DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS 322

RAGNE OJA

Consequences of supplementary feeding of wild boar – concern for ground-nesting birds and endoparasite infection





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LIST OF ORIGINAL PUBLICATIONS

The thesis includes the following papers, which are referred to in the thesis by their Roman numerals.

- I. Oja, R., Kaasik, A., Valdmann, H. (2014) Winter severity or supplementary feeding which matters more for wild boar? *Acta Theriol* 59: 553–559.
- **II.** Oja, R., Soe, E., Valdmann, H., Saarma, U. (2017) Non-invasive genetics outperforms morphological methods in faecal dietary analysis, revealing wild boar as a considerable conservation concern for ground-nesting birds. *PLoS ONE* 12: e0179463.
- **III.** Oja, R., Zilmer, K., Valdmann, H. (2015) Spatiotemporal effects of supplementary feeding of wild boar (*Sus scrofa*) on artificial ground nest depredation. *PLoS ONE* 10: e0135254.
- IV. Oja, R., Velström, K., Moks, E., Jokelainen, P., Lassen, B. (2017) How does supplementary feeding affect endoparasite infection in wild boar? *Parasitol Res* doi:10.1007/s00436-017-5512-0 [In press]

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The participation of the author in preparing the listed publications (* denotes moderate contribution, ** high contribution, *** very high contribution).

	Ι	Π	III	IV
Original idea	**	**	***	***
Study design	**	*	***	**
Data collection	*	**	**	**
Data analysis	**	***	***	**
Manuscript preparation	***	***	***	***

1. INTRODUCTION

The Eurasian wild boar (Sus scrofa) is the most widespread species in the Suidae family, its range extending from Western Europe to the Far East and insular South-east Asia with introduced populations in Australia, New Zealand, and the Americas (Wilson and Mittermeyer 2011). Wild boar disappeared from northern areas soon after the end of the Middle Ages due to a period of extraordinarily cold winters, but returned to its former range or escaped from enclosures (see Thurfiell et al. 2009) in the 20th century and established viable populations (Lepiksaar 1986). At a biogeographical scale, western Eurasian wild boar populations today are primarily limited by winter harshness and vegetation productivity, whereas the presence of wolves (Canis lupus) only has a weak limiting effect on population densities (Melis et al 2006). Mortality from wolf predation is minor compared to the influence of hunting (see also Selva 2004; Nores et al. 2008), which has a strong effect on wild boar mortality (Nores et al. 2008), activity (Sodeikat and Pohlmeyer 2003; Keuling et al. 2008; Scillitani et al. 2010; Thurfjell 2011; Saïd et al. 2012), and possibly even reproductive tactics (see Servanty et al. 2009; Gayet et al. 2016).

During the second half of the 20th century, wild boar abundance increased markedly throughout Europe (Boitani et al. 1995; Fruzinski 1995; Neet 1995; Geisser and Reyer 2005, Massei et al. 2015). This population increase has been associated with a decrease in the relative impact of hunting, mild winters, and increased availability of the anthropogenic foods originating from agriculture and supplementary feeding (Massei et al. 2015). Such population increase can potentially result in an intensification of human-wildlife conflicts as wild boar is considered a major agricultural pest (Geisser and Reyer 2004; Cellina 2008; Chauhan et al. 2009; Lindblom 2011). Additionally, it can cause damage to hardwood plantations by uprooting and feeding on seedlings (Mayer et al. 2000) and even attack humans (Chauhan et al. 2009). Also, more negative consequences on other species are likely to occur – in addition to direct predation (see Briedermann 1990; Giménez-Anaya et al. 2008; Wilcox and van Vuren 2009; Экономов 2016), wild boar can affect other animals indirectly through changes in vegetation (see Singer et al. 1984; Kotanen 1995).

1.1 The effect of wild boar diet on abundance, reproduction and habitat use

Wild boar are opportunistic omnivores and dietary generalists (Senior et al. 2016), whose diet composition depends largely on the availability of different food types, including seasonal and geographic variability in various parts of its range (Schley and Roper 2003; Baubet et al. 2004; Cellina 2008; Ballari et al. 2015). Consequently, landscape diversity is a key factor in determining wild boar abundance, probably acting through the availability of food resources and

protective cover (Acevedo et al. 2006). Seasonal differences in habitat selection are also related to changes in the availability of food and shelter (Meriggi and Sacchi 2001; Keuling 2009; Thurfjell et al. 2009), but broadleaved (deciduous) and mixed forest are used for all activities (Abaigar et al. 1994; Meriggi and Sacchi 2001; Merli and Meriggi 2006; Thurfjell et al. 2009; Borowik et al. 2013). The majority of diet consists of vegetal matter, including both aboveand below-ground parts of plants, fruits, and seeds (Briedermann 1990; Fournier-Chambrillon et al. 1995; Schley and Roper 2003; Baubet et al. 2004). Natural mast foods, mostly in the form of acorns (mainly *Querqus petrea* and *Q. robur*) and beechnut *Fagus sylvatica*, constitute an important food category for wild boar, whereas acorns occur more often and in larger quantities (Cellina 2008).

Numerous studies have highlighted the importance of food resource (particularly mast) availability for wild boar (Mexia-de-Almeida et al. 2004; Geisser and Rever 2005; Acevedo et al. 2006; Melis et al. 2006; Fonseca 2008; Rosvold and Andersen 2008). Wild boar abundance is positively affected by vears of high production of mast (Gethöffer et al. 2007; Cutini et al. 2013), which has a strong influence on the reproductive phenology (Massei et al. 1996; Servanty et al. 2009; Canu et al. 2015; Frauendorf et al. 2016; Gamelon et al. 2017). Interestingly, an increase in reproductive performance has been associated with consumption of acorns, but not beechnut (Frauendorf et al. 2016; Gamelon et al. 2017). This difference could potentially be related to high levels of lysine in acorn and its effect on reproductive traits (Gamelon et al. 2017). The effect of mast production in current and previous year can differ in populations of varying mast availability, so that the reproductive traits of adult females in a resource-limited population are influenced by seed availability in both current and previous years, whereas in a population of abundant resources, only seed availability in the current year has an effect (Gamelon et al. 2017). Climatic conditions such as temperature and rainfall can also affect the proportion of females that reproduce (Servanty et al. 2009; Canu et al. 2015), but this effect might act indirectly through the nutritional conditions.

A significant proportion of juvenile females in the population can reproduce (Gethöffer et al. 2007; Servanty et al. 2009; Gamelon et al. 2017). They have to reach a threshold body mass of 27–33 kg before breeding for the first time (Servanty et al. 2009), but lower weight values of 20 kg (Gethöffer et al. 2007) and 17 kg (Cellina 2008) have also been recorded to mark the start of puberty in females. This comprises about a third of adult body mass, and is relatively low compared to 80%, which has been reported in other ungulates (Servanty et al. 2009). Females with a good food supply start to breed earlier (Briedermann 1990) and drive population growth under good conditions (Bieber and Ruf 2005). Although wild boar females have been known to exhibit reproductive season in young sows (Gethöffer et al. 2007; Cellina 2008). However, once sexual maturity has been reached, female wild boar attempt to reproduce every year whatever the environmental conditions (Servanty et al. 2009). Juvenile females

produce similar-sized litters independent of food availability, but adult females produce highly diversified offspring within a litter in years of abundant mast production and similar-sized litters in years of poor mast production (Gamelon et al. 2013).

The absence of mast is most pronounced on the juveniles (Groot Bruinderink and Hazebroek 1994) and following a poor mast year, wild boar can increase their consumption of foods of anthropogenic origin. For example, in France wild boar compensated lack of acorns by feeding on grapes in the vineyards (Fournier-Chambrillon et al. 1995). Wild boar inhabiting a mosaic forestfarmland habitat can substitute much of the natural food with crops and cereals (Merta et al. 2014), which are consumed year-round when available (Schley and Roper 2003; Herrero et al. 2006, Cellina 2008). The increased use of fields in summer is strictly related to ripening of the crops (Thurfjell et al. 2009; Keuling et al. 2010). However, not all animals increase their use of agricultural fields - a significant amount of wild boar can shift their home ranges entirely to fields, whereas some move between forest and fields, and some remain in the forest (Keuling et al. 2009). When hunting pressure is low, ripe crops can be used for both forage and cover (Keuling et al. 2008; Thurfjell et al. 2009). A clear preference is shown for certain crops - maize is the most frequently damaged, followed by durum wheat, oats, barley, and soft wheat (Amici et al. 2012). Also, wheat and barley are consumed only when these crops are maturing between May and August (Herrero et al. 2006). The type of crops can even affect the diurnal activity of wild boar – in Germany, despite being mostly nocturnal, higher daytime activity was recorded near wheat, oat, and rapeseed fields compared to other agricultural habitats (Keuling et al. 2008).

In addition to crops, supplementary feeding can constitute a major food category for wild boar through-out the year, although mast and standing crops, especially maize, are preferred to supplemental maize (Cellina 2008). Evidence from stomach analysis of wild boar shot at baited sites suggests that they visit more than one supplementary feeding site during the night (Cellina 2008).With ad libitum feeding, supplementary food satisfies an average of one third to two thirds of wild boar energy requirements, but depending on the year and season, total satiation can be reached (Andrzejewski and Jezierski 1978). Older animals tend to feed more on supplemental food and less on agricultural crops (Cellina 2008). The temporal patterns of supplementary feeding vary in different study systems - in Poland, maximum feeding took place from May to September, when natural food was abundant (Andrzejewski and Jezierski 1978), in Luxembourg, supplementary food was least important from July to September, when agricultural crops became available (Cellina 2008), in Spain, feeding was carried out in summer, when natural food is scarce (Navarro-Gonzalez et al. 2013), and in the Czech Republic, supplementary food was most important in winter (Ježek et al. 2016).

