eriti järsk muutus leidis aset enne surma. On võimalik, et haiguse hilisemas staadiumis välja kujunenud septiline šokk muutis nakatunud kährikkoerad pea liikumisvõimetuks.

Võttes kokku Eestis, aga ka mujal Euroopas läbi viidud uuringute tulemused, võib väita, et nii elupaigavaliku kui ka toitumise poolest on kährikkoera näol tegemist oportunistliku liigiga, kes võimalusel eelistab viibida veekogude läheduses ning sellest lähtuvalt võib ta kiskjana ohustada seal pesitsevaid veelinde ja kahepaikseid. Taoline negatiivne mõju on aga reeglina lokaalse ning sesoonse iseloomuga ning seetõttu kährikkoer kohalikule faunale laiemat ohtu ei kujuta, kui tegemist pole just isoleeritud aladega, nt. väikesaartega. Küll aga on kährikkoer mitmete, muuhulgas ka inimesele ohtlike parasiitide kandjaks ning levitajaks. Kuna haiguste levik on suuresti seotud nende kandjate asustustihedusega, siis on oluline hoida kõrge sigimispotentsiaaliga kährikkoerte arvukus ning selle tõusu soodustavad tegurid (näiteks söödaplatside arv) kontrolli all.

REFERENCES

Abuladze, K.I. (1964). Common Cestodology, Part 4: *Taeniidae* – tapeworms of animals and humans and causal agents of their illnesses. Nauka, Moscow, 530 pp. (in Russian)

Aebicher, N.J., Robertson, P.A., Kenward, R.E. (1993). Compositional analysis of habitat use from animal radio-tracking data. Ecology, 74, 1313–1325.

Al-Sabi, M.N.S., Chriel, M., Jensen, T.H., Enemark, H.L. (2013). Endoparasites of the raccoon dog (*Nyctereutes procyonoides*) and the red fox (*Vulpes vulpes*) in Denmark 2009–2012 – A comparative study. International Journal for Parasitology: Parasites and Wildlife, 2, 144–151. doi: 10.1016/j.ijppaw.2013.04.001

Aul, J., Ling, H., Paaver, K., (1957). Eesti NSV imetajad. [Mammals of Estonian SSR]. Eesti Riiklik Kirjastus, Tallinn, pp. 256–257. (in Estonian)

Bagrade, G., Šnabel, V., Romig, T., Ozolinš, J., Hüttner, M., Miterpakova, M., Ševcova, D., Dubinsky, P. (2008). *Echinococcus multilocularis* is a frequent parasite of red foxes (*Vulpes vulpes*) in Latvia. Helminthologia, 45, 157–161.

Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of Royal Statistical Society B, 57, 289–300.

Bružinskaite-Schmidhalter, R., Šarkunas, M., Malakauskas, A., Mathis, A., Torgerson, P.R., Deplazes, P. (2012). Helminths of red foxes (*Vulpes vulpes*) and raccoon dogs (*Nyctereutes procyonoides*) in Lithuania. Parasitology, 139, 120–127.

Ćirović, D. (2006). First record of the raccoon dog (*Nyctereutes procyonoides* Gray, 1834) in the former Yugoslav Republic of Macedonia. European Journal of Wildlife Research, 52, 136–137.

Genovesi, P., Carnevali, L., Alonzi, A., Scalera, R. (2012). Alien mammals in Europe: updated numbers and trends, and assessment of the effects on biodiversity. Integrative Zoology, 7, 247–253.

Eckert, J., Gemmell, M.A., Meslin, F.-X., Pawłowski, Z.S. (2001). WHO/OIE Manual on Echinococcosis in Humans and Animals: A Public Health Problem of Global Concern. World Organisation for Animal Health and World Health organiszation. Paris, 286 pp.

Drygala, F. (2009). Space use pattern, dispersal and social organisation of the raccoon dog (*Nyctereutes procyonoides* Gray, 1834) an invasive, alien canid in Central Europe. PhD thesis. Technische Universität Dresden, Dresden, Germany.

Drygala, F. and Zoller, H. (2013). Spatial use and interaction of the invasive raccoon dog and the native red fox in Central Europe: competition or coexistence? European Journal of Wildlife Research, 59, 683–691.

Drygala, F., Stier, N., Zoller, H., Bögelsack, K., Roth, M. (2008a). Spatial organization and intra-specific relationship of the raccoon dog *Nyctereutes procyonoides* in Central Europe. Wildlife Biology, 14, 457–466.

