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EFFECTS OF SUPERABUNDANT FOOD SUPPLIES ON LARGE UNGULATES, WITH CERTAIN EMPHASIS ON WILD BOAR (SUS SCROFA)

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ABSTRACT

During recent years, supplemental feeding of wildlife has become a common management practice all over the world. Supplemental feeding is normally conducted in order to support and to be supplementary to natural forage or divert animals away from sensitive habitats, but the effects of feeding are both debated and controversial. An evaluation of the published literature on the effects of supplementary feeding large ungulates show that artificial food resources could, similar to natural foods, affect species demography and spatial behaviour, although the understanding of the ecological effects is yet very limited. The effects of supplemental feeding on reproduction could be expected to be influenced by reproductive strategy of the target species as well the timing of feeding. Additional food tends to have an in general positive influence in wild boar reproductive output. Diversionary feeding has shown low efficiency and in the scientific literature it seems to be generally accepted that crop damage is not avoided through supplementary feeding. Reviewed literature show that the mechanisms behind consumer response to pulsed resources are highly complex and there may be numerous unintentional side effects. Furthermore, there are severe management implications with this practice and there is an important trade-off between short-term benefits and long-term costs of feeding.

1. INTRODUCTION

The spatial behaviour of an animal is influenced by a range of decisions, many of which can be explained by the optimal foraging theory (MacArthur and Pianka 1966). In the absence of predation risk, the highest quality habitat should be selected as animals are expected to maximize net benefit in terms of resource allocation. The sum of cost and benefits depend on species, and a behaviour will be favoured only when its benefits outweigh its costs (Barnard 2004, Krebs and Davies 1993). The optimal foraging strategy for a species will be that which maximizes net energy intake, but as predation risk may influence habitat use the net intake might be reduced when including the risk of foraging. There is often a trade-off between security and food. Consequently, the observed foraging behaviour is a result of decisions made by individual animals as they search for food or other limiting resources. The food intake must be balanced to fulfil two goals; to gain enough energy to support growth, development, and reproduction and to gain the right nutrients. In addition to the optimal foraging theory, the central-place foraging theory also predicts space use and foraging decisions as a function of the distance from a focal point (Orians and Pearson 1979, Schoener 1979). The focal point is typically a nest or a den, but any key resource that acts as an attraction point may give rise to a space-use pattern resembling central-place foraging (Rosenberg and McKelvey 1999).

Foraging efficiency and availability of food resources have a major influence on activity patterns. Variation in food availability influences movement and habitat selection in numerous wildlife species (Krebs and Davies 1993) and is considered a primary factor in herbivore space use (McLoughlin and Ferguson 2000, Tufto et al. 1996). Food choice is in ungulates constrained by for example nutrient need, digestive limits and energy limits

(Krebs and Davies 1993). Foraging theory predicts that confined food resources, natural or artificial, may act as attraction points and give rise to a space-use pattern resembling central-place foraging. The expected behaviour from a central-place forager is a declining usage of locations with increasing distance from the focal point. Home range size is predicted to decrease with forage abundance (Ford 1983) and is a key trait with important implications for ecological processes as well as in population management.

Ungulates are generally increasing across Europe (Apollonio et al. 2010, Massei et al. 2015). With several species showing rapid population growths we face potentially large habitat and biodiversity impacts, resulting in increasing conflicts of land use. During recent years, supplemental feeding of wildlife has become a common management practice all over the world. Supplemental feeding is normally conducted in order to support and to be supplementary to natural forage or divert animals away from sensitive habitats or from certain areas, but the effects of feeding are both debated and controversial. It has been suggested to lead to both positive and negative effects on animals, their surroundings and human activities. Feeding has also been suggested to have similar effects as naturally occurring superabundant food resources such as forest mast seeding, offering abundant high-quality food resources all year round. Understanding the responses and adaptations of consumers to pulsed resources is essential for an effective management of these species.

OBJECTIVES AND QUESTIONS

The objectives of this review are to define superabundance (natural and artificial) and summarize existing research on the effects of superabundant food supplies on species abundance (reproduction and survival) and spatial behaviour with certain emphasis on ungulates. This essay will further review the available literature to evaluate the effects of artificial feeding on abundance (reproduction and survival) and spatial behaviour (including damage prevention) in ungulate species to identify prevailing knowledge gaps.

Questions:
1. How do superabundant food supplies alter species abundance (reproduction and survival) and spatial behaviour?
2. What empirical evidence can be found in the published literature on prevailing assumptions of artificial feeding effects?

2. METHODS

This essay describes the dynamics and causes of a number of different superabundant food resources as well as its effects on species abundance and animal spatial behaviour. When reviewing the effects, the emphasis focus on wild ungulates and particularly wild boar (*Sus scrofa*). Included studies were found mainly through database search but also by looking up original references in review articles and adding relevant papers cited in key articles on the subject. For chapter *4.3. Effects of artificial feeding,* a separate systematic review was conducted. The following methods describe this part of the essay.

I reviewed articles in the peer-reviewed literature that provided empirical evidence of the effects of feeding ungulates. Articles were identified through a search in Web of Science (Web of Science Core Collection) and manually evaluated for inclusion. The search terms were TOPIC: (supplement* OR diversion* OR artificial*) AND TOPIC: (feed* OR

forage*) and results were refined by: TOPIC: ("red deer" OR "roe deer" OR "fallow deer" OR "wild boar” OR moose OR ungulate) AND TOPIC: (survival OR "body condition" OR "body weight" OR reproduct* OR fertility OR "spatial ecology" OR movement OR damage) AND DOCUMENT TYPES: (ARTICLE). Timespan: 1990-2019.
All articles were manually screened and evaluated for inclusion at three levels: 1. Title, 2. Abstract, 3. Full text.
In order to be included, each article had to pass each of the following criteria:

Relevant type of study: Primary field studies (modelling studies and reviews excluded).