Supplementary food and crops are not the only alternative to mast. In the absence of supplementary food, wild boar increase their intake of roots and broadleaved grasses accordingly (Groot Bruinderink and Hazebroek 1994). In a

population without access to foods of anthropogenic origin, wild boar were observed to actively consume pine seeds, even when their availability was low (Massei et al. 1996). And in poor mast years, the importance of animal food increases, being more important for the juveniles (Groot Bruinderink and Hazebroek 1994). Animal food is consumed frequently and in greater proportions in the introduced range, reaching up to 33% by volume, whereas in the native range its volume varies from 1% to 16% (Ballari and Barrios-García 2014). However, the proportion of animal food can be easily underestimated, because of its rapid or entire digestion (Fournier-Chambrillon et al. 1995).

Wild boar are known to consume both vertebrates and invertebrates to a varying degree. Invertebrates include gastropods, earthworms, myriopods, insects and larvae (Briedermann 1990; Schley and Roper 2003, Cellina 2008). When available, year-round consumption of snails (Herrero et al. 2006) and earthworm (Baubet et al. 2003) has been observed. Earthworm appears to be one of the most important sources of animal food and its frequency in wild boar diet can reach up to 92% (Baubet et al. 2003). Vertebrate diet includes mostly small mammals such as rodents, moles, and shrews, birds and ungulates, whereas fish, reptiles and amphibians are only seldom preyed upon (Briedermann 1990; Schley and Roper 2003; Cellina 2008; Wilcox and Van Vuren 2008; Ballari et al. 2015). Season has a strong effect on the frequency of different animal foods due to availability. For example, earthworm consumption increases in spring, reaching a maximum in summer and autumn (Baubet et al. 2003) and bird consumption is most frequent in late spring and summer (Herrero et al. 2006; Ballari et al. 2015).

Various studies have shown that wild boar can predate on birds and their eggs, particularly grouse (Briedermann 1990; Svobodová et al. 2012; Carpio et al. 2014; Экономов 2016; Senserini and Santilli 2016) and waterfowl (Purger and Mészáros 2006; Giménez-Anaya et al. 2008), but a variety of passerines, pigeons, woodpeckers, and owls has also been recorded in wild boar diet (Cellina 2008; Ballari et al. 2015). However, they are often neglected in conservation management of ground-nesting birds. For example, although wild boar is recognised as an occasional nest predator of capercaillie (*Tetrao urogallus*) (Saniga 2002), mesopredators such as pine marten (*Martes martes*) and red fox (*Vulpes vulpes*), as well as goshawk (*Accipiter gentilis*), are believed to have the most effect (Summers et al. 2004; Wegge and Rolstad 2011; Moreno-Opo 2015).

1.2 Effects of supplementary feeding

Supplementary feeding in general means that additional food is provided for wild animals in their natural habitat. Depending on the ultimate purpose of the feeding, Cellina (2008) has categorised different kinds of supplementary feeding as followed: a) dissuasive feeding, b) baiting, c) massive feeding, d) provision of game meadows, e) feeding to avoid food distress or famine, f) providing

minerals/salt, and g) vaccination. All of these have been used for wild boar, but to meet their goal, differences in the period and amount of food availability must be taken into account. However, although essentially different in theory, in practice these categories cannot always be easily distinguished.

Long-term supplementary feeding can lead to an increase in the reproductive potential of female wild boar (Cellina 2008). A comparison of two wild boar populations from southern Poland has shown that wild boar whose diet consists mostly of crops and cereals are heavier and have a larger kidney fat index than those inhabiting a large compact forest and feeding on natural plants (Merta et al. 2014). These attributes are directly related to reproductive traits in wild boar (see chapter 1.1). Similarly, cessation of supplementary feeding can lead to increased variation in weight of even-aged cohorts of different years of birth and a decrease in recruitment, but the effect is not as strong if wild boar have access to other anthropogenic food sources (Groot Bruinderink and Hazebroek 1994).

Dissuasive feeding has been suggested as a means to reduce damage to crops and there is some literature to support this practice (see Andrzejewski and Jezierski 1978; Calenge et al. 2004). However, in the long term, the positive effect of supplementary feeding on wild boar reproduction and the subsequent increase in abundance seems to outweigh the potential deterring effect. In Switzerland, more damages to crops tend to occur in areas with more supplementary feeding (Geisser and Reyer 2004). Ripe crops, which are most sensitive to damage, are preferred to supplemental food by wild boar (Cellina 2008), so that feeding has the least effect on deterring wild boar from fields during the period, when it matters the most. And in a study of damage patterns, the distance to a supplementary feeding site was one of the most important factors to explain the severity of damage to an agricultural field, being the most severe between 750 m and 1500 m from the feeding site (Lindblom 2011).

Supplementary feeding has also been suggested as a means to decrease nest predation, but the effects of this practice range from decreased (Vander Lee et al. 1999) to increased nest predation (Cooper and Ginnett 2000; Jones et al. 2010; Selva et al. 2014), or no effect (Greenwood et al. 1998; Jones et al. 2002). This is probably due to similar reasons as with the use of dissuasive feeding to reduce damage to crops. But additionally, supplementary feeding can potentially also concentrate non-target species, capable of predating on birds and their nests. In Estonia, supplementary feeding sites of wild boar are actively used by raccoon dogs (*Nyctereutes procyonoides*) (Süld et al. 2014) and raccoons (*Procyon lotor*) caused major nest loss near deer feeders in USA (Cooper and Ginnett 2000).

Depending on the overall resource availability, supplementary feeding can influence wild boar space use and daily activity. Wild boar are mostly nocturnal (Boitani et al. 1994), but if the same feeding site is visited by a large number of wild boar groups, which lack tolerance for other groups, these sites can also be visited during daytime (Andrzejewski and Jezierski 1978). Female groups with access to artificial food sources use the core areas of their home range more consistently than males, who tend to wander over the entire range (Boitani et al.

1994). Also, the annual home range of wild boars which receive supplementary food can be half the size of that used by animals without artificial feeding (Prévot 2010). Wild boar groups with frequent and year-round access to artificial food source have also failed to show seasonal patterns in home range use, which are characteristic of other wild boar (Boitani et al. 1994), and can increase their use of nutritionally unrewarding habitats (Thurfjell et al. 2009).

Wild boar host various parasites and can be a vector and reservoir for numerous pathogens shared between wildlife, livestock, and humans (Martin et al 2011). Supplementary feeding can potentially facilitate the transmission of various diseases in wildlife (Sorensen et al. 2014). Solitary males tend to avoid each other, but habitat use of different family groups can overlap (Boitani et al. 1994) and when a feeding site is visited by several groups of wild boar (Andrzejewski and Jezierski 1978), increased contact rate of separate groups can lead to increased risk of infection (Arneberg 2001; Arneberg 2002; Roberts et al. 2003). With the current spread of the African swine fever (ASF) in Europe, it is recommended to limit supplementary feeding of wild boar (Gavier-Widén et al. 2015), although it seems to be one of the least effective measures in controlling the continued spread of this disease (Guinat et al. 2017).

1.3 Status of wild boar in Estonia

Wild boar first reached Estonia in the late-Preboreal stage of the Postglacial thermal period (9,500 BP), when the abundance of hazel *Corylus* sp. groves created favourable conditions for many omnivorous animals by the production of hazelnuts and humus, which is rich in worms, insects and molluscs (Lepiksaar 1986). Broadleaved forests are essential for wild boar (Abaigar et al. 1994; Meriggi and Sacchi 2001; Merli and Meriggi 2006; Thurfjell et al. 2009) – this is also demonstrated by the distribution of wild boar in Norway, which was restricted to broadleaved forests even during the most favourable climatic period of the Holocene (Rosvold et al. 2010). Presently, wild boar in Estonia live close to the northern limit of the species range, and the climate reflects a transition between continental and maritime influences with an average air temperature of 16 °C to 17 °C in July and -6 °C to -7 °C (East and Central Estonia) or -2 °C to -4 °C (West Estonia) in January. The northernmost populations inhabit Karelia (Danilkin 2001).

Nearly half of Estonia is covered with forests, the most common forest tree species being Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birch (*Betula* sp.) and aspen (*Populus tremula*). However, mast trees (common hazel *Corylus avellana* and English oak *Q. robur*), although present in the parks, are uncommon in the wild. The highest proportion of forests containing oak occur in the island Saaremaa and also cover over 1 % of the area in the Lääne, Rapla and Harju counties. Reed (*Phragmites australis*) shoots and roots provide a natural energy-rich food source, but in general, mast foods have been substituted by foods of anthropogenic origin – seasonally available agricultural

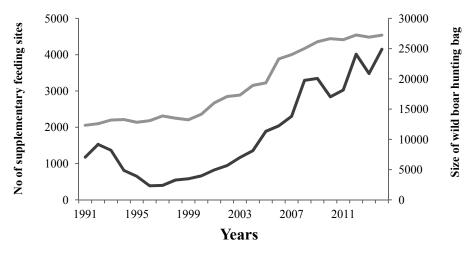
crops and supplementary feeding. Both, agricultural production and supplementary feeding are associated with wild boar presence in unfavourable habitats and increased abundance (Fruziński and Łabudzki 2002; Melis et al. 2006; Cellina 2008; Rosvold and Andersen 2008). Evidence from boar remains suggests that wild boar benefited from the availability of anthropogenig food as early as in the Subboreal climatic period (5,000 to 2,500 BP), when refuse heaps near human dwellings might have served as supplementary feeding sites (Lepiksaar 1986).

Extraordinarily cold winters during the Little Ice Age reduced the populations of ungulates to a minimum, whereas wild boar disappeared shortly after the end of the Middle Ages (Lepiksaar 1986). Low temperatures can impose strong constraints on the energy budget of wild boar (Lemel et al. 2003) and snow depths of 40–50 cm have been considered as a limiting factor of wild boar range (Danilkin 2001). Deep snow makes foraging energetically costly and difficult, and can cause rapid deterioration of body condition, increased susceptibility to disease, and starvation (Jedrzejewski et al. 1992). After climate amelioration, wild boar returned to Estonia about 1930 and soon established a large population despite a temporary decrease during the severe winters of 1939–1941 (Lepiksaar 1986). During the time of this study, hunters' estimation of adult and yearling wild boar abundance before the birthing period in spring was about 22,000, while yearly hunting bags ranged from 17,000 to 25,000 (Fig 1). In Estonia, wild boar are preved upon mainly by wolf (Valdmann et al. 1998) and only occasionally by brown bear (Ursus arctos) (Vulla et al. 2009) and Eurasian lynx (Lynx lynx) (Valdmann et al. 2005). However, in general, large carnivores seem unlikely to be capable of limiting boar numbers in Estonia and hunting is probably the most important cause of mortality. Today, the abundance of wild boar has been strongly influenced by the rapid spread of the ASF virus and hunters' estimates of abundance have decreased in all counties except on the island Hiiumaa (Veeroja and Männil 2016), which has remained an ASF-free area.