Drygala, F., Stier, N., Zoller, H., Bögelsack, K., Mix, M.H., Roth, M. (2008b). Habitat use of the raccoon dog (*Nyctereutes procyonoides*) in north-eastern Germany. Mammalian Biology, 73, 371–378.

Helle, E. and Kauhala, K. (1995). Reproduction in the raccoon dog in Finland. Journal of Mammology, 76, 1036–1046.

Heptner, V.G. and Naumov, N.P. (1998). Mammals of the Soviet Union. Volume II, Part 1a: Sirenia and Carnivora. Smithsonian Institution Libraries and The National Science Foundation, Washington DC, pp 82–123.

Hofer, S., Gloor, S., Müller, U., Mathis, A., Hegglin, D., Deplazes, P. (2000). High prevalence of *Echinococcus multilocularis* in urban red foxes (*Vulpes vulpes*) and voles (*Arvicola terrestris*) in the city of Zurich, Switzerland. Parasitology ,120, 135–142.

Holmala, K. (2009). The community of medium-sized carnivores: the interactions between species, habitats and rabies. Academic dissertation. Helsinki University Printing House, Helsinki.

Holmala, K. and Kauhala, K. (2006). Ecology of wildlife rabies in Europe. Mammal Review, doi: 10.1111/j.1365-2907.2006.00078.x

Holmala, K. and Kauhala, K. (2009). Habitat use of medium-sized carnivores in Southeast Finland – key habitats for rabies spread? Annales Zooloogici Fennici, 46, 233–246.

Hrčkova, G., Miterpakova, M., O'Connor, A., Šnabel, V., Olson, P.D. (2011). Molecular and morphological circumscription of *Mesocestoides* tapeworms from red foxes (*Vulpes vulpes*) in central Europe. Parasitology, 138, 638–647.

Hurnikova, Z., Miterpakova, M., Chovancova, B., 2009. The important zoonoses in the protected areas of the Tatra National Park (TANAP). Wiadomoci Parazytologicne, 55, 395–398.

Ikeda, H. (1983). Development of young and parental care of raccoon dog, *Nyctereutes procyonoides viverrinus* Temminck, in captivity. Journal of Mammalogy, 9, 229–236.

Jacobs, J. (1974). Quantitative measurements of food selection. A modification of the forage ratio and Ivlev's selectivity index. Oecologia, 14, 413–417.

Jedrzejewska, B. and Jedrzejewski, W. (1998). Predation in vertebrate communities: The Bialowieza Primeval Forest as a case study. Ecological Studies, vol 135. Springer-Verlag, Berlin, 452 pp.

Judin, V.G. (1977). Raccoon dog in Primorje and Priamurye. Izd. Moscow: Nauka, pp 76–98. (in Russian)

Jõgisalu, I. (2012). Mandri-Eesti mägralinnakute levik, olukord ja elupaiga iseloom. Environment Agency, Tartu, Estonia. (in Estonian), 17 pp.

Kaal, M. (1981). Eesti imetajate määramistabelid. Eesti NSV Põllumajandusminis-teeriumi Info– ja Juurutisvalitsus, Tallinn. (in Estonian)

Kauhala, K. (1996a). Introduced carnivores in Europe – a review. Wildlife Biology, 2, 197–204.

Kauhala, K. (1996b). Reproductive strategies of the raccoon dog and the red fox in Finland. Acta Theriologica, 41, 51–58.

Kauhala, K. (2004). Removal of medium-sized predators and the breeding success of ducks in Finland. Folia Zoologica, 53, 367–378.

Kauhala, K. and Auniola, M. (2001). Diet of raccoon dogs in summer in the Finnish archipelago. Ecography, 24, 151–156.

Kauhala, K. and Holmala, K. (2006). Home ranges and densities of medium–sized carnivores in south-east Finland, with special reference to rabies spread. Acta Theriologica, 51, 1–13

Kauhala, K. and Holmala, K. (2008). Optimal radio-tracking strategy—the best results with the least effort? Acta Theriologica, 53, 333–341.

Kauhala, K. and Auttila, M. (2010). Habitat preferences of the native badger and the invasive raccoon dog in southern Finland. Acta Theriologica, 55, 231–240.