Relevant type of outcome:
Effects of feeding on body weight and condition.
Effects of feeding on winter survival.
Effects of feeding on fertility or reproductive output.
Effects of feeding on spatial ecology (movement, habitat use).
Effects of feeding on habitat damage prevention.

Language: Full text written in English.

Only studies on ungulate species occurring wild in Sweden were included (reindeer excluded) for the review to be relevant to Scandinavian conditions. However, this does not mean that the review is limited to Scandinavian literature.

34 articles were included for full-text reading (based on title and abstract), 12 articles were excluded after reading full-text, resulting in a total of 22 articles included for final review.

3. SUPERABUNDANT FOOD SUPPLIES

3.1. What is a superabundant food supply?

Superabundant, or pulsed, food resources can be explained by a temporary availability of dramatically higher than normal levels of resources which then become quickly depleted with time (Ostfeld and Keesing 2000). Such extreme resource abundance often results in an extraordinary flush of nutritious foods for consumers. Today, many wildlife populations are completely dependent on superabundant food supplies and these occurrences may have impacts on population dynamics of consumer species. Superabundant food resources can be divided into natural or anthropogenic/artificial. One of the most common natural superabundant food resources is forest mast seeding, meaning the recurrent and synchronous production of large seed crops by plant populations (Janzen 1976, Silvertown 1980). Other examples include periodic irruptions of insects or wind-induced transport of marine resources to terrestrial systems, e.g. Schlacher et al. (2013). The extent of pulsed food resources may also be strongly influenced or enhanced by climatic factors such as periodically heavy rains. This review gives particular emphasis to the natural food resource mast seeding. In the modern agricultural landscape, the most common artificial (and unintentional) superabundant food resource is agricultural crops. During a limited time when crops are ripe, these areas offer easily accessible and energy-rich food to a variety of animal communities.

3.2. Causes of superabundant food supplies

Many forest tree populations produce seed crops synchronously at irregular intervals. This large-scale phenomenon occurs in the northern hemisphere (Piovesan and Adams 2001) and tends to occur more frequently with time (Övergaard 2012). It has shown to be related to climate events (Cutini et al. 2015, Piovesan and Adams 2001, Övergaard 2012). The causes of masting events are poorly known and many explanations have been suggested, although most common theories hypothesize that masting by trees is a defensive strategy by predator satiation or a behaviour to improve pollination (Kelly 1994, Silvertown 1980).

3.3. Effects of superabundant food supplies

Effects on demographic factors

The relationships between food, growth and reproduction is important for assessing the regulation of population dynamics. Population growth rate is strongly dependent on age at first reproduction, litter size and (winter) survival early in life. In turn, reproductive rate is dependent on the availability of energy-rich food. The species most likely to respond to pulsed resources are trophic generalists as they can be supported by non-pulsed resources during other periods. As most Nordic ungulates are income breeders (sensu Jönsson 1997), adjusting food intake concurrently with breeding, they respond directly to and show large population fluctuations because of resource variation. Hence, these populations are strongly influenced by the spatial distribution and seasonal variation of resource availability (Tufto et al. 1996). The wild boar, however, is a capital breeder using energy stores built up before reproduction to breed and could therefore, at least in theory, be expected to respond differently to temporal resource variation.

Forest mast seeding is a known key food resource for numerous small mammal and bird communities (Clotfelter et al. 2007). The effects of mast seeding on ungulate foraging is less documented (with a few exceptions), although several studies show that acorns, beech and chestnuts form a significant portion of the diet of different ungulate species when available (white-tailed deer: McCullough 1985, Harlow et al. 1975, McShea and Schwede 1993, wild boar: Bieber and Ruf 2005, Massei et al. 1996, Schley and Roper 2003). Most of the published literature describing the influence of mast seeding on reproduction and survival is concentrated on the wild boar. Little is available on other ungulate species but a few publications describe the effects of acorn mast availability on white-tailed deer (Odocoileus virginianus) and roe deer (Capreolus capreolus). Feldhamer et al. (1989) and Wentworth et al. (1992) found that birth weight and fawn survival in white-tailed deer in deciduous hardwood forests were positively related with the abundance of previous year's hard-mast crops. Similarly, favourable mast conditions enhanced body mass in roe deer with heavier fawns after mast years (Kjellander 2000, Kjellander et al. 2005) and in mast richer habitat (Pettorelli et al. 2001). In contrast, Campbell and Wood (2013) found that annual fluctuations in oak mast had no influence on body weights of fawn and yearling in white-tailed deer.