During the 2000s, the number of supplementary feeding sites increased two-fold and by the time of this study there were over 4,500 supplementary feeding sites for wild boar in Estonia (Fig 1). These sites mostly provided grain and vegetables (usually potatoes), but apples, acorns and residues from food processing industries were also offered, depending on the season and availability. The majority of feeding was carried out in winter with the purpose of baiting animals for easier hunting, decreasing mortality during food distress, and preventing damage to farmland (dissuasive feeding). Although these aims require feeding that differs in the amount and period when food is available for animals (see also Cellina 2008), they resulted in year-round *ad libitum* feeding. Supplementary feeding was mostly unregulated by law and was restricted only in the areas where capercaillie leks were protected (since 2007). Today, supplementary feeding of wild boar has been regulated by decree of the Environmental Board in order to prevent the spread of ASF – feeding is allowed only for the purpose of baiting with a maximum of 5 kg of supplementary food

available and a density of one feeding site per 1000 ha (see also Gavier-Widén et al. 2015).

A study carried out in an isolated population on the island Saaremaa in western Estonia showed that a majority of wild boar are infected with lungworm *Metastrongylus* sp. (prevalence 82 %), whereas three different species were identified: *M. pudendotectus, M. elongates*, and *M. salmi* (Järvis et al. 2007). The same study also identified *Dicrocoelium dendriticum, Taenia hydatigena, Trichuris suis*, and *Ascaris suum*. In the mainland, *Trichocephalus suis, Oeso-phagostomum dentatum*, and *Physocephalus sexalatus* are also present (Järvis 1993). Wild boar in Estonia are a reservoir for *Trichinella* spp. (Kärssin et al. 2016) and *Toxoplasma gondii* (Jokelainen et al. 2015). Several viral and bacterial diseases share similar transmission routes with parasites and endoparasite infections can indirectly contribute to disease severity in wild boar (Risco et al. 2014). However, until the outbreak of the ASF in September 2014, wild boar population in Estonia had not suffered from increased mortality due to pathogens or disease in recent decades.



— No of supplementary feeding sites —— Size of wild boar hunting bag

Fig 1. The number of supplementary feeding sites for wild boar and hunting bag size in Estonia, both increased markedly during the 2000s. Data from Statistics Estonia and Estonian Environment Agency.

1.4 The objectives of this thesis

The main objectives of this thesis were to examine:

- the effect of extensive supplementary feeding of wild boar on predation of ground-nesting birds;
- the effects of concentrating animals to feeding sites and increased overall host abundance on wild boar infection with endoparasites.

To achieve these aims, wild boar density in Estonia was modelled in paper I, using generalised linear models with mixed effects (GLMM). An abundance index from a winter wildlife census programme, based on track counts, was used to indicate wild boar abundance and various management- and climate-related factors were included as explanatory variables.

To study the behaviour of wild boar as a predator and to investigate the effect of supplementary feeding on ground-nesting birds, wild boar spring diet was studied and experiments with artificial nests were carried out. In paper II, wild boar faeces were collected from protected capercaillie leks and surrounding areas that have restrictions against supplementary feeding, and analysed using a morphological method as well as a newly developed molecular method. In addition to the samples used in paper II, stomachs were collected from wild boar shot by hunters and faeces were collected from hunting districts that had no restrictions against supplementary feeding.

In paper **III**, two separate artificial nest experiments were carried out to estimate the spatiotemporal effects of concentrating wild boar and other predators of ground-nesting birds around supplementary feeding sites. The first experiment was used to study nest predation in the immediate vicinity up to 400 m from the feeding sites. The second experiment was used to compare predation risk in the immediate vicinity of active feeding sites and near abandoned feeding sites that are no longer used for hunting purposes. Predation risk was modelled using GLMM.

To examine the effects of supplementary feeding on parasite infections in paper **IV**, endoparasite eggs and oocysts were counted in wild boar faecal samples. The role of host density and number of feeding sites on the risk and mean abundance of infection was modelled using generalized linear models (GLM).

All data were collected before the outbreak of the ASF virus in Estonia.

2. MATERIALS AND METHODS

2.1. Wild boar abundance

In paper I, data from the winter wildlife census programme in Estonia was used, the study period covered six years (2006–2011), including three harsh winters with deep snow cover and low temperatures. Every year, local hunters counted 383 permanent 12-km-long routes for tracks 24 h after snowfall. The method provides an abundance index (AI), which corresponds to the number of tracks per km. In the analysis, AI was calculated for each year by averaging wild boar track counts from all valid routes in each county in Estonia. All points with missing data were excluded from the analysis, leaving 80 data points to represent Estonia on the county level across a 6-year period.

Seven independent variables representing hunting, food, habitat and predators were used in the analysis: the size of the hunting bag (BH), the number of hunting stands (HS) and supplementary feeding sites (FS), which were each calculated per 1,000 ha of forest, the proportions of the area covered with agricultural fields (AGRI) and forests (FOR), and the AIs for wolf and Eurasian lynx. Two variables were used to describe the climate – mean January temperature (current and previous year summed; TEMP) and the sum of mean monthly snow depth during the previous year (SNOW). Wild boar AI was Intransformed prior to analysis in order to normalise the distribution of the model residuals.

Generalized linear mixed models were used to investigate variations in wild boar abundance based on AI, year was used as a random effect. Models were ranked by the Akaike information criterion corrected for finite sample sizes (AICc) (Burnham and Anderson 2004) and maximum likelihood estimation was used for model parameter estimation to allow comparison of models with different fixed effect structure. R version 3.0.1 (R Development Core Team 2013), with the package nlme (Pinheiro *et al.* 2011), was used for statistical analyses.

2.2. Wild boar diet

2.2.1. Morphological analysis of wild boar diet

In paper II, the data consisted of 109 wild boar faeces collected from seven protected capercaillie lekking areas in central, eastern, and southern Estonia, which had been monitored for three years (2013–2015) from the end of March to the middle of June. The period corresponds to capercaillie displaying and breeding in Estonia. Faeces were stored at -80 °C before analysis. In addition to the faeces analysed in the paper, a separate sample of wild boar faeces (N = 26) was collected from hunting districts in southern and south-eastern Estonia in April–May 2015. Also, 77 stomach contents (N₂₀₁₂ = 60, N₂₀₁₄ = 17) from eight

counties (Harju, Järva, Jõgeva, Pärnu, Põlva, Rapla, Tartu, Valga) were collected from wild boar shot in May–June 2012 or 2014 for additional analysis.

Faeces and full stomach contents were washed on a metal sieve (0.8 mm mesh size) and identifiable objects were divided into eight categories: greens (above-ground plant material, except for tree leaves and needles), roots (in faeces only), supplementary (grain from feeding sites), invertebrates (earth-worm, arthropod wings and leg segments, fragments of chitin), mammals (hair, teeth and bone fragments; undigested skin fragments in stomachs only), birds (feathers, bone and eggshell fragments; partly digested bird foetuses in stomachs only), birds/reptiles (reptilian-like scales crushed into fragments too small for certain identification, in faeces only), reptiles (reptilian skin fragments, in stomachs only), and other (digested fragments of tree leaves and needles, small stones, etc.).

To quantify diet composition, frequency of occurrence (FO = number of faeces or stomachs containing each food category / total number of faeces or stomachs) and volume of each food category were measured. Volumetric evaluation was used for the faeces (see article **II** for specifics) and visual evaluation (as in Cellina 2008) for the stomachs. Owing to the difference in size, relative volume percentage was calculated, using the formula $V_a \% = 100 \times \frac{\Sigma V_a}{V}$, where $V_a \%$ is the percentage volume of a food category, ΣV_a is the volume of objects in a category, and V is the total volume of objects in all categories. Chi-squared test was used to compare the proportion of different food categories in faeces (N = 135, faeces from protected areas and hunting districts summed) and stomachs, and R 3.4.0 was used for all analyses (R Development Core Team 2017).

2.2.2. Molecular method for detection of bird in mammalian faeces

In paper II, mitochondrial DNA was extracted from 109 faeces collected from capercaillie lekking areas and taxon-specific primers were used for molecular identification of avian prey in wild boar faeces. The method is universal for mammals and birds and can be used for a wide range of mammalian and avian species. After sequencing, mammal and bird taxa were determined to the species level. To evaluate the sensitivity of the molecular method, the frequency of bird occurrence was compared in corresponding datasets used in the molecular and morphological analyses.

2.3. Artificial nest experiments

2.3.1. Study design

In paper III, two different artificial nest experiments were carried out in four hunting districts in south-eastern Estonia to investigate the effect of supple-

mentary feeding on ground nest predation. The first experiment was conducted to investigate the key factors associated with predation risk in the forest surrounding supplementary feeding sites, and the second experiment was conducted to investigate long-lasting effects of abandoned feeding sites. For the first experiment, a total of 312 nests were placed in the vicinity of 12 supplementary feeding sites in May 2012. Two parallel transects, containing 26 artificial nests with approximately 40 m between the nearest neighbouring nests, started at the proximity of each site and led into the forest interior. The quantity of available food, distance to the feeding site, ground cover, and forest type were determined for each artificial nest.

For the second experiment, a total of 306 artificial nests were placed in the vicinity of active (N = 12) and abandoned feeding sites (no supplementary feeding for at least one year; N = 10) and control sites (located >500 m from the nearest feeding site; N = 9) in 2010, 2012, and 2013. Artificial nests were placed in a 3 by 3 pattern with approximately 30 m between the nearest neighbouring nests. Forest type was determined for each artificial nest, the age of the feeding site, defined as the time in years that had passed from abandonment, was determined for nests placed in the vicinity of abandoned feeding sites.