Kauhala, K. and Kowalczyk, R. (2011). Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: History of colonization, features behind its success, and threats to native fauna. Current Zoology, 57, 584–598.

Kauhala, K. and Saeki, M. (2016). Nyctereutes procyonoides. The IUCN Red List of Threatened Species 2016: e.T14925A85658776. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T14925A85658776.en.

Kauhala, K., Kaunisto, M., Helle, E. (1993). Diet of the raccoon dog, *Nyctereutes procyonoides,* in Finland. Zeitschrift für Säugetierkunde, 58, 129–136.

Kauhala, K., Piätila, H., Helle, E. (1998a). Time allocation of male and female raccoon dogs to pup rearing at the den. Acta Theriologica, 43, 301–310.

Kauhala, K., Laukkanen, P., von Rége, I. (1998b). Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. Ecography, 21, 457–463.

Kauhala, K., Holmala, K., Schrege, J. (2007). Seasonal activity patterns and movements of the raccoon dog, a vector of diseases and parasites, in southern Finland. Mammalian biology, 72, 342–353.

Kauhala, K., Schregel, J., Auttila, M. (2010). Habitat impact on raccoon dog *Nyctereutes procyonoides* home range size in southern Finland. Acta Theriologica, 55, 371–380.

Keller, R.P., Geist, J., Jeschke, J.M., Kühn, I. (2011). Invasive species in Europe: ecology, status, and policy. Environmental Sciences Europe 23, 23. doi:10.1186/2190-4715-23–23

Kido, N., Kamegaya, C., Omiya, T., Wada, Y., Takahashi, M., Yamamoto, Y. (2011). Hematology and serum biochemistry in debilitated, free-ranging raccoon dogs (*Nyctereutes procyonoides*) infested with sarcoptic mange. Parasitology International, 60, 425–428.

Knapp, J., Gottstein, B., Saarma, U., Millon, L. (2015). Taxonomy, phylogeny and molecular epidemiology of Echinococcus multilocularis: from fundamental knowledge to health ecology. Veterinary Parasitology, 213, 85–91. doi: http://dx.doi.org/10.1016/j.vetpar.2015.07.030

Kolodziej-Sobocinska, M., Zalewski, A., Kowalczyk, R. (2014). Sarcoptic mange vulnerability in carnivores of the Białowieża Primeval Forest, Poland: underlying determinant factors. Ecological Research, 29, 237–244.

Kozlov, D.P. (1977). Key to helminths of carnivorous mammals of USSR. Nauka, Moscow, 231pp. (in Russian)

Kowalczyk, R., Jędrzejewska, B., Zalewski, A., Jędrzejewski, W. (2008). Facilitative interactions between the Eurasian badger (*Meles meles*), the red fox (*Vulpes vulpes*), and the invasive raccoon dog (*Nyctereutes procyonoides*) in Białowieża Primeval Forest, Poland. Canadian Journal of Zoology, 86, 1389–1396.

Kraabøl, M., Gundersen, V., Fangel, K., Olstad, K. (2015). The taxonomy, life cycle and pathology of *Sarcoptes scabiei* and *Notoedres cati* (Acarina, Sarcoptidae): A review in a Fennoscandian wildlife perspective. Fauna Norvegica, 35, 21–33.

Laanetu, N. (1986). Ondatra – kiskja saakloom. Eesti Ulukid 4, 15–30. (in Estonian)

Laos, L. and Männil P. (2017). Kährikkoera ja teiste liikide kiskluse mõju kahepaiksetele ja rannaniidul pesitsevatele lindudele. Rakendusuuringu aruanne. Environment Agency, Tartu, Estonia, 21 pp. (in Estonian)

Laurimaa, L., Davison, J., Plumer, L., Süld, K., Oja, R., Moks, E., Keis, M., Hindrikson, M., Kinkar, L., Laurimäe, T., Abner, J., Remm, J., Anijalg, P., Saarma, U. (2015a). Non-invasive molecular diagnostics identifies *Echinococcus multilocularis* spillover to an urban area in Estonia. Emerging Infectious Diseases, 21, 163–164. doi:10.3201/eid2101.140136

Laurimaa, L., Davison, J., Süld, K., Plumer, L., Oja, R., Moks, E., Keis, M., Hindrikson, M., Kinkar, L., Laurimäe, T., Abner, J., Remm, J., Anijalg, P., Saarma, U. (2015b). First report of highly pathogenic *Echinococcus granulosus* genotype G1 in dogs in European urban environment. Parasites & Vectors, 8, 182. doi:10.1186/s13071-015-0796-3

