Wildlife Biology 20: 326–334, 2014
doi: 10.2981/wlb.00053

Subject Editor: John Ball. Accepted 27 July 2014

How important is supplementary feed in the winter diet of red deer? A test in Hungary

Krisztián Katona, Anikó Gál-Bélteki, Attila Terhes, Kálmán Bartucz and László Szemethy

K. Katona (orcid.org/0000-0002-7300-2504)(katonak@ns.vvt.gau.hu), A. Gál-Bélteki, A. Terhes, K. Bartucz and L. Szemethy, Inst. for Wildlife Conservation, Szent István Univ., Páter Károly Street 1, HU-2100 Gödöllő, Hungary

Winter supplementary feeding is widespread in large game management. As it is very expensive, it is important to know how essential this feeding may be for populations of game like red deer *Cervus elaphus*. Game managers typically observe only the disappearance of feed, but do not measure the consumption from the perspective of the animal, so the importance of feeding programs is often uncertain. During the winter of 2007–2008 we determined the consumption by red deer of two feed types (maize silage and apple pomace which is the residue from pressing apples) commonly offered at feeding plots in Hungary in two study areas. We simultaneously utilised two complementary methods: microhistological analysis of faeces and rumen content, and macroscopic observation of natural and artificially mixed food markers. Based on our analyses, 20 to 90% of the red deer (among different dates and measures) had eaten the supplementary food. However, the proportion of supplementary food in the red deer droppings collected in the immediate surroundings of the feeding plots was always very low (< 10%). This indicates that not every individual of the red deer population visits the feeders, or if does, eats a rather small amount of the provided food. Our data strongly suggests that supplementary food did not play a large role in the diet of the red deer individuals regularly visiting these sites. We emphasise that the mere observation that supplementary food regularly vanishes from the feeder does not necessarily mean that even one individual red deer has gained a significant biological advantage which would result in additional financial profit for the game manager later. Managers considering supplementary feeding should evaluate the quality of the forest area because the natural food supply can greatly influence the use of the feeding plots.

Practical deer management requires understanding the relationship between the quantity and quality of the available food and resource use by deer in the habitat (Tremblay et al. 2004, Sahlsten et al. 2010). Although red deer *Cervus elaphus* is an intermediate feeder (Hofmann 1989) which primarily forages on browse (Gebert and Verheyden-Tixier 2001), supplementation by non-browse food is very common among game managers (Rajský et al. 2008). A part of the food requirement of game used to be satisfied by agricultural crops produced in special open fields called game fields (Točka 1983). Supplementary winter feeding by readily-available crops (e.g. corn *Zea mays*, wheat *Triticum aestivum*, oat *Avena sativa*, rye *Secale cereale*) or cheap by-products is also a widespread practice in central Europe (Csányi and Lehoczki 2010) as well as in the US (Brown and Cooper 2006, Timmons et al. 2010). Despite the popularity of supplementary feeding, there are very few direct studies of its utility or effect on wildlife populations.

According to the common opinion of Hungarian game managers (for some details see Heltay 2000, Faragó 2002), grasses, agricultural crops, crops grown in game fields, and supplementary winter feed are all considered important in the diet of red deer in Hungary. It is also a commonly-accepted idea among game managers and nature conservationists that winter feeding greatly contributes to local density increases (Sanchez-Prieto et al. 2004, Luccarini et al. 2006) and overabundance of large game (Putman and Staines 2004, Geisser and Reyer 2005, Gortázar et al. 2006). Winter feeding of red deer is generally considered as an efficient method to reduce bark stripping and browsing damage, but it has often been found to be counter-productive in preventing negative ungulate impact (Reimoser 2003, Putman and Staines 2004, Rajský et al. 2008). In small-bodied herbivores Boutin (1990) reviewed 138 food-addition experiments. He found that the typical population response to food supplementation was two- to three-fold increase in density, but no change in the pattern of population dynamics.

Our previous research on the same study areas indicates that in forest habitats and in every season, red deer feed mainly on woody plant species from the shrub layer (Mátrai and Kabai 1989, Szemethy et al. 2003, Katona et al. 2013). Furthermore, the contribution of supplementary feed to the diet was not large, only alfalfa *Medicago sativa* was found in the diet of red deer in a proportion of 10 to 20% (Mátrai et al. 2002). In spite of this, game density in the game fields may be much higher than in neighbouring forest areas, likely due to the wallows and salt stations established there in addition to the provided food (Bleier et al. 2006). In neighbouring Slovenia, Jerina (2012) also reported that supplementary feeding decreases annual home ranges of red deer much more than expected based on consumption and energetic value of supplementary food.