2.3.2. Statistical analysis

Generalized linear models with binomial distribution were used for predicting the probability of nest predation. In each experiment, nest fate was a binary dependent variable (0 – nest survived; 1 – nest depredated) and study plot was used as a random factor. Study plot referred to each individual supplementary feeding site or control plot.

In the first experiment, the fixed factors were: the quantity of available food (INT, large sites providing >50 kg supplemental food per week, small sites providing <25 kg supplemental food per week), distance from the feeding site (DIST; linear, quadratic, cubic and quartic functions), herbaceous plant cover (%; COV), forest type (FT), fate of the nearest neighbouring nest (0 – nest survived; 1 – nest depredated; NF) and study area (Tähtvere or Valga; SA). Interactions between DIST × COV, DIST × INT and COV × INT were also included.

In the second experiment, the fixed factors were: type of the study plot (feeding site or control area; TYPE), period of non-use of the feeding site (time in years after the abandonment of a feeding site, "0" for both active feeding sites and control areas; AGE) and forest type (FT) as well as the interactions between $AGE \times FT$ and $TYPE \times FT$.

Alternative models were ranked according to AICc (Burnham and Anderson 2004) and R 3.0.1 (R Development Core Team 2013) with the package lme4 (Bates *et al.* 2015) was used for all analyses.

2.4. Wild boar endoparasites

2.4.1. Sample collection and parasitological analysis

In paper IV, a total of 201 fresh-looking wild boar faeces were collected from April to early June in 2013–2015. The majority of samples correspond to the faecal samples described in paper II and chapter 2.2.1. The study area covered 12 hunting districts in six counties (Ida-Viru, Jõgeva, Rapla, Tartu, Viljandi, Võru) in central and south-eastern Estonia. Faecal samples were collected by searching the forest and the immediate vicinity of supplementary feeding sites was avoided in order to prevent contamination in potentially high-risk areas.

Faecal samples were stored at +4 °C and analysed using the concentration McMaster technique. Parasite eggs and oocysts were identified on the basis of morphological features (Roepstorff and Nansen 1998). A parasitological finding of endoparasite eggs/oocysts in the faeces was assumed to have been indicative of true infection.

2.4.2. Statistical analysis

Generalized linear models with binomial and negative binomial distributions were used for predicting the probability of endoparasite infection and infection intensity in wild boar. The models were ranked according to AICc (Burnham and Anderson 2004). Mixed models would have been preferable in our study design, however, the inclusion of 'hunting district' or 'year' as a random factor did not improve the models in terms of AICc, and the confidence interval for the variance of the random effect contained zero.

Models were built using the presence or number of endoparasite eggs/ oocysts as a dependent variable and one independent factor to represent either wild boar (host) density or feeding site density. Two separate factors were used to represent wild boar density: wild boar hunting bag (hunting) and hunters estimates of wild boar population size (abundance). Two factors represented supplementary feeding: number of supplementary feeding sites (feeding) and number of salt provision sites (minerals). All four factors (feeding, minerals, hunting, and abundance) were calculated per 1000 ha of each investigated hunting district to account for variation in the size of different sampling areas.

All statistical analyses were carried out using R 3.2.2 (R Development Core Team 2015), package "MASS" (Venables and Ripley 2002) was used to construct negative binomial regression models.

3. RESULTS

3.1. Wild boar abundance

Habitat- (FOR, AGRI) and management-related variables (FS, HS, BH) were very strongly correlated (in most cases r > 0.5), and these variables were not used in the same model to avoid multicollinearity. Lynx AI was not used in the same model with any of the habitat- and management-related variables due to strong intergroup correlations. This left a total of 26 models to be ranked by AICc (see Table 2 in article I for specifics).

AICc identified two top models (M₁: FS + TEMP and M₂: FS + TEMP + WOLF), whereas wild boar AI was increased by more supplementary feeding (M₁: $\beta = 0.380$, SE = 0.065, p < 0.001; M₂: $\beta = 0.387$, SE = 0.065, p < 0.001) and warmer January temperature (M₁: $\beta = 0.036$, SE = 0.010, p < 0.001; M₂: $\beta = 0.035$, SE = 0.010, p < 0.001). WOLF (p > 0.4) represented a redundant variable and did not improve the goodness of fit of the second model – the difference in AICc values was less than two units. The highest-ranking model FS + TEMP was over ten times more likely to represent the best model than FS + SNOW (evidence ratio ER = 10.82) and had an ER > 750 over any of the models that included habitat-related variables (see Table 2 in a paper I for specifics).

Therefore, wild boar abundance in Estonia is primarily determined by supplementary feeding and temperature, which dominate over other management- and habitat-related variables and the negative effects of deep snow cover and predators.

3.2. Wild boar diet

3.2.1. Morphological analysis of wild boar diet

The majority of wild boar diet consisted of plants and included items from both natural and supplementary sources (Table 1). Roots were not detected in stomachs, but occurred in similar proportion to greens in faeces ($\chi^2_1 = 0.77$, p = 0.381). The proportion of supplementary food was similar to natural plants (greens) in stomachs ($\chi^2_1 = 0.28$, p = 0.600) and faeces in general ($\chi^2_1 = 1.28$, p = 0.259), but occurred significantly less frequently in faeces collected from protected areas ($\chi^2_1 = 9.61$, p = 0.002).

The proportion of animal matter in wild boar diet is low compared to plants, but the frequency of occurrence is substantial (Table 1). Invertebrates were detected significantly less frequently in faeces than stomachs ($\chi^2_1 = 35.68$, p < 0.001), but mammals occurred in similar proportion in both faeces and stomachs ($\chi^2_1 = 0.34$, p = 0.558). Objects in the category bird were significantly more frequent in stomachs than faeces ($\chi^2_1 = 12.72$, p < 0.001). However, it is difficult to say if bird occurred more frequently in stomachs than faeces due to

the category bird/reptile in faeces, which contained reptilian-like scales that had degraded too much for certain identification. Seven of the stomachs contained bird foetuses and only three contained bird bone fragments (two chicks, one adult), which indicates that in a majority of cases wild boar did not act as a scavenger, but actively predated on the nests and chicks of ground-nesting birds. Mostly, bird consumption left only trace amounts (<5 % by volume) of material (egg-shell fragments with a diameter less than 2 mm, 2–3 bird foetuses) and species identification was not possible based on morphology due to digestive degradation of the study material.

Two of the analysed stomachs and six of the faeces collected from protected areas (5.5%) contained no plant material, which indicates a deliberate consumption of animal matter as opposed to the opportunistic predation while browsing for other foods. Both of the stomachs contained vertebrates, but one indicated nest predation and the other was probably carrion consumption (roe deer *Capreolus capreolus*). Two faeces contained bird and invertebrates, one indicated both nest and mammal predation (field vole *Microtus agrestis*, identified by teeth morphology), and three consisted of bird/reptile, carrion (roe deer) or invertebrates in addition to plant material.

	FO (%)			Volume (%)			
Category	Faeces		Stomachs	Faeces		Stomachs	
	N = 109	N = 26	N = 77	N = 109	N = 26	N = 77	
Greens	46.8	19.2	67.5	38.2	16.7	43.0	
Roots	37.6	26.9	n.p.	23.6	16.6	n.p.	
Supplementary	25.7	69.2	72.7	21.2	66.8	47.3	
Invertebrate	25.7	3.8	63.6	3.5	< 0.1	6.3	
Mammal	7.3	n.p.	11.7	1.9	n.p.	1.1	
Bird	4.6 *	n.p.	15.6	1.2 *	n.p.	0.9	
Bird/Reptile	15.6	n.p.	n.p.	6.9	n.p.	n.p.	
Reptile	0,9 *	n.p.	1.3	0.5 *	n.p.	0.1	
Amphibian	n.p.	n.p.	2.6	n.p.	n.p.	0.1	
Other	21.1	11.5	9.1	3.0	< 0.1	1.2	

Table 1. Results of the morphological analysis of wild boar diet based on faecal and stomach analysis.

* Molecular analysis was used to identify two samples from the bird/reptile category in the faecal analysis – one of the samples belonged to bird and the other to reptile. FO (%) – frequency of occurrence; V (%) – relative volume percentage; n.p. – not present

3.2.2. Molecular method for detection of bird in mammalian faeces

Of the 109 faecal samples analysed with the molecular method in paper II and belonging to wild boar based on morphology, 49 were identified as wild boar and of these six contained bird DNA. Additionally, among the samples that gave negative result in mammalian PCR, the method identified bird DNA in three samples. Wild boar faeces are morphologically easily distinguishable from other mammalian predator in three samples, they clearly belonged to wild boar. Thus, bird DNA was identified in nine out of 52 wild boar samples and bird occurred $4.5 \times$ more frequently than suggested by morphological analysis in the same set of samples (FO_{molecular} = 17.3% and FO_{morphological} = 3.8%).

Five of the bird samples were determined to species level: three capercaillie, one black grouse (*Tetrao tetrix*), and one hazel grouse (*Tetrastes bonasia*). The other four bird samples were determined to genus level due to partial sequences (DNA degradation): three to *Tetrao* and one to *Corvus*.

3.3. Artificial nest experiments

3.3.1. Spatial patterns of increased depredation risk

224 out of 312 nest were depredated (72%) in the first experiment and depredation risk was independent of the proximity of the nearest neighbouring nest (p > 0.05). Predation risk varied significantly in relation to distance, when moving from the feeding sites into the forest interior – the effect of distance from the feeding site was best explained by the cubic function.

Feeding regime proved to be the most important factor to predict predation risk in the vicinity of supplementary feeding sites and dominated over all other factors. Three good models ($\Delta AICc < 2.0$) were distinguished based on AICc values: M₁ INT+DIST+DIST²+DIST³|SP, M₂ INT+DIST+DIST²+DIST³+COV|SP, and M_3 INT|SP. Removal of the factor INT resulted in models with the lowest AICc scores (see Table 1 in article III). Models M₁ and M₂ were similar in terms of goodness-of-fit ($\chi^2_1 = 1.21$, p = 0.271), therefore COV can be dropped and the simpler model preferred. Model M₃ differed significantly from model M_1 in terms of goodness-of-fit ($\chi^2_1 = 7.86$, p = 0.049), thus the factor DIST cannot be dropped from the model. However, models with DIST were good only if INT was also included (see Table 1 in paper III). According to model M_1 , supplementary feeding sites concentrated potential nest predators, including wild boar, whereas sites with more food available had a much stronger effect – nest depredation risk was significantly lower in the vicinity of small feeding sites compared to large sites ($\beta = -2.563$, SE = 0.394, p < 0.001), nest depredation reached a local maximum at approximately 150 m and was lowest at approximately 380 m. This variation in predation risk was observed only in the vicinity of small feeding sites (see Fig 2 in paper III).