Laurimaa, L., Süld, K., Moks, E., Valdmann, H., Umhang, G., Knapp, J., Saarma, U. (2015c). First report of the zoonotic tapeworm Echinococcus multilocularis in raccoon dogs in Estonia, and comparisons with other countries in Europe. Veterinary Parasitology, 212, 200−205. doi: 10.1016/j.vetpar.2015.06.004

Laurimaa, L., Moks, E., Soe, E., Valdmann, H., Saarma, U. (2016). Echinococcus multilocularis and other zoonotic parasites in red foxes in Estonia. Parasitology, 143, 1450–1458. doi:10.1017/S0031182016001013

Lavrov, N.P. (1971). Results of raccoon dog introductions in different parts of the Soviet Union. Trudy Kafedry Biologii MGZPI 29, 101–160. (In Russian)

Loos-Frank, B. (2000). An up-date of Verster's (1969) 'Taxonomic revision of the genus Taenia Linnaeus' (Cestoda) in table format. Systematic Parasitology, 45, 155–183.

Machnicka-Rowinska, B., Rocki, B., Dziemian, E., Kolodziej-Sobocinska, M. (2002). Raccoon dog (*Nyctereutes procyonoides*) – the new host of *Echinococcus multilocularis* in Poland. Wiadomoci Parazytologicne, 48, 65–68.

Marcinkute, A., Šarkunas, M., Moks, E., Saarma, U., Jokelainen, P., Bagrade, G., Laivacuma, S., Strupas, K., Sokolovas, V., Deplazes, P. (2015). *Echinococcus* infections in the Baltic region. Veterinary Parasitology, 213, 121–131. doi: http://dx.doi.org/10.1016/j.vetpar.2015.07.032

Matsuyama, R., Yabusaki, T., Kuninaga, N., Morimoto, T., Okano, T., Suzuki, M., Asano, M. (2015). Coexistence of two different genotypes of *Sarcoptes scabiei* derived from companion dogs and wild raccoon dogs in Gifu, Japan: the genetic evidence for transmission between domestic and wild canids. Veterinary Parasitology, 212, 356–360.

Mazza, G., Tricario, E., Genovesi, P., Gherardi, F. (2014). Biological invaders are threats to human health: an overview. Ethology, Ecology & Evolution, 26, 112–129.

Melis, C., Herfindal, I., Dahl, F., Ahlen, P.-A. (2015). Individual and temporal variation in habitat association of an alien carnivore at its invasion front. PLoS ONE, 10: e0122492

Micali, G., Lacarrubba, F., Verzì, A.E., Chosidow, O., Schwartz, R.A. (2016). Scabies: advances in noninvasive diagnosis. PLoS Neglected Tropical Diseases, 10(6): e0004691. doi: 10.1371/journal.pntd.0004691

Moks, E. (2004). Heminth fauna of the red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), grey wolf (*Canis lupus*) and lynx (*Lynx lynx*) in Estonia. University of Tartu, Master thesis. 49 pp. (in Estonian)

Moks, E., Saarma, U., Valdmann, H. (2005). *Echinococcus multilocularis* in Estonia. Emerging Infectious Diseases, 11, 1973–1974. doi: http://dx.doi.org/10.3201/eid1112.050339.

Moks, E., Jõgisalu, I., Valdmann, H., Saarma, U. (2008). First report of *Echinococcus granulosus* G8 in Eurasia and a reappraisal of the phylogenetic relationships of "genotypes" G5–G10. Parasitology, 135, 647–654. doi: http://dx.doi.org/10.1017/S0031182008004198.

Moks, E., Jõgisalu, I., Saarma, U., Talvik, H., Järvis, T., Valdmann, H. (2006). Helminthologic survey of the wolf (*Canis lupus*) in Estonia, with an emphasis on *Echinococcus granulosus*. Journal of Wildlife Diseases, 42, 359–365. doi: http://dx.doi.org/10.7589/0090-3558-42.2.359

Mustonen, A.M., Asikainen, J., Kauhala, K., Paakkonen, T., Nieminen, P. (2007). Seasonal rhythms of body temperature in the free-ranging raccoon dog (Nyctereutes procyonoides) with special emphasis on winter sleep. Chronobiology International, 24, 1095–1107. doi: 10.1080/07420520701797999 PMID: 18075801

Mustonen, A.M., Lempiäinen, T., Aspelund, M., Hellstedt, P., Ikonen, K., Itämies, J., Vähä, V., Erkinaro, J., Asikainen, J., Kunnasranta, M., Niemelä, P., Aho, J., Nieminenet, P. (2012). Application of change-point analysis to determine winter sleep patterns of the raccoon dog (*Nyctereutes procyonoides*) from body temperature recordings and a multi-faceted dietary and behavioral study of wintering. BMC Ecology, 12, 27. doi: 10.1186/1472-6785-12-27.