For a manager, provision of extra food in addition to the natural supply has significant costs (Calenge et al. 2004). Therefore, preparing a feeding management plan based on harvest requirements should consist of measuring natural food availability (Feuereisel 2005, Feuereisel and Ernst 2009) and estimating the costs of game field cultivation and artificial feeding (Kim et al. 1996, Osborn and Jenks 1998). However, many supplementary feeding programs in Hungary and elsewhere proceed without such data collection. The supplementary feeding program is often not adapted to the specific goals of local management, the size of game populations, or their requirements, and is mainly the result of management habits which are not investigated for cost-efficiency (Page and Underwood 2006, Biró et al. 2010, Csányi and Lehoczki 2010).

In this study our main aim was to determine the importance of supplementary feed in the diet of the red deer in two different areas. Based on the intensive feeding programs we hypothesised that supplementary food is the dominant component in the winter diet of red deer, and it is consumed by the majority of the individuals. In order to evaluate the possible returns of game feeding we investigated: 1) the proportion of the supplementary food compared to that of natural ones in the red deer diet and 2) the proportion of the individuals using the feeding plots and consuming supplementary feed.

Material and methods

Study areas

Part of the research was carried out at Hajósszentgyörgy (46°24′N, 19°07′E) situated between the Danube and Tisza rivers. The site of 14 600 ha is mainly a forested area located in two blocks around Hajósszentgyörgy (Table 1). The forested areas grow on extremely dry sand dunes where no natural water courses are found. The forests in the surroundings of the town of Hajós were established in the second half of the 20th century in places less suitable for agricultural use. These are mainly black locust *Robinia pseudoacacia* and pine *Pinus sylvestris* and *P. nigra* woodlands. In addition, smaller stands of poplar *Populus* spp. plantations and oak *Quercus* spp. woodlands can be found. Parallel to this, red deer came to the Hajósszentgyörgy area partly by continuous spreading from the south from the famous floodplain area of Gemenc, and partly by the introduction of animals rescued from the floods. The quality of trophies of the red deer population has been outstanding for a long time, but in recent years it has fallen somewhat. The estimated density of the red deer population within the area of the game management unit was 7.67 individuals 100 ha^{-1}; meanwhile the total ungulate density reached 17.09 individuals 100 ha^{-1} in 2007 (according to the Hungarian National Game Management Database).

The other forested area (near Valkó, 47°33′N, 19°29′E) included in our investigation is situated in the Gödöllő

Table 1. Population densities (individuals 100 ha^{-1}) of different game species calculated from the reported number of estimated and shot animals, availability of game fields and pastures (ha 100 ha^{-1}), amount of supplementary feed provided (kg/estimated ungulate individuals/year) and size of the game management unit (ha) in the two study areas in 2007. Data derives from the game management units utilizing our study areas (based on the National Game Management Database).

Species	Population density (ind. 100 ha^{-1})	Hajósszentgyörgy	Valkó
Red deer	estimated	7.67	2.44
	shot	2.59	1.14
Roe deer	estimated	5.03	1.64
	shot	1.78	0.55
Fallow deer	estimated	0.00	0.30
	shot	0.00	0.04
Mouflon	estimated	0.00	0.32
	shot	0.00	0.08
Wild boar	estimated	4.38	2.57
	shot	4.45	2.79
Available game fields and pastures (ha 100 ha^{-1})		1.51	1.11
Supplementary feed provided (kg/estimated ungulate ind./year)		301.4	929.29
Size of the game management unit (ha)		14 600	19 240

Hills, an area of 19 240 ha (Table 1). The size of area suitable for management is 16 279 hectares and is comprised of 11 855 ha of forest, 3200 ha of arable land, 1014 ha of grasslands and 88 ha of reed-bed and ponds. In the area used for game management, mainly maple *Acer campestre* and oak, lime *Tilia cordata* and oak, unmixed Scots and black pine and unmixed black locust woodlands can be found. All five medium to large game species (red deer, roe deer *Capreolus capreolus* and fallow deer *Dama dama*, wild boar *Sus scrofa*, mouflon *Ovis ammon musimon*) occur in the area. According to the estimates performed in 2007, the density of the red deer population was 2.44 individuals 100 ha^{-1}; meanwhile the total ungulate density was 7.28 individuals 100 ha^{-1} in the game management unit, respectively.