3.3.2. Temporal patterns of increased depredation risk

In the second experiment, 168 out of 306 nests were depredated (55%), and depredation risk varied significantly between active and abandoned feeding sites, as well as control plots – 75% and 48% of nests were depredated in the vicinity of active and abandoned feeding sites respectively, and 38% in control plots. Supplementary feeding sites concentrated nest predators independently of forest type, and this effect persisted for some time after the feeding site had been abandoned by the hunters. According to AICc, the best model was TYPE+ AGE|SP (see also Table 2 in article III), whereas depredation risk was higher in feeding sites than in control plots ($\beta = 1.854$, SE = 0.415, p < 0.001) and decreased with increasing period of non-use at abandoned feeding sites ($\beta = -0.197$, SE = 0.054, p < 0.001), but was significantly higher during the first few years after abandonment (see also Fig 3 in paper III).

3.4. Wild boar endoparasites

3.4.1. Parasitological findings

Eimeria sp. (prevalence 64.2%, CI = 57.1–70.7) was the most widespread and abundant parasite in the 201 wild boar faecal samples, while the most prevalent helminths were *Strongyloides* sp. (prevalence 57.2%, CI = 50.1–64.1) and *Metastrongylus* sp. (prevalence 47.8%, CI = 40.7–54.9). *A. suum* and *T. suis* were also detected, but were not modelled due to low prevalence (10.5%, CI = 6.7–15.7 and 9.0%, CI = 9.0, CI = 5.6–14.0 respectively).

3.4.2. Probability of infection and mean infection abundance

Correlations between the different indicators of wild board density (hunting and abundance) were weak (Spearman rank correlation (r_s) = 0.19, p = 0.007). However, moderate correlations existed between the density of supplementary feeding sites and hunting bag (Spearman rank correlation r_s = 0.44, p < 0.001) and hunters estimation of population size (Spearman rank correlation r_s = 0.34, p < 0.001). Hunting bag size is likely to reflect the amount of supplemental food provided by the hunters.

Eimeria sp. infection was best predicted by factors associated with the density of wild boar (see also Table 2 in paper **IV**), whereas hunting bag produced the best model fit. Larger hunting bag size increased both the probability of infection ($\beta_{hunting} = 0.919$, SE = 0.193, p < 0.001) and mean infection abundance ($\beta_{hunting} = 0.465$, SE = 0.139, p = 0.001). Higher estimates of abundance also increased infection probability ($\beta_{abundance} = 0.291$, SE = 0.119, p = 0.014) and mean infection abundance ($\beta_{abundance} = 0.404$, SE = 0.161, p = 0.012), but resulted in models with significantly lower weight.

Two equally good models predicted *Metastrongylus* sp. infection probability (see also Table 2 in paper **IV**) – higher density of supplementary feeding sites ($\beta_{\text{feeding}} = 2.000$, SE = 0.855, p = 0.019) and larger hunting bag size ($\beta_{\text{hunting}} = 0.279$, SE = 0.106, p = 0.008) both increased the probability of being infected. The effects of host density and supplementary feeding sites cannot be separated completely due to correlation between these two variables. Mean infection abundance was not modelled for *Metastrongylus* sp. due to loss in the accuracy of faecal egg count.

4. DISCUSSION

4.1. The role of supplementary feeding and other factors in determining wild boar abundance

In Estonia, wild boar abundance was determined by two major factors – supplementary feeding and winter temperature – and the importance of habitatrelated variables was relatively low (I). Supplemental food comprises a very important food category for the Estonian wild boar, not only in hunting districts, but in protected areas as well, although limited access to supplemental food has resulted in its lower proportion in samples collected from protected areas (II, chapter 3.2.1). Widespread practice of supplementary feeding has probably helped ameliorate the effect of harsh winters on wild boar mortality, which are most detrimental to juvenile wild boar (Andrzejewski and Jezierski 1978; Jędrzejewski et al. 1992, Selva 2004), and increased the reproductive potential of the female wild boar (Celline 2008). Under good environmental conditions, population growth is primarily driven by juveniles (Bieber and Ruf 2005) and the high proportion of juvenile females participating in breeding in the Estonian population (Veeroja and Männil 2014) illustrates this effect of both intensive and extensive supplementary feeding.

The negative effect of the mean January temperature (I) on wild boar abundance can reflect the effects of mortality from harsh winters (Andrzejewski and Jezierski 1978; Jędrzejewski et al. 1992, Okarma et al. 1995; Selva 2004), as well as the availability and distribution of resources (Acevedo et al. 2006). Indeed, the relatively milder climate in the western parts of Estonia co-occurs with the highest numbers of wild boar hunted per area and the proportion of forests containing oak (see chapter 1.3). The importance of acorns has been previously highlighted in numerous studies on wild boar diet and reproductive output (Gethöffer et al. 2007; Cellina 2008; Rosvold et al. 2010; Cutini et al. 2013; Frauendorf et al. 2016; Gamelon et al. 2017). These areas will probably also be the least affected by the current restrictions on supplementary feeding in Estonia.

The mean depth of the snow cover had very little effect in determining wild boar abundance (I). This is in contrast with a study from Italy, where snow depth was one of the key factors and correlated negatively with wild boar abundance (Cutini et al. 2013). In this study, supplementary feeding sites acted as concentration centres for wild boar (III), who are known to alter their habitat use on a relatively small scale in relation to human disturbance (Keuling et al. 2008; Ohashi et al. 2012). However, when supplementary food is available, wild boar can also limit their movements in snow (Thurfjell 2011; Prévot 2010; Jezek et al. 2013). Therefore, the benefit from supplementary feeding in winter is twofold for wild boar – complementary nutrition during a period, when natural food is scarce, and avoidance of increased energy cost when foraging in deep snow (see Jędrzejewski et al. 1992; Melis et al. 2006; Cellina 2008). Similarly, Okarma et al. (1995) found that snow depth has an essential role in wild boar mortality in extreme winters (snow cover over 70 cm lasting for two months with a maximum snow depth up to 100 cm, such conditions were not reached in this study), but in milder winters food abundance becomes the most important factor. Incidentally, wild boar have also been known to increase scavenging when snow is deepest (Selva 2004), thus taking advantage of easy-access protein-rich diet in harsh climate.

Although the abundance index of wolf appeared in one of the top models, the role of predators seems to have had very little impact on the wild boar population at the height of its abundance in Estonia (I). Wild boar are the preferred prey of wolves in certain locations (Valdmann et al. 1998, Mattioli et al. 2011), but they prey mostly on juvenile wild boar (Jędrzejewski et al. 1992, Barja 2009), whose reproductive output is low compared to adults (see chapter 1.1), and in Estonia, roe deer occurs by far more frequently in the wolves' diet (Valdmann et al. 1998), whereas wild boar is the most significant prey item in Italy (Cutini et al. 2013). In Poland, where wild boar is also not the dominant prey item for wolf, death from factors other than predation prevail in the wild boar population (Jędrzejewski et al. 1993, Okarma et al. 1995; Selva 2004).

Habitat-related factors had very little impact on wild boar abundance (I). These results differ from other studies that have highlighted the positive effects of agriculture and forest cover (Borowik et al. 2013). However, agricultural fields constitute an important habitat for wild boar only during the period, when crops are ripe (Neet 1995; Geisser and Reyer 2005, Cellina 2008; Thurfjell et al. 2009; Keuling et al. 2010). In Estonia, this time-frame could be too short to have a significant effect on population abundance, particularly, when supplementary food is available year-round. This can also be explained by the low availability of maize, which is preferred to other crops (Herrero et al. 2006; Cellina 2008; Amici et al. 2012) and probably has the potential to influence wild boar population the most, but was grown on less than 1 % of agricultural fields in Estonia during the time of the study (data from Statistics Estonia). In Poland, forest cover of up to 40 % increased wild boar abundance, which reached a relatively stable plateau at higher levels (Borowik et al. 2013). However, in Estonia, nearly half of the area is covered with forests, thus cover hardly seems to be the limiting factor.

4.2. The role of supplementary feeding on ground-nesting birds

Wild boar is a known predator of ground-nesting birds and their nests (Briedermann 1990; Purger and Mészáros 2006; Giménez-Anaya et al. 2008; Svobodová et al. 2012; Carpio et al. 2014; Экономов 2016; Senserini and Santilli 2016, II), thus supplementary feeding can affect the birds in two ways. First, increased abundance of wild boar resulting from supplementary feeding (I) can raise the overall predation risk. Second, concentration of wild boar and other predators (see also Cooper and Ginnett 2000) near feeding sites can create predation hot-spots (Cooper and Ginnett 2000; Selva et al. 2014, III). In Estonia, non-target visitors include small mammals, red fox, raccoon dog, and various birds (Oja 2010; Süld et al. 2014). Third, extensive supplementary feeding (I, II, chapter 3.2.1) can attract wild boar to forests that they would not frequent as much otherwise (Geisser and Reyer 2004; Thurfjell et al. 2009).

This can cause a problem for the conservation of gallinaceous birds, who have long been of conservation concern (Moss et al. 2010) because of a marked decrease of abundance through-out the world due to loss of habitat (Storch 2007) as well as various predators (Sirkiä et al. 2010; Wegge and Rolstad 2011). Forest grouse prefer spruce-dominated habitats (Sachot et al. 2003) and a significant proportion of the Baltic capercaillie population inhabits coniferous forests (Lõhmus et al. 2017). This habitat is used by wild boar for daytime resting (Thurfjell et al. 2009, Keuling 2010), but has limited feeding opportunities. In the scarcity of the preferred food items, ground-nesting birds and their nests can be used as alternative prey (Šalek et al. 2004). The effect of concentrating nest predators near feeding sites in Estonia was independent of forest type (III), but the effect of supplementary feeding on the overall predator abundance is likely to be the most evident in poor and nutritionally unrewarding habitats. Although supplementary feeding has been prohibited in capercaillie lekking areas, where faecal samples were collected, they still contain grain from supplementary feeding sites (II). This suggests that the current buffer zone of 1 km is too small to prevent wild boar from taking advantage of supplemental food. This is not surprising, because they can travel up to 12 km during nightly feeding searches (Boitani et al. 1994).