The wild boar is omnivorous, although plant matter comprises the majority of their diet (Schley and Roper 2003). Additionally, it is an opportunistic species, feeding on a variety of plants and animals depending on availability, meaning that wild boar can take great advantage of superabundant food supplies. Wild boar shows intense responses to food pulses, e.g. Bieber and Ruf (2005), Cutini et al. (2013), Geisser and Reyer (2005), Massei et al. (1996) and several studies have showed a clear association between beech or acorn crop availability and population growth rates in central European wild boar populations (Feichtner 1998, Massei et al. 1996, Jędrzejewska et al. 1997, Okarma et al. 1995). Under good conditions, wild boar juveniles have an extensive potential to gain weight and advance puberty as this seem to depend more on weight than on actual age (Briedermann 1990, Fernández-Llario and Mateos-Quesada 1998, Malmsten and Dalin 2016). Several studies have reported a relationship between mast occurrence and mean body weight in the wild boar (Groot Bruinderink et al. 1994, Massei et al. 1996). Correspondingly, tree mast is typically followed by high rates of reproduction (Briedermann 1990, Andrzejewski and Jezierski 1978, Jędrzejewska et al. 1997, Groot Bruinderink et al. 1994, Massei et al. 1996). Cutini et al. (2013) evaluated the interaction between mast seeding and wild boar in the Mediterranean region and found that mast seeding positively affected piglet density. Similarly, Massei et al. (1996) found that high production of acorns resulted in more breeding females and larger litter sizes. In addition, high seed production has shown to positively affect winter survival (Okarma et al. 1995, Jędrzejewska et al. 1997, Feichtner 1998). Bieber and Ruf (2005) concluded that a future increase in the frequency of full mast years would likely lead to a rapid acceleration of population growth in wild boar. Also, population dynamics of a related suid, the bearded pig (Sus barbatus), is known to be strongly affected by tree seeding with high fruit supplies causing population eruptions (Hancock et al. 2005). Few studies are available on the direct effects of agricultural crop diet on ungulate population densities but Geisser and Reyer (2005) reported a wild boar population increase correlated with an increase in the area of maize cultivation in Switzerland.

Effects on spatial behaviour

Forage availability is one of the most important factors shaping animal spatial behaviour, e.g. Mikulka et al. (2018). Bisi et al. (2018) revealed that mast seeding influences the spatial behaviour of wild boar with home range size negatively correlated to increasing resources. This is in agreement with previous studies on other ungulate species where home range sizes showed to be correlated to biomass production (elk (*Cervus elaphus*): Anderson et al. 2005, white-tailed deer: McShea and Schwede 1993, roe deer: Morellet et al. 2013, Said et al. 2009). Little is available on the effects of agricultural crop availability on ungulate spatial behaviour. However, the importance of cereals and maize in the diet of wild boar has been reported (Ballari and Barrios-García 2014, Schley and Roper 2003) and in the agricultural landscape, crops seasonally dominate the diet of the wild boar (Malmsten 2017, Mikulkla et al. 2018). It is also known that wild boar selects for agricultural fields during season when crops are ripe (Thurfjell et al. 2009).

Ecological consequences of superabundant food supplies

Pulses of heavy seed production are widespread and may have important consequences for the population dynamics of several species within an ecosystem. High seed abundance often leads to peaks in population sizes in the mast consumer species. However, population sizes respond to fluctuating resource levels with a time lag, meaning that by the time the consumer population has increased in density, pulsed resource levels have already begun to decline. This often leads to a switch to alternative resources by the consumer and thus resulting in a strongly fluctuating impact on alternative resources (Ostfeld and Keesing

2000). Furthermore, generalist predators are expected to respond to these fluctuations of mast consumers (Kjellander and Nordström 2003). Jędrzejewska and Jędrzejewski (1998) found that several mammalian and avian predators responded to prey population fluctuations of mast consumers in Bialowieza Primeval Forest. This shows that pulsed resources may also affect densities of secondary consumers.

4. ARTIFICIAL FEEDING

4.1. What is artificial feeding?

Supplementary feeding of game animals is a common practice throughout northern Europe and parts of North America. Feeding is normally associated with diverting, maintaining or increasing densities of wildlife, through: (*i*) maintaining or increasing body weights and condition overwinter; (*ii*) improving reproductive performance and fertility; (*iii*) increasing overwinter survival; and (*iv*) reducing levels of damage caused to agriculture and forestry. Artificial feeding consists of human provision of additional food for wild animals. Like mast seeding events, artificial provision of feed is offering energy-rich food during periods of normal food shortage, possibly buffering negative impact of years with poor conditions. Such a constant superabundance of food could in this sense be compared to a continuous forest mast and further argued to have similar effects.

Animals are provided additional food for different purposes, and feeding practices can thus be divided into a number of different kinds. Although the phrasing varies strongly throughout literature, the most typical types of feeding strategies used in the context of free-living ungulate species are:

- Supplementary. Food provided *ad libitum* over the whole year, often in feeding devices.
- Diversionary feeding. Prevention of environmental damage.
- Unintentional feeding (e.g. unprotected agricultural crops and garbage dumps).
- Baiting. Small quantities of food offered to attract animals for hunting. Baiting can sometimes be used also for scientific reasons, for example observing or catching animals. Baiting will not be further assessed in this essay, however, as it is considered mainly a hunting practice and likely affects the spatial behaviour of the target species for a limited time of the year.

4.2. Reasons for artificial feeding

The purpose of feeding varies from place and time, as well does the feeding practice. The feed offered varies in type, quality and amount. The type of food provided varies widely from hay and silage, root crops and corn to a variety of different commercially produced livestock forages or specially designed wildlife pellets. Intended effects of supplemental feeding (sometimes winter feeding or massive feeding) are in general to maintain or increase population size and abundance. In theory increased availability of food resources would lead to improved body condition and increased survival and reproductive rates (Bayliss and Choquenot 2002). Hence, by preventing starvation during the winter season when the availability of natural foods is low, we would expect increasing overwinter survival and maintained or increased body weights and condition overwinter. Feeding may also be designed in a diversionary way (sometimes intercept feeding or dissuasive feeding) with the purpose to attract animals away from sensitive areas to reduce environmental damage, particularly to agriculture, forestry and habitats of high conservation value, or to reduce animal-vehicle collisions. The main goals of diversionary feeding are to reduce traffic collision rate and reduce crop, forest or habitat damage by controlled spatial distribution and diet shift to provided feed. This essay will focus on the effectiveness of habitat damage prevention.

4.3. Effects of artificial feeding

In total, 22 articles were included for evaluation of the effects of feeding ungulates. Reviewed articles studied red deer (*Cervus elaphus*), roe deer, fallow deer *(Dama dama*), wild boar and moose (*Alces alces*).