Naaber, J. (1971). Kährikkoer. Eesti Loodus 14, 449–455. (in Estonian)

Naaber, J. (1972). Kährikkoer Eesti NSV-s. Metsamajanduslikud uurimused, IX. Tallinn, pp 254–276.

Naaber, J. (1974). Rebane ja kährikkoer meie looduses. Jaht ja Ulukid. Eesti NSV Jahimeeste Seltsi aastaraamat 1969–1972. Valgus, Tallinn, pp 102–115.

Nakagawa, T.L.D.R., Takai, Y., Kubo, M., Sakai, H., Masegi, T., Yanai, T. (2009). A pathological study of sepsis associated with sarcoptic mange in raccoon dogs (*Nyctereutes procyonoides*) in Japan. Journal of Comparative Pathology, 141, 177–181.

Nasimovič, A.A. and Isakov, J.A. (1985). Arctic fox, red fox and raccoon dog: distribution of populations, ecology and preservation. Moscow, Nauka, 116–145. (in Russian).

Neronov, V.M., Khlyap, L.A., Bobrov, V.V., Warshavsky, A.A. (2008) Alien species of mammals and their impact on natural ecosystems in the biosphere reserves of Russia. Integrative Zoology, 3, 83–94.

Oivanen, L., Kapel, C.M.O., Pozio, E., La Rosa, G., Mikkonen, T., Sukura, A. (2002). Associations between *Trichinella* species and host species in Finland. Journal of Parasitology, 88, 84–88.

Oja, R. (2012). Side effects of supplementary feeding of wild boar (*Sus Scrofa*) on ground-nesting birds, other mammals and plants. M.Sc. Thesis, University of Tartu. (in Estonian)

Oja, R., Velström, K., Moks, E., Jokelainen, P., Lassen, B. (2017). How does supplementary feeding affect endoparasite infection in wild boar? Parasitology Research. doi:10.1007/s00436-017-5512-0

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner. (2012) vegan: Community Ecology Package. R package version 2.0–5. http://CRAN.Rproject.org/package = vegan.

Opermanis, O., Mednis, A., Bauga, I. (2001). Duck nests and predators: interaction, specialisation and possible management. Wildlife Biology, 7, 87–96.

Pannwitz, G., Mayer-Scholl, A., Balicka-Ramisz, A., Nöckler, K. (2010). Increased prevalence of *Trichinella* spp., northeastern Germany, 2008. Emerging Infectious Diseases, 16, 936–942. doi: 10.3201/eid1606.091629

Parre, J. (1985). Veterinary Parasitology. Valgus, Tallinn, 439 pp. (in Estonian).