In this study, birds were present in both stomachs and faeces, but based on morphology, were detected significantly less in the latter (II, chapter 3.2.1). However, molecular analysis on wild boar faeces revealed that the proportion of bird was approximately $4.5 \times$ higher than suggested by morphology alone. Stomachs and faeces have previously been considered adequate and comparable in wild boar diet analysis (Baubet et al. 2004; Zeman et al. 2016). However, it seems that in this study faecal analysis suffered more from the rapid digestion of animal food (Fournier-Chambrillon et al. 1995). A majority of stomachs contained bird foetuses, which were never observed in faeces and were probably fully digested, whereas bone fragments and feathers of birds were detected in both faeces and stomachs. These results indicate that previous studies on wild boar diet that have relied on faecal analysis instead of stomachs might have underestimated the consumption of bird by wild boar. What is more, when only a subsample is used in stomach analysis (as in Cellina 2008), the frequency of occurrence can be underestimated, because bird consumption may leave only small traces in the stomachs (see chapter 3.2.1).

When mast production is low, wild boar increase their intake of animal foods (Groot Bruinderink and Hazebroek 1994), which suggests that supplemental food could be used to deter wild boar from areas with increased density of ground-nesting birds (Vander Lee et al. 1999) and concentrate them around

supplementary feeding sites (III). However, access to foods of anthropogenic origin does not always result in a decreased consumption of animal foods. A comparison of two wild boar populations from southern Poland showed that the consumption of both animal and anthropogenic food sources were higher in the population inhabiting a forest-farmland environment (Merta et al. 2014). Similarly, wild boar inhabiting an urban area prefered natural food to anthropogenic, which they used only, when natural resources were limited (Stillfried et al. 2017). In this study, supplementary food was consumed in proportion similar to natural plants, although significantly less in protected areas with limited access to supplemental food (chapter 3.2.1). These results indicate that the Estonian wild boar also prefer natural food and supplementary feeding could not be provided as a substitute for ground-nesting birds and their eggs.

4.3. Wild boar - predator or scavenger?

Despite its low volume, animal matter constitutes an important food item for wild boar and can occur in very high frequency. For example, in the introduced range (USA), animal matter was recorded in 94 % of stomachs collected during the spring and summer season (Howe et al. 1981), and a similar frequency has been found for earthworm in the native range (Baubet et al. 2003). Based on volume, however, animal food seems to be more important in the introduced range and can be acquired by predation or scavenging (Ballari and Barrios-García 2014). In this study, faeces and stomachs both contained samples consisting entirely of animal matter (**II**, chapter 3.2.1), which indicates deliberate consumption of animals. When wild boar have consumed vertebrates, it can be difficult to determine, whether they were killed by wild boar or some other predator and consumed as carrion, but the distinction is necessary for conservation planning – if wild boar acted exclusively as a scavenger, who takes over prey from smaller and/or solitary predators, then it would influence the birds only through the predator species.

Small mammals, such as rodents and invertebrates are common in wild boar diet (Briedermann 1990; Schley and Roper 2003; Cellina 2008; Wilcox and Van Vuren 2008; Ballari et al. 2015; **II**, chapter 3.2.1) and due to their small size it is highly unlikely that they are consumed as carrion. Wilcox and van Vuren (2009) found that small mammals appeared in large numbers in stomach analysis and were actively preyed upon. It is noteworthy, that animals in poorer physical condition were more likely to prey on vertebrates (Wilcox and van Vuren 2009), which corresponds to the increased consumption of animal matter in years of poor mast availability in wild boar without access to supplementary food (Groot Bruinderink and Hazebroek 1994). When the availability of acorns decreases, wild boar can take advantage of acorn hoards buried by small mammals (Focardi et al. 2000) and are likely to predate occasionally on mammals that remain in the burrows that are excavated during the search for acorns.

In addition to small mammals, wild boar are known to scavenge on ungulates and occasionally other mammals. In the introduced range, they consume domestic animals as carrion and are believed to prey on sheep, but the few cases attributed to wild boar had not in fact been predated (Herrero and De Luco 2003). In addition to domestic cattle, red deer (Cervus elaphus) and badger (Meles meles) have been discovered as carrion (Herrero et al. 2005). In the Białowieża Primeval Forest in Poland, the main guild of scavengers includes wild boars, which show a strong preference for animals killed by predators, mostly lynx (Selva 2004). Roe deer remains found in this study were also probably consumed as carrion (II, chapter 3.2.1). Roe deer is the dominant prev item of lynx in the region (Valdmann et al. 2005) and wild boar, which are highly social and live in tight groups (Boitani et al. 1994; Keuling 2009), typically also scavenge in groups, and can appropriate the kills from lynx and consume these completely (Jedrzejewski et al. 1993). Cannibalism is also not uncommon in wild boar, however, although wild boar remains have been found in diet analysis (Ježek et al. 2016), they have been shown to prefer red deer and European bison (Bison bonasus) for scavenging, and avoid the carcasses of conspecifics (Selva 2004). However, infanticide can occur in wild boar kept in enclosures and it seems to be part of the normal behavioural pattern (Andersson et al. 2011). Thus, predation cannot be excluded.

When birds are involved, it can be even more difficult to decide, whether they were consumed as carrion or predated. When dead birds become seasonally available, wild boar have been reported to scavenge on bird carrion (Cellina 2008; Ballari et al. 2015). Other studies, however, describe wild boar as predators of birds and their nests (Briedermann 1990; Saniga 2002; Экономов 2016; Giménez-Anaya et al. 2008). In this study, wild boar probably acted as a predator in most cases of bird consumption. Firstly, the period of sample collection (spring and early summer) coincides with the period when eggs and chicks of ground-nesting birds become available. Secondly, the high proportion of bird foetuses and chicks among stomach samples suggests either nest or chick predation (chapter 3.2.1). Similarly, the lack of evidence of bird consumption in the morphological analysis compared to molecular (II) suggests that the remains were digested quickly (Fournier-Chambrillon et al. 1995), feathers and bones of adult birds should have been detected in the faeces. Thirdly, the species composition of consumed birds includes mainly ground-nesting birds, with the exception of one case, when an adult bird (based on morphologic evidence) of the genus Corvus (identified with the molecular method) was consumed (II). However, predation cannot be excluded even in this case, because wild boar have been observed to attack ravens at carcasses (Selva 2004). And finally, it is highly unlikely that wild boar fed on the carcasses of groundnesting birds, because they need more time than foxes or corvids (ravens and jays), also present and abundant in the study area, to locate the carrion (Selva 2004). However, because bird carcasses are small, the first scavengers to arrive will probably consume the dead birds completely.

4.4. The role of supplementary feeding sites in disease transmission

High overall host abundance (I) and concentration of wild boar around supplementary feeding sites (III) increase the contact rate of hosts and can therefore also increase the risk of parasitic helminth infections (Arneberg 2001; Arneberg 2002; Roberts et al. 2003, IV). What is more, the concentrating effect did not disappear immediately after a feeding site was abandoned by the hunters, but remained up to two years after abandonment (III). Such concentration centres together with increased host population density have previously been associated with increased risk of disease transmission (Pyziel et al. 2011; Navarro-Gonzalez et al. 2013; Sorensen et al. 2014). However, increased contact at feeding sites can also influence parasite infections directly, even if supplementary feeding has no effect on the population density of hosts (Gompper and Wright 2005). In this study, the effect of supplementary feeding was not universal for all parasites, but depended on the life-cycle of the parasite (IV).

The probability of infection and mean infection abundance of *Eimeria* sp. was primarily determined by the overall wild boar density (IV). Similarly, Popiołek et al. (2010) found that A. suum, which also has a direct life-cycle, had a higher prevalence in wild boar living in higher density. In Spain, however, directly transmitted strongyle infection depended positively on the density of supplementary feeding sites, and was unaffected by host abundance (Navarro-Gonzalez et al. 2013). Firstly, these contrasting results suggest geographic differences in the pattern of wild boar visits to feeding sites. However, although the majority of feeding in Estonia takes place in winter (summer in Spain), diet analysis shows that the wild boar in this study had visited supplementary feeding sites recently (II, chapter 3.2.1) and had, therefore, been in contact with a high-risk environment. Secondly, it is possible that the accumulation of Eimeria sp. oocysts and helminth eggs in Estonia is hindered by their limited survival in natural conditions (Larsen and Roepstorff 1999), especially since wild boar grubbing constitutes a disruptive event that can expose eggs from deeper levels of soil to the environment. Indeed, compared to previous studies (Fernandez-de-Mera et al. 2004; Gasso et al. 2015), egg counts were relatively low in this study (IV).

The probability of lungworm *Metastrongylus* sp. infection was determined by both the density of feeding sites and the density of wild boar (**IV**). However, these results must be treated with some care, because the host-density indicator used in this study (number of wild boar hunted, see also Acevedo et al. 2009; Mentaberre et al. 2014) is very strongly related to supplementary feeding. This variable probably reflects the amount of supplemental food – a factor that is both unavailable for researchers and often unknown even by the local hunters. Hunters' estimation of abundance was used as an alternative indicator of abundance, but its efficiency was relatively poor. Winter tracking index, although used in previous studies and a good indicator of abundance on a large scale (see Bobek et al. 2014; **I**, Bragina et al. 2015; Deryabina et al. 2015), is inferior to hunting bag size on the hunting district level. Because density of wild boar has had little to no effect on lungworm infection in previous studies (Acevedo et al. 2007; Popiołek et al. 2010), and the model using hunters' estimation of abundance had little weight, then it cannot be concluded that host density has more influence on lungworm infection in the Estonian wild boar population than in other studies.