In this review, 9 studies have been conducted on the effects of feeding on population size and demography and 13 studies on spatial-temporal behaviour or habitat damage prevention.

Effects on demographic factors

Reviewed studies on the effects of feeding on body weights and condition show various results. Supplemental feeding has shown to have a positive influence on body weight and other condition parameters in fallow deer (Bovolenta et al. 2013, Pavlik et al. 2018, Ru et al. 2003) and red deer (Santos et al. 2013, Schmidt and Hoi 2002), while Groot Bruinderink et al. (2000) found neither body growth rate nor weight of red deer and wild boar to be affected by supplementary feeding. Furthermore, Smith et al. (1997) found that rates of supplementary feeding had no effect on birth weight of red deer calves. The research available on effects of feeding on reproductive output mainly focuses on wild boar and Oja et al. (2014) shows that supplemental feeding contributes to an increase in population size by increased relative abundance. It has also been confirmed that feeding may under certain circumstances increase reproductive rates (Groot Bruinderink et al. 1994, Groot Bruinderink et al. 2000), but only during periods of natural resource limitation. The review included no articles on effects of feeding on winter survival.

Effects on spatial behaviour

Most of the research on effects of feeding on spatial behaviour support that supplemental feeding strongly influences ungulate spatial ecology (e.g. red deer: Arnold et al. 2018, Sánchez-Prieto et al. 2004, moose: Sahlsten et al. 2010). Many studies describe a concentrated space-use or reduced home range size with increased feeding (moose: van Beest et al. 2010, red deer: Jerina 2012, Reinecke et al. 2014, roe deer: Ossi et al. 2017). Reinecke et al. (2014) also found that feeding affected seasonal adjustments in habitat-use in red deer as individuals supplied with supplementary food during winter did not alter their home range size seasonally in contrast to individuals in areas with no or little feeding. However, other studies failed to show any strong effect of feeding on spatial behaviour (moose: van Beest et al. 2011, roe deer: Ossi et al. 2015). Evidence for effectiveness of diversionary feeding in prevention of environmental damage is inconclusive, with some studies showing a decrease in damage caused (red deer and roe deer: Borowski et al. 2019, wild boar: Calenge et al. 2004) and others showing no effect (moose: van Beest et al. 2010, Gundersen et al. 2004, wild boar: Geisser and Reyer 2004). Additionally, some studies show that feeding can be effective in redistributing animals and mediating habitat selection

(Arnold et al. 2018, Sahlsten et al. 2010) although not testing for the direct effects on damage prevention. The reviewed literature indicates that there is a lack of a clear relationship between the diversionary feeding of ungulates and the reduction of damage caused by them.

5. DISCUSSION

Although controversial, supplemental feeding is applied to varying extent throughout Europe and parts of North America. Its effects are debated and most of the research available on this subject describes the level of influence rather than actual effects.

The effects of artificial feeding are often argued to be similar to those of naturally occurring superabundant food supplies, such as forest mast. However, the effects of mast seeding on ungulate demographics and spatial behaviour is scarcely documented in other ungulate species than wild boar and is not particularly conclusive. More species are represented within reviewed articles on effects of artificial feeding, although with ambiguous results. The fact that the scientific results on the subject are so inconclusive makes it difficult not only to evaluate the consequences but also to compare responses to natural food supplies with those of anthropogenic origin. For the specific case of wild boar, however, effects of high natural food availability and the availability of supplementary feed seem to align relatively well.

Effects on demographic factors

Food conditions are known to be important factors for the population dynamics of many ungulate species and may influence demography in several ways. Firstly, favourable conditions can reduce juvenile mortality, allowing juveniles to reach the minimal body weight until autumn that is necessary to survive the cold winter months, and secondly, food availability strongly affects reproductive output and age at first reproduction. Very few publications available describes the effects of additional food (both from naturally pulsed resources or by human provision) on the demographic parameters body weight, condition and overwinter survival in ungulates. The effects on reproductive output and fertility seem to be better explored although these studies have concentrated primarily on wild boar. Numerous studies show that this species exhibits strong responses to food pulses and the importance of high food availability for reproductive output in wild boar is evident. Compared to other wild ungulates of similar body size, the wild boar has a high reproductive capacity where large litter sizes and puberty at an early age are considered important factors contributing to the high reproductive potential (Malmsten et al. 2017, Mauget 1982, Servanty et al. 2007). The onset of sexual maturity in wild boar females strongly depends on resource availability (Pépin and Mauget 1989, Malmsten and Dalin 2016) and additional food, in particular, is likely to boost reproductive success through younger age at first reproduction and earlier onset of oestrus (Andrzejewski and Jezierski 1978, Briedermann 1990, Geisser and Reyer 2005, Saether 1997). Additionally, wild boar females in good condition and with access to high food supply tend to have larger litter sizes (Fernández-Llario and Mateos-Quesada 1998, Massei et al. 1996, Servanty et al. 2007). When discussing the influence of food conditions on reproductive output, it is important to consider the alternative strategies of resource use in reproduction (capital and income breeding sensu Jönsson 1997) as it may be of great importance for species population dynamics. There is clear evidence that tree mast has a very strong influence on wild boar reproductive output. Also, artificial feeding tends to have an in general positive influence on wild boar reproduction, but these results are more disperse and there is no consensus on the effects of natural versus artificial supply of food. This could be argued to be due to the timing of feeding as there are certain key periods during the wild boar reproduction cycle when food abundance could be expected to be especially important. The main tree mast crop is available during autumn which is not only a crucial time for the wild boar to build up fat reserves before winter but also the start of the main wild boar oestrus period (Figure 1).