Pence, D.B. and Ueckermann, E. (2002). Sarcoptic mange in wildlife. Revue scientifique et technique (International Office of Epizootics), 21, 285–398.
Portier, J., Jouet, D., Ferte, H., Gibout, O., Heckmann, A., Boireau, P., Vallee, I. (2011). New data in France on the trematode *Alaria alata* (Goeze, 1792) obtained during *Trichinella* inspections. Parasite, 18, 271–275.
Pärtel, A. (2013). Self-declaration by Estonia on the recovery of its rabies-free status. OIE Bulletin, 3, 58–61.
Reig, S. and Jedrzejewski, W. (1988). Winter and early spring food of some carnivores in the Bialowieza National Park, Eastern Poland. Acta Theriologica, 33, 57–65.
Riehn, K., Hamedy, A., Große, K., Zeitler, L., Lücker, E. (2010). A novel detection method for *Alaria alata* mesocercariae in meat. Parasitology Research 107, 213–220.
Remonti, L., Balestrieri, A., Domenis, L., Banchi, C., Valvo, T., Robetto, S., Orusa, R. (2005). Red fox (*Vulpes vulpes*) cannibalistic behaviour and the prevalence of *Trichinella britovi* in NW Italian Alps. Parasitology Research, 97, 431–435.
Robardet, E., Picard-Meyer, E., Dobroštana, M., Jaceviciene, I., Mähar, K., Muižniece, Z., Pridotkas, G., Masiulis, M., Niin, E., Olševskis, E., Cliquet, F. (2016) Rabies in the Baltic States: Decoding a Process of Control and Elimination. PLOS Neglected Tropical Diseases, 10(2): e0004432.
Rätsepp, M. (2005). Kährikkoera (*Nyctereutes procyonides*) ja punarebase (*Vulpes vulpes*) talvine toitumine Eestis. Bachelor thesis. University of Tartu. (in Estonian)
Saarma, U., Jõgisalu, I., Moks, E., Varcasia, A., Lavikainen, A., Oksanen, A., Simsek, S., Andresiuk, V., Denegri, G., Gonzalez, L.M., Ferrer, E., Garate, T., Rinaldi, L., Maravilla, P. (2009). A novel phylogeny for the genus *Echinococcus*, based on nuclear data, challenges relationships based on mitochondrial evidence. Parasitology, 136, 317–328.
Saito, M.U. and Sonoda, Y. (2017). Symptomatic raccoon dogs and sarcoptic mange along an urban gradient. EcoHealth, 30. doi: 10.1007/s10393-017-1233-1.
Sato, Y., Mano, T., Sieki, T. (2000). Applicability of the point-frame method for quantitative evaluation of bear diet. Wildlife Inventory and Techniques, 28, 311–316.
Schwarz, S., Sutor, A., Staubach, C., Mattis, R., Tackmann, K., Conraths, F.J. (2011). Estimated prevalence of *Echinococcus multilocularis* in raccoon dogs (*Nyctereutes procyonoides*) in northern Brandenburg, Germany. Current Zoology, 57, 655–661.
Seaman, D.E. and Powell, R.A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology, 77, 2075–2085.
Selva, N. (2004). The role of scavenging in the predator community of Bialowieza primeval forest. PhD thesis, Polish Academy of Sciences.
Selva, N., Jedrzejewska, B., Jedrzejewski, W., Wajrak, A. (2005). Factors affecting carcass use by guild of scavengers in European temperate woodland. Canadian Journal of Zoology, 83, 1590–1601.
Shimalov, V.V. and Shimalov, V.T. (2002). Helminth fauna of the racoon dog (*Nyctereutes procyonoides* Gray, 1834) in Belorussian Polesie. Parasitology Research, 88, 944–945. doi: 10.1007/s00436-001-0582-3
Sidorovich, V.E., Solovej, I.A., Sidorovich, A.A, Dyman, A.A. (2008a). Seasonal and annual variation in the diet of the raccoon dog *Nyctereutes procyonoides* in northern Belarus: The role of habitat type and family group. Acta Theriologica, 53, 27–38.
Sidorovich, V.E., Sidorovich, A.A, Ivanovskij, V.V., Pikulik, M.M., Shinkevich, E.P. (2008b). The structure of vertebrate predator community in north-eastern Belarus

before and after naturalization of the American mink and raccoon dog. Folia Zoologica, 57, 373–391.

Simpson, K., Johnson, C.N., Carver, S. (2016). *Sarcoptes scabiei*: The mange mite with mighty effects on the common wombat (*Vombatus ursinus*). PLoS ONE, 11(3): e0149749. doi: 10.1371/journal.pone.0149749

Skorodumov, A.N. (1939). Propagation of ussurian raccoon dogs. VKOI, Moscow. 67 pp. (in Russian)

Stahler, D.R., Smith, D.W., Guernsey, D.S. (2006). Foraging and feeding ecology of the gray wolf (*Canis lupus*): lessons from Yellowstone National Park, Wyoming, USA. The Journal of Nutrition, 136, 1923S–1926S.

Stone, L. and Roberts, A. (1990). The checkerboard score and species distributions. Oecologia, 8, 74–79.

Su, H., Su, Y., Huffman, M.A. (2013). Leaf swallowing and parasitic infection of the Chinese lesser civet *Viverricula indica* in northeastern Taiwan. Zoological Studies, 52, 22. doi: 10.1186/1810-522X-52-22

Sueda. K.L.C., Hart, B.L., Cliff, K.D. (2008). Characterisation of plant eating in dogs. Applied Animal Behaviour Science, 111, 120–132.