Lungworm infection is acquired by consuming earthworms that have been infected with *Metastrongulus* sp. larvae. In Estonia, supplementary feeding sites are typically located in forest edges and open areas for easier access, coinciding with a higher density and biomass of earthworm than in the forest interior (Zeithaml et al. 2009). Earthworms inhabiting wild boar feeding sites have a higher infection rate with *Metastrongylus* sp. (Humbert and Henry 1989; Nagy et al. 2015). Thus, earthworms act as a reservoir of infection – when visiting wild boar defecate, lungworm eggs are excreted into the soil, consumed by earthworms, which become infected, and are later consumed by wild boar grubbing around the feeding ground. Interestingly, in Spain, where earthworm consumption is minimal due to concrete bases built at the feeders, supplementary feeder density had no role in lungworm infection (Navarro-Gonzalez et al. 2013).

4.5 Conclusions

Supplementary feeding has a strong effect on increasing wild boar abundance and can exceed the effect of climate, namely harsh winters that otherwise play an important role in wild boar mortality. This can lead to inhabiting poor environments and possibly the expansion of the natural range. In addition to the overall high abundance, supplementary feeding influences the space use of wild boar and other predators, so that locally high predation rates occur near supplementary feeding sites. This can affect ground-nesting birds in two ways. Firstly, high abundance of wild boar and other predators taking advantage of supplementary feeding will increase the overall predation risk. And secondly, because supplementary feeding sites can become predation hot-spots, birds will suffer from the decrease in the quality of potential habitat for nesting.

Although dissuasive feeding has been suggested as a means to decrease predation risk of ground-nesting birds, the results of this study do not support the practice of that method. Wild boar consumed birds and other animal matter despite having access to supplementary food. Based on literature, wild boar prefer natural food to supplemental grain and long-term feeding will evidently result in increased abundance. Incidentally, although birds can be consumed by scavenging in addition to predation, wild boar mostly acted as a predator of ground-nesting birds in this study. What is more, the molecular method for diet analysis showed that birds were consumed significantly more often than suggested by the classic morphological analysis of the faeces. This indicates that other studies, which have relied on morphology, might have strongly underestimated the role of wild boar on bird predation. Based on the results of this study, wild boar must be reckoned with in planning conservation of groundnesting birds.

The overall high abundance and concentration of wild boar near feeding sites also plays an important role in parasite infections. However, the effect of supplementary feeding depends on various life cycles of the parasites. Lungworm infection, which requires an intermediate host, is directly related to visits to permanent feeding sites, which can easily become hot-spots for acquiring an infection. This is due to a suitable habitat for the intermediate hosts – earthworms – at the feeding sites. However, for parasites with a direct life-cycle, which depend on survival in the environment, the effect of supplementary feeding was intermediated by the increased host abundance. Such indirect effects could be ameliorated by increased hunting.

SUMMARY

With a wide range that covers most of Eurasia and reaches North-Africa, and many introduced populations over the world, Eurasian wild boar is the most widespread species of the pig family. Its dependence on fluctuating energy-rich food resources (mast) has led to a reproductive strategy that promotes fast population increase in nutritionally rewarding and stable environments. Female wild boar can start breeding early, often in their first year, and adult wild boar increase their litter size in response to an abundance of food. Females have to reach a threshold body mass before breeding for the first time, but once puberty has been reached, wild boar attempt to breed every year, whatever the environmental conditions.

In the second half of the 20^{th} century, wild boar populations increased significantly – a change that has been largely associated with the continuing spread of agriculture, as well as the widespread practice of supplementary feeding, which often occurs year-round and in unlimited amounts. Currently, wild boar abundance in the native range is mostly determined by the amount of food and temperature, which can increase mortality in harsh winters and affect productivity of the environment. Predators, mostly wolf, can affect the abundance locally, but their overall influence is low, and hunting is the most important cause of mortality in addition to death from malnutrition and/or disease.

Increased abundance of wild boar can result in an intensification of humanwildlife conflicts, because wild boar can cause considerable damage to farmland and is generally considered an agricultural pest. Wild boar is a reservoir of various pathogens shared between wildlife and domestic animals and can play an important role in disease outbreaks, thus causing economic loss. However, due to its omnivorous behaviour, high population density of wild boar can also have disastrous effects on other animals, particularly ground-nesting birds, whose populations have suffered from loss of habitat as well as predation. So far, the effect of wild boar has been considered to have been minor compared to mesopredators, and the species is at best considered as an occasional nest predator. However, the proportion of animal food in wild boar diet can be underestimated due to its fast digestion rate compared to vegetal matter and consumption of bird nests can easily remain undetected.

The purpose of this thesis was to examine the effects of supplementary feeding of wild boar in an environment, where natural mast foods (acorns, hazelnuts) are scarce and harsh winters with low temperature and deep snow can have detrimental effects on wild boar. The effects of feeding on the overall wild boar abundance and small-scale changes in relative density were studied, with emphasis on potential consequences for ground-nesting birds. Additionally, because increased overall abundance of wild boar and increased contact rates at feeding sites can promote the spread of various diseases, wild boar infection with endoparasites was investigated with regards to the effects of supplementary feeding.

To achieve these aims, wild boar abundance was modelled, using various management and climate related factors as explanatory variables (I). Food items in faecal samples and stomachs were categorized based on morphology to investigate the importance of supplemental food and proportion of bird in wild boar diet (II, chapter 2.2.1). To estimate the potential error of the proportion of bird consumed by wild boar in morphologic analysis of faeces, resulting from fast digestion rate of animal matter, a newly developed molecular method was applied (II). Because supplementary feeding sites can concentrate predators of ground-nesting birds, relative predation risk was measured in the vicinity of active and abandoned feeding sites, where supplemental food was no longer provided, by using predation rates from artificial nest experiments as a proxy of relative predator abundance (III). Finally, wild boar infection with endoparasites was investigated with emphasis on the separate effects of increased overall host abundance resulting from supplementary feeding and high-risk environment in the vicinity of supplementary feeding sites acting as infection hot-spots (IV).

According to paper I, abundance was determined by two factors – winter temperature and supplementary feeding, whereas the effect of predators, habitat, and other management-related factors was minor. Supplementary feeding could even overcome the effect of harsh winters, probably acting through the highly nutritional and easily accessible supplemental food, which allows wild boar to limit their movements in deep snow. According to paper II and chapter 3.2.1, supplemental food constituted a major food category even in the warm season and its proportion was similar to natural plants. The negligible effect of predators in the models in paper I is probably a result of their low abundance and strong impact of hunting on wild boar mortality. Forest cover, which has been a key factor in other studies in determining wild boar abundance, did not have a limiting effect in this study, because nearly half of Estonia is covered with forests. Similarly low importance of agriculture is probably related to the limited time, when crops are available in summer.

In this study, ground nesting birds were predominantly consumed among vertebrates (**II**, chapter 3.2.1) and various grouse, mainly capercaillie, constituted the majority of birds identified from faeces. What is more, wild boar acted as a predator in the majority of such cases and presumed carrion consumption was a rare event. The morphological method of diet analysis failed to detect nest predation in most cases and is therefore unsuitable for detecting birds from the faeces of the omnivorous wild boar. The molecular method used in this study proved to be much more efficient in detecting birds from faeces and resulted in an estimated frequency of occurrence that was $4.5 \times$ higher than indicated by the morphological method (**II**). Thus, wild boar is an important predator of groundnesting birds and their nests and must be reckoned with, when planning conservation management of ground-nesting birds.

Intensive supplementary feeding can influence ground-nesting birds in several ways. Wild boar can increase their use of nutritionally poor habitats that they would generally avoid or use to a lesser degree, resulting in higher relative abundance in areas that are predominantly used by ground-nesting birds. Extensive supplementary feeding can contribute to the population increase and high overall abundance of wild boar (I) and other non-target species that can increase predation risk for ground-nesting birds at large. The concentration of wild boar and other predators near feeding sites (III) can result in locally increased predation risk in otherwise suitable habitat for ground-nesting birds and thus contribute to loss of habitat, which is already considered to be one of the most important causes of the declining grouse populations.

Similar effects that contribute to increased nest predation can also promote endoparasite infections in wild boar. Supplementary feeding sites acted as hotspots of lungworm *Metastrongylus* sp. infection (IV) through the concentrating effect on wild boar (III). These parasites use earthworms as intermediate hosts and supplementary feeding sites constitute a suitable habitat for earthworms, which are one of the most frequently consumed animal foods by wild boar. Thus, when wild boar infected with lungworm excrete parasite eggs at feeding sites and these are later consumed by earthworm, then infection can be transferred to other visiting wild boar, which grub for earthworm in the vicinity of these sites. Interestingly, although the effect of concentrating wild boar near supplementary feeding sites persists up to two years after feeding has been discontinued by the hunters (III), their role in the transmission of parasites with a direct life-cycle was indirect and acted through increased host abundance (IV). High overall abundance of wild boar (I) played the key role in determining both the probability and mean infection abundance with the protist *Eimeria* sp (IV). This can be caused by the limited survival of infectious life stages of parasites in the soil of supplementary feeding sites, which is frequently overturned by the visiting animals grubbing for food, thus exposing these to various environmental conditions.

In conclusion, supplementary feeding had a key role in determining wild boar abundance in Estonia. But this practice can have serious consequences for other species due to increasing the overall abundance and concentration of wild boar and other animals near feeding sites. Wild boar is a predator of groundnesting birds and grouse were targeted the most in this study. In addition to its contribution to increased predation of ground-nesting birds, supplementary feeding was shown to influence endoparasite infection in wild boar both directly and indirectly through increased abundance, and these effects should be reckoned with in wild boar management.