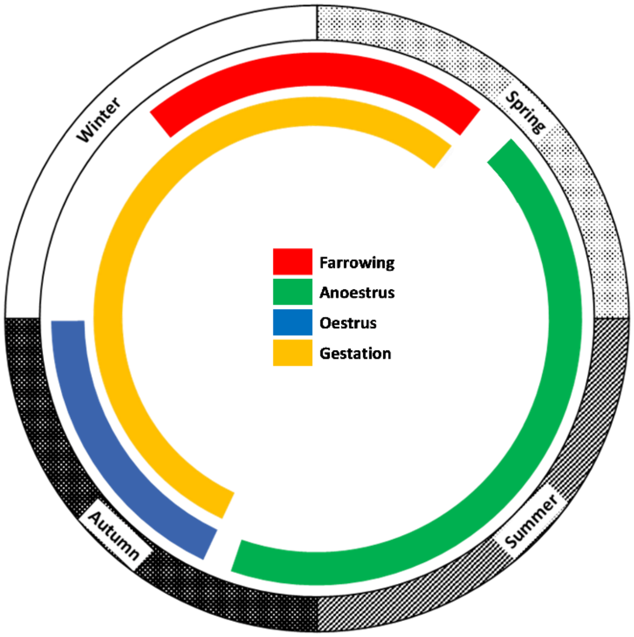

Figure 1. The wild boar seasonal reproductive pattern, adapted from Malmsten et al. (2017) and Mauget (1982).

Additional food during this time offers a nutritional flush at a critical period for a capital breeder and thus enabling an improved reproductive output. Supplemental feed during other seasons may provide less additional resource advantages and could possibly explain the inconsistency among results on the subject. However, it has been suggested that the onset of the wild boar breeding season is related to the level of available food in that a high access to food can cause a shortened anoestrus period (Sabrina et al. 2009) and that human food provision may offset the naturally occurring seasonal pattern. Hence, this question remains to be unravelled. Very few studies were found on the effects of additional food (both of natural and anthropogenic origin) on reproductive output in other ungulate species, making it hard to evaluate any principal demographic responses further.

There are no clear conclusions regarding the demographic consequences of feeding large ungulates. Also, other reviews on this topic show various results. For example, Putman and Staines (2004) reported relatively little effect of feeding on body weight, survival as well as reproduction in red deer while a more recent review by Milner et al. (2014) found strong evidence that supplementary feeding enhanced reproduction and population growth in wild ungulates under certain conditions. Supplementary feeding could provide an important artificial food supply during periods of natural food shortage. Likewise, agricultural crops could theoretically buffer the negative impact of years with poor conditions, as would be the case with natural food conditions. But the availability of natural feed in Scandinavia is generally very high and the summer months, when agricultural crops are available, are holding particularly favourable environmental conditions with a long vegetation period and rarely extensive drought. Moreover, during the summer months, the majority of ungulate females are anoestral (Asher 2011, Mauget 1982, Malmsten et al. 2014, Malmsten et al. 2017) why agricultural crops could be expected to have limited influence on reproductive output. Overall, supplemental feeding is likely to contribute to increases in ungulate population densities merely during periods of natural food shortage (autumn and winter months) when such a resource provision may contribute by improved survival, and in terms of reproduction mainly during key reproductive stages such as beginning of oestrous.

Effects on spatial behaviour and effectiveness in environmental damage prevention

The effects of pulsed food resources on spatial ecology have been variously evaluated among wild ungulates with some species more represented than others in the published literature. However, there is strong evidence that the provision of additional forage at focal points in the landscape can alter the animal distribution and natural foraging behaviour, regardless of species. The general consequence is a concentrated space-use or reduced home range size. The fact that feeding stations restrict space-use this way suggests that these sites can be resembled as a central-place attraction point and further that basic foraging theories could be a useful tool when predicting habitat selection patterns for ungulate species using feeding sites.

Although the research available shows that both natural and artificial superabundant food supplies may strongly influence the spatial behaviour among ungulate species, this review found possible consequences of diversionary feeding to be scarcely documented or with low effectiveness. Other reviews on this topic show similar results, e.g. Milner et al. (2014), Putman and Staines (2004). Even though the diversionary methods may work locally or distract animals temporarily (Andrzejewski and Jezierski 1978), they do not help to solve the problem in the long-term. It may, in fact, be counterproductive and increase future damage to farmland as abundant food supply can enhance population growth through improved survival and reproductive output (Geisser and Reyer 2004, Geisser and Reyer 2005, Groot Bruinderink et al. 1994). The effectiveness of diversionary feeding also seems to be influenced by feed type in relation to the grazing or browsing strategy of the target species (Milner et al. 2014), which further highlights the complexity of this issue.

Unintentional side effects

Supplementary feeding can also have a number of unintended side effects with ecological implications. Many studies report an increase in browsing intensity on natural vegetation adjacent to supplemental feeding sites (as a consequence of the redistribution of animals in the landscape and increased density at these sites), e.g. Garrido et al. (2014), Gundersen et al. (2004), Sahlsten et al. (2010) and van Beest et al. (2010). In this sense, feeding is here creating a problem that it is in other places intended to prevent. Other studies show that feeding stations may have an impact on non-target species, e.g. Pedersen et al. (2014). Other trophic levels may be affected, causing cascading effects where secondary consequences are triggered by the impact of one or several key species in the ecosystem. Moreover, spatial aggregations and increased contact rates around feeding sites may create situations favourable to the spread of directly transmitted diseases and parasites within populations or between different species that utilize the same feeding sites (Milner et al. 2014). However, these aspects were not further evaluated in this essay as it was not within the scope of the objectives.