Sutor, A., Kauhala K., Ansorge, H. (2010). Diet of raccoon dog *Nyctereutes procyonoides* – a canid with opportunistic foraging strategy. Acta Theriologica, 55, 165–167.

Sutor, A. and Schwarz, S. (2012). Home ranges of raccoon dogs (*Nyctereutes procyonoides*, Gray, 1834) in Southern Brandenburg, Germany. European Journal of Wildlife Research, 58, 85–97.

Sutor, A., Schwarz, S., Conraths, F.J. (2014). The biological potential of the raccoon dog (*Nyctereutes procyonoides*, Gray 1834) as an invasive species in Europe – new risks for disease spread? Acta Theriologica 59, 49–59. doi: 10.1007/s13364-013-0138-9

Tamminga, N., Bierman, W.F.W., de Vries, P.J. (2009). Cutaneous larva migrans acquired in Brittany, France. Emerging Infectious Diseases 15, 1856–1858. doi: 10.3201/eid1511.090261

Teerink, B.J. (1991). Hair of West-European mammals: atlas and identification key. Cambridge University Press, p 223.

Theiss, T., Schuster, R., Nöckler, K., Mix, H. (2001). Helminth findings in indigenous raccoon dogs *Nyctereutes procyonoides* (Gray, 1834). Berliner und Münchener Tierärztliche Wochenschrift, 114, 273–276. (in German)

Veeroja, R. and Männil, P. (2015). Ulukiasurkondade seisund ja küttimissoovitus 2016 [Status of game populations in Estonia and proposal for hunting in 2015]. Estonian Environment Agency. (in Estonian)

Veeroja, R. and Männil, P. (2016). Ulukiasurkondade seisund ja küttimissoovitus 2016 [Status of game populations in Estonia and proposal for hunting in 2016]. Estonian Environment Agency. (in Estonian)

Veeroja, R. (2015). Metssea karja tegevuspiirkond, elupaigakasutus ja mõju teistele liikidele erinevate lisasöötmisrežiimide tingimustes. Estonian Environment Agency. (in Estonian)

Vila M., Basnou C, Gollasch S, Josefsson M., Pergl J., Scalera R. (2008). One hundred of the most invasive alien species in Europe. In: Drake, J.A., eds. Handbook of Alien Species in Europe. Springer, Netherlands, pp. 265–268.

Vilà, M., Basnou, C., Pyšek, P., Josefssona, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E., and DAISIE partners. (2010).

How well do we understand the impacts of alien species on ecosystem services? A pan-European cross-taxa assessment. Frontiers in Ecology and the Environment, 8, 135–144.

Ward, O.G. and Wurster-Hill, H. (1990). Mammalian Species: *Nyctereutes procyonoides*. The American Society of Mammalogists, 358, 1–5.

Wasiluk, A. (2009). Alariosis – newly diagnosed trematodiasis. Wiadomoci Parazytologicne, 55, 349–352.

Zhang, H.-H., Liu, X.-P., Dou, H.-S., Zhang, C.-D., Ren, Y. (2009). Food composition and food overlap of three kinds of canidae. Acta Ecologica Sinica, 29, 347–350.

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Süld, K., Saarma, U., Valdmann, U. (2017). Home ranges of raccoon dogs in managed and natural areas. PloS ONE 12(3): e0171805. doi: 10.1371/jpurnal.pone.0171805

Laurimaa, L., Süld, K., Davison, J., Moks, E., Valdmann, H., Saarma, U. (2016). Alien species and their zoonotic parasites in native and introduced ranges: the raccoon dog example. Veterinary Parasitology 219, 24–33

Laurimaa, L., Davison, J, Süld, K., Plumer, L., Oja, R., Moks, E., Keis, M., Hindrikson, M., Kinkar, L., Laurimäe, T., Abner, J., Remm, J., Anijalg, P., Saarma, U. (2015). First report of highly pathogenic Echinococcus granulosus genotype G1 in dogs in European urban environment. Parasites & Vectors, 8 (182), 182, 10.1186/s13071-015-0796-3

Laurimaa, L., Süld, K., Moks, E., Valdmann, H., Umhang, G., Knapp, J., Saarma, U. (2015). First report of the zoonotic tapeworm Echinococcus multilocularis inraccoon dogs in Estonia, and comparisons with other countries inEurope. Veterinary Parasitology, 212, 200−205, 10.1016/j.vetpar.2015.06.004