SUMMARY IN ESTONIAN

Metssigade lisasöötmise tagajärjed – oht maaspesitsevatele lindudele ja roll siseparasiitidega nakatumisel

Metssiga on kõige levinum liik sigalaste sugukonnast, kelle looduslikule areaalile, mis katab suurema osa Euraasiast ja ulatub isegi Põhja-Aafrikasse, lisandub hulgaliselt introdutseeritud populatsioone üle maailma. Sõltumine muutliku kättesaadavuse ja kõrge energiasisaldusega toiduallikast (tammetõrud, pähklid jm.) on kujundanud metssigadel paljunemisstrateegia, mis soosib rohke toidubaasiga stabiilses keskkonnas väga kiiret arvukuse tõusu. Noored emised võivad alustada sigimist vara, sageli juba esimesel eluaastal, ning täiskasvanud metssigadel on toidurohketel aastatel pesakonnad suuremad. Enne esmakordselt viljastumist peavad emised saavutama kindla kehamassi, kuid pärast murdeiga üritavad nad keskkonnatingimustest sõltumata osaleda sigimises igal aastal.

Metssigade arvukus tõusis XX sajandi teisel poolel oluliselt – muutus, mida on seostatud nii põllumajanduse üha jätkuva intensiivistumise kui ka laialt levinud lisasöötmisega, mis toimub tihtipeale aastaringselt ja piiramatutes kogustes. Tänapäeval piiravad metssigade arvukust nende looduslikus levilas peamiselt toidu saadavus ja madal temperatuur, mis võib suurendada suremust karmidel talvedel ja mõjutada ka keskkonna tootlikkust. Kiskjad, kellest olulisim on hunt, võivad küll paiguti metssigade arvukust reguleerida, kuid üldiselt on nende mõju nõrk ning nälgimise ja/või haiguste kõrval on küttimine kõige sagedasem surma põhjus.

Kuna põllukultuure kahjustavatesse metssigadesse suhtutakse kui põllumajandus-kahjuritesse, võivad nende arvukuse suurenemisega sageneda konfliktid inimese ja looduse vahel. Metssiga on ühtlasi reservuaar paljudele metsja koduloomadel levinud haigustele ja võib seetõttu mängida tähtsat rolli uutes haiguspuhangutes ning põhjustada seega majanduslikku kahju. Kuna metssiga on kõigesööja, võivad tema kõrge asustustihedusega kaasneda probleemid ka teistele loomadele, eriti maaspesitsevatele lindudele, kelle arvukus on oluliselt vähenenud nii elupaiga kadumise kui kiskjate rohkuse tõttu. Seni on arvatud, et metssigade mõju on keskmise kehasuurusega kiskjatega võrreldes väheoluline ja äärmisel juhul peetakse teda vaid juhuslikuks pesarüüstajaks. Kuid loomsete objektide osakaalu metssea toidus võidakse kergesti alahinnata, sest nende seedimisprotsess on kiirem kui taimsetel ning linnupesade rüüste võib ka toitumisanalüüsis kergesti märkamata jääda.

Selle doktoritöö eesmärk oli uurida metssigade lisasöötmise mõjusid keskkonnas, kus looduslikku kõrge energiasisaldusega toitu (tammetõrud, pähklid) napib ning külmadel ja lumerikastel talvedel võib suremus metssigade populatsioonis olla suur. Uuriti lisasöötmise mõju metssigade üldisele arvukusele ja ühtlasi ka metssigade suhtelise esinemissageduse muutusi söötmiskohtade vahetus läheduses, pöörates rõhku sellele, millist mõju võivad need avaldada maaspesitsevatele lindudele. Lisaks uuriti, kuidas mõjutab metssigade lisasöötmine nende nakatumist siseparasiitidega, sest metssigade üleüldiselt kõrge arvukus ja sagedasem kokkupuude liigikaaslastega söötmiskohtades võivad soodustada mitmesuguste haiguste levikut.

Nende eesmärkide saavutamiseks kasutati metssigade arvukuse modelleerimisel erinevaid ulukite majandamist ja ilmastikku kirjeldavad tegureid ja hinnati nende mõju (I). Lisasööda ja lindude osakaalu leidmiseks metssea toidus, määrati metssigade roojaproovides ja magudes leiduvad toiduobjektid morfoloogia alusel eri kategooriatesse (II, peatükk 2.2.1). Loomsete toiduobjektide kiirest seedimisest põhjustatud vea hindamiseks metssea toidus leiduvate lindude osakaalu määramisel kasutati lindude tuvastamiseks roojast uut molekulaarset meetodit ja võrreldi sel viisil saadud hinnangut lindude esinemissagedusele morfoloogilise analüüsi tulemustega (II). Kuna maaspesitsevate lindude kiskjad võivad koonduda söötmiskohtade ümbrusesse, mõõdeti suhtelist kisklusohtu nii kasutuselolevate kui endiste söötmiskohtade läheduses, kus lisasöötmist enam ei toimunud, kasutades kiskjate suhtelise arvukuse kirjeldamiseks tehispesakatsete tulemusel leitud rüüstemäärasid (III). Lõpuks uuriti ka metssigade nakatumist siseparasiitidega, pöörates tähelepanu lisasöötmise tagajärjel suurenenud lõpp-peremeeste (metssiga) arvukuse suurenemisest tuleneva mõju eristamisele söötmiskohtade kui nakatumiskeskuste toimest (IV).

Artikli I andmetel määras metssigade arvukust kaks peamist tegurit – talvine temperatuur ja lisasöötmine, kusjuures kiskjate, elupaiga ja teiste jahimajanduslike faktorite olulisus oli väike. Lisasöötmise tähtsus võis isegi ületada karmide talvede mõju – tõenäoliselt võimaldas metssigadel paksus lumes liikumist piirata suure energiasisaldusega ja kergesti kättesaadava toidu olemasolu. Artikli II ja peatüki 3.2.1 põhjal moodustas lisasööt väga olulise toidukategooria isegi soojal aastaajal ja selle esinemissagedus oli võrreldav looduslike taimedega. Kiskjate pea olematut mõju artiklis I kirjeldatud mudelites võib seletada nende madala arvukuse ja küttimise suure osakaaluga metssigade suremuses. Metsasus, mis on olnud varasemates töödes metssigade arvukuse kujunemisel määrava tähtsusega, ei piiranud selles töös nende arvukust, sest metsamaa hõlmab pea poole Eesti pindalast. Põllumajanduse sarnaselt vähene mõju on tõenäoliselt seotud suhteliselt lühikese perioodiga suvel, mil küps vili põldudel kättesaadav on.

Käesolevas töös olid linnud kõige sagedasem kategooria selgroosete toiduobjektide seas (II, peatükk 3.2.1), kusjuures kanalised, peamiselt metsis, moodustasid väljaheidetest määratud lindudest enamiku. Lisaks oli valdav osa linde söödud murdmise tulemusel ja raipesöömist esines harva. Klassikaline morfoloogiline toitumisanalüüs ei tuvastanud enamikul juhtudel pesarüüstet ja ei sobi seega omnivoorse metssea väljaheidetest lindude määramiseks. Doktoritöös kasutatud molekulaarne meetod oli lindude tuvastamisel väljaheidetest märksa efektiivsem ja hindas nende esinemissagedust $4,5 \times$ kõrgemaks kui morfoloogilise meetodi tulemused (II). Seega on metssiga maaspesitsevate lindude murdja ja pesarüüstaja ning lindude kaitsetegevuse kavandamisel tuleb sellega arvestada.

Intensiivne lisasöötmine võib mõjutada maaspesitsevaid linde mitmeti. Metssead võivad hakata kasutama toiduvaeseid elupaiku, mida nad ilma lisasöödata väldiksid või kasutaksid harvem, mistõttu võib tõusta nende suhteline esinemissagedus aladel, mida eelistavad maaspesitsevad linnud. Laialdane lisasöötmine võib soodustada metssigade (I) ja ka teiste söötmiskohti kasutavate maaspesitsevaid linde ohustavate liikide üleüldist arvukuse tõusu. Kui metssiga ja teised kiskjad koonduvad söötmiskohtade ümbrusesse (III), võib maaspesitsevatele lindudele muidu sobivas keskkonnas suureneda oht kiskja saagiks langeda ja seega väheneb sobivate elupaikade pindala – muutus, mida seostatakse juba praegu kanaliste arvukuse vähenemisega.

Sarnased tegurid, mis suurendavad pesarüüste ohtu, võivad soosida ka nakkuste levikut metssigade populatsioonis. Loomi koondava mõju tõttu (III) olid söötmiskohad muutunud kopsuussidega Metastrongylus sp. nakatumise keskusteks (IV). Nende parasiitide vaheperemehed on vihmaussid, kes kasutavad söötmiskohtade pinnast elupaigana ja moodustavad metssea poolt tarbitavatest loomsetest toiduobjektidest kõige olulisema kategooria. Seega, kui parasiitide munad satuvad kopsuussidega nakatunud metssigade väljaheidetega söötmiskohtade pinnasesse, kus need hiljem vihmausse nakatavad, võib nakkus kanduda edasi teistele metssigadele, kes söötmiskoha ümbruses tuhnides ka vihmaussidest toituvad. Kuid kuigi metssigade söötmiskohtade koondav mõju võib püsida veel kuni kaks aastat pärast söötmise lõpetamist (III), on nende roll pinnase kaudu levivate parasiitidega nakatumisel kaudne ja toimib läbi metssigade arvukuse suurenemise (IV). Metssigade kõrge arvukus (I) määras algloomaga Eimeria sp. nakatumise tõenäosuse ja nakkusintensiivsuse (IV). Seda võib seletada parasiitide nakkusohtlike elujärkude hävinemisega söötmiskohtade pinnases, mida toitu otsivad loomad pidevalt ümber pööravad, muutes need seega erinevatele keskkonnateguritele vastuvõtlikumaks.

Kokkuvõttes kandis lisasöötmine metssigade arvukuse kujundamisel Eestis põhirolli. Selle jahimajandusliku meetodi rakendamine võib põhjustada tõsiseid tagajärgi teistele liikidele nii metssigade üleüldise arvukuse suurenemise kui metssigade ja teiste loomade koondumise tõttu söötmiskohtade ümbrusesse. Metssiga on maaspesitsevate lindude murdja ja doktoritöö raames kogutud andmete põhjal langesid saagiks peamiselt kanalised. Lisaks maaspesitsevate lindude kisklusohu suurendamisele, mõjutab lisasöötmine ka metssigade nakatumist siseparasiitidega nii otseselt kui kaudselt läbi suurenenud arvukuse ning neid mõjusid tuleb metssea majandamisel arvesse võtta.

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