Conclusions and future research

Many pulsed resources occur naturally and similarly to natural foods, artificial food resources can affect species demography and spatial behaviour. The understanding of the ecological effects of supplementary feeding of wildlife, both effectiveness of intended effects and risk of unintended effects, is very limited. Effects of artificial feeding are caused by many different factors of which the relative importance differs between species and study systems, making them hard to predict. The effects of supplemental feeding on reproduction could be expected to be influenced by reproductive strategies of the target species as well the timing of feeding. Diversionary feeding has shown low efficiency and in the scientific literature, it seems to be generally accepted that crop damage is not avoided through supplementary feeding. It may instead be counterproductive through a positive effect on population growth. Hence, there is an important trade-off between short-term benefits and long-term costs of feeding. Additionally, many authors point out the complexity of supplemental feeding on species ecology and severe management implications with this practice. There may be numerous unexpected consequences, not only on the target species but also on other trophic levels. Considering that supplemental feeding is mainly intended to compensate for scarcity of resources in winter, it may also be important to evaluate the role of supplemental feeding in light of climate change. A future with less winter severity may reduce the need for supplemental food to prevent starvation.

Understanding the responses and adaptations of consumers to pulsed resources is essential for an effective management practice. The mechanisms behind are highly diverse and complex why there is a need for a more mechanistic insight to better understand obtained responses. Another useful contribution would be to further investigate the role of additional food in the onset of the breeding season in wild boar for a better understanding of its effect on population dynamics of this species. Improvements can also be done in unintentional side effects of feeding and particularly the impacts of feeding sites on non-target species.

LITERATURE LIST

Anderson D.P., Forester J.D., Turner M.G., Frair J.L., Merrill E.H., Fortin D., Mao J.S. and Boyce M.S. 2005. Factors influencing female home range sizes in elk (Cervus elaphus) in North American landscapes. Landscape Ecology 20: 257–271

Andrzejewski R. and Jezierski W. 1978. Management of a wild boar population and its effects on commercial land, Acta theriologica 23, 19: 309–339

Arnold J.M., Gerhardt P., Steyaert S.M.J.G. and Hochbichler E. 2018. Diversionary feeding can reduce red deer habitat selection pressure on vulnerable forest stands, but is not a panacea for red deer damage. Forest Ecology and Management 407: 166-173.

Asher G.W. 2011. Reproductive cycles of deer. Animal Reproduction Science 124: 170–175

Bayliss P. and Choquenot D. 2002. The numerical response: Rate of increase and food limitation in herbivores and predators. Philosophical transactions of the Royal Society of London. Series B, Biological sciences. 357. 1233–48

Barnard C. 2004. Animal Behaviour: mechanism, development, function and evolution. Pearson, Prentice Hall, Harlow

van Beest F.M., Gundersen H., Mathisen K.M., Milner J.M. and Skarpe C. 2010. Long-term browsing impact around diversionary feeding stations for moose in Southern Norway. Forest Ecology and Management 259: 1900–1911

van Beest F.M., Rivrun I.M., Loe, L.E., Milner J.M. and Mysterud, A. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? Journal of Animal Ecology 80:771-785

Bieber C. and Ruf T. 2005. Population dynamics in wild boar Sus scrofa: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. Journal of Applied Ecology 42: 1203–1213

Bisi F., Chirichella R., Chianucci F., Von Hardenberg J., Cutini A., Martinoli A. and Apollonio M. 2018. Climate, tree masting and spatial behaviour in wild boar (Sus scrofa L.): insight from a long-term study. Annals of Forest Science 75:46

Borowski Z., Balazy R., Ciesielski M. and Korzeniewski K. 2019. Does winter supplementary feeding affect deer damage in a forest ecosystem? A field test in areas with different levels of deer pressure. Pest Manag Sci 2019; 75: 893–899

Bovolenta et al. 2013 Bovolenta S., Corazzin M., Messina M., Focardi S. and Piasentier E. 2013. Supplementary Feeding of Farmed Fallow Deer: Effect on Milk Composition and Fawn Performance. Italian Journal of Animal Science 12:4

Calenge C., Maillard D., Fournier P. and Fouque, C. 2004. Efficiency of spreading maize in the garrigues to reduce wild boar (Sus scrofa) damage to Mediterranean vineyards. European Journal of Wildlife Research 50: 112–120

Campbell S.A.B. and Wood T.C. 2013. Influences of recipitation, temperature, and acorn mast on white-tailed deer body weight in the northern piedmont of Virginia. Northeastern Naturalist 20: 469–477

Charnov E.L. 1976. Optimal foraging: the marginal value theorem. Theoretical Population Biology 9:129–136

Clotfelter E.D., Pedersen A.B., Cranford J.A., Ram N., Snajdr E.A., Nolan V. Jr and Ketterson E.D. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. Oecologia 154: 493–503

Cutini A., Chianucci F., Chirichella R., Donaggio E., Mattioli L. and Apollonio M. 2013. Mast seeding in deciduous forests of the northern Apennines (Italy) and its influence on wild boar population dynamics. Annals of Forest Science 70: 493–502

Feldhamer G.A., Kilbane T.P. and Sharp D.W. 1989. Cumulative effect of winter on acorn yield and deer body weight. The Journal of Wildlife Management 53: 292–295

Fernández-Llario P. and Mateos-Quesada P. 1998. Body size and reproductive parameters in the wild boar Sus scrofa. Acta Theriologica 43: 439–444

Ford R.G. 1983. Home range in a patchy environment: optimal foraging predictions. American Zoologist 23: 315–326

Jędrzejewska B., Jędrzejewski W., Bunevich A.N., Miikowski L. and Krasiński Z.A. 1997. Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. Acta Theriologica 42: 399–451