Laurimaa, L., Davison, J., Plumer, L., Süld, K., Oja, R., Moks, E., Keis, M., Hindrikson, M., Kinkar, L., Laurimäe, T., Abner, J., Remm, J., Anijalg, P., Saarma, U. (2015). Noninvasive detection of Echinococcus multilocularis

tapeworm in urban area, Estonia. Emerging Infectious Diseases, 21, 163−164, 10.3201/eid2101.140136
Süld, K., Valdmann, H., Laurimaa, L., Soe, E., Davison, J., Saarma, U. (2014). An invasive vector of zoonotic disease sustained by anthropogenic resources: the raccoon dog in Northern Europe. PLoS ONE 9(5): e96358. doi: 10.1371/journal.pone.0096358

Conference presentations:

Karmen Süld, Harri Valdmann, John Davison, Leidi Laurimaa, Epp Moks, Urmas Saarma. "Diet and parasites of an introduced species raccoon dog in Estonia" 16.–18.10.2014/ Daugavpils, Latvia/ 9th Baltic Theriological Conference. Oral presentation.

Karmen Süld, Harri Valdmann, John Davison, Urmas Saarma. "Raccoon dog (*Nyctereutes procyonoides*) diet in Estonia: the impact of sarcoptic mange and wild boar feeding sites" 31.03–4.04. 2014/ Kirkkolahti, Republic of Karelia, Russia/ 6th International Symposium. "Dynamics of Game Animals Populations in Northern Europe". Oral presentation.

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Süld, K., Saarma, U., Valdmann, U. (2017). Home ranges of raccoon dogs in managed and natural areas. PloS ONE 12(3): e0171805. doi: 10.1371/jpurnal.pone.0171805

Laurimaa, L., Süld, K., Davison, J., Moks, E., Valdmann, H., Saarma, U. (2016). Alien species and their zoonotic parasites in native and introduced ranges: the raccoon dog example. Veterinary Parasitology 219, 24–33.

Laurimaa, L., Davison, J, Süld, K., Plumer, L., Oja, R., Moks, E., Keis, M., Hindrikson, M., Kinkar, L., Laurimäe, T., Abner, J., Remm, J., Anijalg, P., Saarma, U. (2015). First report of highly pathogenic Echinococcus granulosus genotype G1 in dogs in European urban environment. Parasites & Vectors, 8 (182), 182, 10.1186/s13071-015-0796-3

Laurimaa, L., Süld, K., Moks, E., Valdmann, H., Umhang, G., Knapp, J., Saarma, U. (2015). First report of the zoonotic tapeworm Echinococcus multilocularis inraccoon dogs in Estonia, and comparisons with other countries inEurope. Veterinary Parasitology, 212, 200−205, 10.1016/j.vetpar.2015.06.004

Laurimaa, L., Davison, J., Plumer, L., Süld, K., Oja, R., Moks, E., Keis, M., Hindrikson, M., Kinkar, L., Laurimäe, T., Abner, J., Remm, J., Anijalg, P., Saarma, U. (2015). Noninvasive detection of Echinococcus multilocularis tapeworm in urban area, Estonia. Emerging Infectious Diseases, 21, 163−164, 10.3201/eid2101.140136

Süld, K., Valdmann, H., Laurimaa, L., Soe, E., Davison, J., Saarma, U. (2014). An invasive vector of zoonotic disease sustained by anthropogenic resources: the raccoon dog in Northern Europe. PLoS ONE 9(5): e96358. doi: 10.1371/journal.pone.0096358

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Karmen Süld, Harri Valdmann, John Davison, Leidi Laurimaa, Epp Moks, Urmas Saarma. "Diet and parasites of an introduced species raccoon dog in Estonia" 16.–18.10.2014/ Daugavpils, Latvia/ 9th Baltic Theriological Conference. Oral presentation.

Karmen Süld, Harri Valdmann, John Davison, Urmas Saarma. "Raccoon dog (*Nyctereutes procyonoides*) diet in Estonia: the impact of sarcoptic mange and wild boar feeding sites" 31.03–4.04. 2014/ Kirkkolahti, Republic of Karelia, Russia/ 6th International Symposium. "Dynamics of Game Animals Populations in Northern Europe". Oral presentation.

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