Garrido P., Lindqvist S. and Kjellander P. 2014. Natural forage composition decreases deer browsing on Picea abies around supplemental feeding sites. Scandinavian Journal of Forest Research. DOI:10.1080/02827581.2014.903993

Geisser H. and Reyer H.U. 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. Journal of Wildlife Management 68: 939–946

Geisser H. and Reyer H.U. 2005. The influence of food and temperature on population density of wild boar Sus scrofa in the Thurgau (Switzerland). Journal of Zoology 267: 89–96

Groot Bruinderink G.W.T.A., Hazebroek E. and Van der Voot A. 1994. Diet and condition of wild boar, Sus scrofa scrofa, without supplementary feeding. Journal of Zoology 233: 631–648

Groot Bruinderink G.W.T.A., Lammertsma D.R. and Hazebroek E. 2000. Effects of cessation of supplemental feeding on mineral status of red deer Cervus elaphus and wild boar Sus scrofa in the Netherlands. Acta Theriologica 45: 71–85

Gundersen H., Andreassen H.P. and Storaas T. 2004: Supplemental feeding of migratory moose Alces alces: forest damage at two spatial scales. Wildlife Biology 10: 213-223

Hancock P.A., Milner-Gulland E.J. and Keeling M.J. 2005. An individual based model of bearded pig abundance. Ecological Modelling, 181: 123–137

Harlow R.F, Whelan J.B., Crawford H.S., and Skeen J.E. 1975. Deer foods during years of oak mast abundance and scarcity. The Journal of Wildlife Management 39: 330–336

Janzen D.H. 1976. Why bamboos wait so long to flower. Annual Review of Ecology and Systematics 7: 347–391

Jędrzejewska B. and Jędrzejewski W. 1998. Predation in vertebrate communities. The Bialowieza Primeval Forest as a case study. Ecological studies, Springer 135: 1–450

Jędrzejewska B., Jędrzejewski W., Bunevich A.N., Miikowski L. and Krasiński Z.A. 1997. Factors shaping population densities and increaseretes of ungulates in Bialowieza Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. Acta Theriologica 42: 399–451

Jerina K. 2012 Roads and supplemental feeding affect home-range size of Slovenian red deer more than natural factors. Journal of Mammalogy 93: 1139–1148

Jönsson K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78: 57–66

Kelly D. 1994. The evolutionary ecology of mast seeding. Trends in Ecology and Evolution 9: 465–470

Krebs J.R. and Davies N.B. 1993. An Introduction to Behavioural Ecology. 3rd ed. Oxford, Blackwell.

Kjellander P. 2000. Density dependence in roe deer population dynamics. PhD Thesis. Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Uppsala. Silvestria 154.

Kjellander P. and Nordström J. 2003. Cyclic voles prey switching in red fox and roe deer dynamics – a test of the alternative prey hypothesis. Oikos 101: 338–344

Kjellander P., Gaillard J.M. and Hewison A.J.M. 2005. Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. Oecologia 146:521–530

MacArthur R.H. and Pianka E.R. 1966. On Optimal Use of a Patchy Environment. American Naturalist 100: 603–609

Malmsten, A. 2017. On the reproduction of female wild boar (Sus scrofa) in Sweden. Doctoral thesis. Swedish University of Agricultural Sciences

Malmsten A. and Dalin A.M. 2016. Puberty in female wild boar (Sus scrofa) in Sweden. Acta Veterinaria Scandinavica, 58:55

Malmsten A., Jansson G., Lundeheim N. and Dalin A.M. 2017. The reproductive pattern and potential of free ranging female wild boars (Sus scrofa) in Sweden. Acta Veterinaria Scandinavica, 59:52

Malmsten J. Söderquist, Thulin C.G., Gavier Widén D., Yon L. and Dalin A.M. 2014. Reproductive characteristics in female Swedish moose (Alces alces), with emphasis on puberty, timing of estrus, and mating. Acta Veterinaria Scandinavica 56: 1–10

Massei G., Genov P.V. and Staines B.W. 1996. Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. Acta Theriologica 41: 307–320

Massei G., Kindberg J., Licoppe A., Gacic D., Sprem N., Kamler J., Baubet E., Hohmann U., Monaco A. Ozolins J., Cellina S., Podgórski T., Fonseca C., Markov N., Pokorny B., Rosell C. and Náhlik A. 2015. Wild boar populations up, numbers of hunters down? A review trends and implications for Europe. Pest Management Science 71: 492–500

Mauget R. 1982. Seasonality of reproduction in the wild boar. Control of Pig Reproduction (eds D.J.A. Cole & G.R. Foxcroft), pp. 509–526. Butterworths, London.

McCullough D.R. 1985. Variables influencing food habits of white-tailed deer on the George Reserve. Journal of Mammalogy 66: 682–692

McShea W.J. and Schwede G. 1993. Variable acorn crops: responses of white-tailed deer and other mast consumers. Journal of Mammology 74: 999–1006

Milner J.M., van Beest F.M., Schmidt K.T., Brook R.K. and Storaas T. 2014. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. Journal of Wildlife Management 78: 1322–1334

Morellet N., Bonenfant C., Borger L., Ossi F., Cagnacci F., Heurich M., Kjellander P., Linnell J.D.C., Nicoloso S., Sustr P., Urban F. and Mysterud A. 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. Journal of Animal Ecology 82: 1326–1339

Oja R., Kaasik A. and Valdmann H. 2014. Winter severity or supplementary feeding—which matters more for wild boar? Acta Theriologica 59: 553–559

Okarma H., Jędrzejewska B., Jędrzejewski W., Krasiński Z. and Milkowski L. 1995. The roles of predation, snow cover, acorn crop, and man-related factors on ungulate mortality in Białowieża Primeval Forest, Poland. Acta Theriologica 40: 197–217

Orians G.H. and Pearson N.E. 1979. On the theory of central place foraging. In: Horn D J, Stairs GR, Mitchell RD (eds) Analysis of ecological systems. Ohio State University Press, Columbus, OH, pp. 155–177

Ostfeld R.S. and Keesing F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Tree 15: 232-237

Ossi F., Gaillard J.M., Hebblewhite M. and Cagnacci F. 2015. Snow sinking depth and forest canopy drive winter resource selection more than supplemental feeding in an alpine population of roe deer. European Journal of Wildlife Research 61:111–124

Ossi F., Gaillard J.M., Hebblewhite M., Morellet N., Ranc N., Sandfort R., Kroeschel M., Kjellander P., Mysterud A., Linnell J.D.C., Heurich M., Soennichsen L., Sustr P., Berger A., Rocca M, Urbano F. and Cagnacci F. 2017. Plastic response by a small cervid to supplemental feeding in winter across a wide environmental gradient. Ecosphere 8(1): e01629

Övergaard R. 2012. Seed production and natural regeneration of beech (Fagus sylvatica) in southern Sweden. Doctoral thesis. Swedish University of Agricultural Sciences.

Pavlik A., Slama P., Bures D. and Kotrba R. 2018. Effect of feeding on growth and blood biochemistry of male fallow deer. Journal of Microbiology, Biotechnology and Food Sciences: 8: 911–913

Pedersen S., Mathisen K.M., Gorini L., Andreassen H.P., Røskaft E. and Skarpe C. 2014. Small mammal responses to moose supplementary winter feeding. European Journal of Wildlife Research 60: 527–534

Pépin D. and Mauget R. 1989. The effect of planes of nutrition on growth and attainment of puberty in female wild boars raised in captivity. Animal Reproduction Science 20: 71–77

Pettorelli N., Gaillard J.M., Duncan P., Oullet J.P. and Van Laer G. 2001. Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. Oecologia 128: 400–405

Piovesan G. and Adams J.M. 2001. Masting behaviour in beech: linking reproduction and climatic variation. Canadian Journal of Botany 79: 1039–1047

Putman R.J. and Staines B.W. 2004. Supplementary winter feeding of wild red deer Cervus elaphus in Europe and North America: justifications, feeding practice and effectiveness. Mammal Review 34: 285–306

Reinecke H., Leinen L., Thißen I., Meißner M., Herzog S., Schütz S. and Kiffner C. 2014. Home range size estimates of red deer in Germany: environmental, individual and methodological correlates. European Journal of Wildlife Research 60: 237–247

Rosenberg D.K. and McKelvey K.S. 1999. Estimation of habitat selection for central-place foraging animals. Journal Wildlife Management 63: 1028–1038

Ru Y.J., Fisher M., Glatz P.C., Wyatt S., Swanson K., Falkenberg S. 2003. Forage intake and nutrient requirements of fallow weaner deer in southern Australia. Asian-Australasian Journal of Animal Science 16: 685–92.

Sabrina S, Gaillard J.M. Toı¨go C., Brandt S. and Baubet E. 2009. Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. Journal of Animal Ecology 78: 1278–1290

Saether B.E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution 12: 143–149.

Sahlsten J. Bunnefeld N, Månsson J., Ericsson G., Bergström R. and Dettki H. 2010. Can supplementary feeding be used to redistribute moose Alces alces? Wildlife Biology 16: 85–92

Sánchez-Prieto C.B., Carranza J. and Pulido F.J. 2004. Reproductive behavior in female Ibearian red deer: effects of aggregation and dispersion of food. Journal of Mammalogy 85: 761–767

Santos J.P.V., Fernandez-de-Meraa I.G., Acevedod P., Boadellaa M., Fierroa Y. , Vicentea J. and Gortazar C. 2013 Optimizing the sampling effort to evaluate body condition in ungulates: A case study on red deer. Ecological Indicators 30: 65–71

Said S., Gaillard J.M., Widmer O., Débias F., Bourgoin G., Delorme D. and Roux C. 2009. What shapes intra-specific variation in home range size? A case study of female roe deer. Oikos 118: 1299–1306.

Schley L. and Roper T.J. 2003. Diet of wild boar Sus scrofa in Western Europe, with particular reference to consumption of agricultural crops. Mammal Review 33: 43-56

Schmidt K.T. and Hoi H. 2002.Supplemental feeding reduces natural selection in juvenile red deer. Ecography 25: 265–272

Servanty S, Gaillard J.M, Allaine´ D., Brandt S. and Baubet E. 2007. Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. Behav Ecol 18: 427–432

Schlacher T.A, Strydom S. and Connolly R.M. 2013. Multiple scavengers respond rapidly to pulsed carrion resources at the land-ocean interface. Acta Oecologica 48: 7–12.

Schoener T.W. 1979. Generality of the size-distance relation in models of optimal feeding. American Naturalist 114: 902–914

Silverton J.W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society 14: 235–50

Smith B.L., Robbins R.L. and Anderson S.H. 1997. Early development of supplementally fed, free-ranging elk. The Journal of Wildlife Management 61: 26–38

Thurfjell H., Ball J.P., Åhlén P.A., Kornacher P., Dettki H. and Sjöberh K. 2009. Habitat use and spatial patterns of wild boar Sus scrofa, (L.): agricultural fields and edges. European Journal of Wildlife Research 55: 517–523

Tufto J., Andersen R. and Linnell J. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology 65: 715–724

Wentworth J.M., Johnson P.E. and Kammermeye K.E. 1992. Relationships of acorn abundance and deer herd characteristics in the Southern Appalachians. Southern Journal of Applied Forestry 16: 5–8.