Our study period (between November 2007 and February 2008) showed significant anomalies in weather conditions. November and December were colder than the average of the last 30 years in Hungary (Schlanger and Kolláth 2008), but January and February were warmer and dryer than in the earlier years (Bella and Kolláth 2009). Mean monthly temperatures averaged in this period 3.4 ± 2.53°C (daily range varied between –10.8 and 19.8°C) in Hajósszentgyörgy and 0.8 ± 2.6°C (daily range varied between –13.7 and 17.8°C) in Valkó. Average monthly precipitation over this time interval was 31.1 ± 22.4 mm in Valkó and 42.6 ± 33.8 mm in Hajósszentgyörgy. The proportion of precipitating days per month was 30 ± 10% for both areas. Nevertheless, the enormous amount of the provided supplementary food reflects that wildlife managers did not expect lower consumption of supplementary food by red deer than usual.

Methods

The consumption of supplementary food can be investigated in many ways: by PIT-tag technology (Newey et al. 2009), the 'video-scale', a motion-activated, infrared video camera combined with a weigh scale (Cooper et al. 2006), detection of food remains in faeces or stomach contents (Groot Bruinderink et al. 1994) and analysis of marker substances (e.g. alkanes, Ru et al. 2002, or stable isotopes, Robb et al. 2011). We used the two latter methods (identification of food remains and markers) in our investigations simultaneously, as together these are suitable for determining the proportion of supplementary food in the individual diet and the proportion of individuals consuming the marked feed. A marker should have no health risk for the animal, not affect the choice of food, and can be identified later in the faeces or rumen content. From among several possible markers we used tiny fragments of rubber, but the supplementary food itself can be appropriate (if it is not available to the animal elsewhere in the habitat and it can be identified in rumen contents or faeces). Total mean retention time of red deer has been estimated to be between 28 and 43 h, while transit time (the interval before first appearance of the consumed food in the faeces) was between 9 and 11 h (Milne et al. 1978, Sibbald and Milne 1993). Consequently, deer had enough time to travel quite a distance after consumption of supplementary feed. In this area the hourly movements of deer could reach 1 km in the most active period after sunset (Katona et al. 2002).

Investigations in Hajósszentgyörgy

In this area two types of supplementary feed were provided during our study period, apple *Malus domestica* pomace and maize *Zea mays* silage. Apple pomace is the residue of apple juice production; it mainly contains apple peel, ovaries and seeds. Maize silage is made by grinding, compressing and fermenting harvested maize plants. The water content of apple pomace was around 75% (Taasoli and Kafilzadeh 2008), while that of maize silage was less than 70% (Haigh 1997).

Supplementary feeding in the area was started in the middle of September 2007, when apple pomace was fed regularly at 17 sites (approx. one site per 200 ha). After the beginning of November, however, apple pomace was supplied at only two game fields (Kukulla and Lugozi, 5 km away from each other). Here, 4000 kg (wet weight) were fed at both game fields, each of five times (20 000 kg per feeder altogether) until the beginning of February 2008. At further two game fields (Kismajor and Tinósi, 2.5 km apart) maize silage marked for research was fed. Between 6 November 2007 and 31 January 2008 an average of 542 ± 52 kg food was applied ten or nine times at the two game fields, respectively (Table 2). Feed was always put down on the ground and thus was available to all ungulates (Table 1). At the game fields of Kismajor and Tinósi from January, 10 to 20 kg rubber scrapings (a filler used at tennis courts using artificial grass) was mixed into the maize silage as marking material (for distinguishing from maize consumed beyond the feeding plots). Before application, rubber scrapings were tested in laboratory conditions and did not lose weight after having been soaked in concentrated hydrochloric acid for 24 h at 40°C, which means it should not disappear during the extreme conditions of digestion.

On the sampling days (22 November, 13–29 December 2007, 14 January, 12 February 2008) we collected faeces in the vicinity (to a maximum distance of 100 m) of the feeding sites to determine the proportion of the supplementary food in the diet of individuals visiting that site. In addition to this, we collected faecal samples on the above mentioned days walking a 5 km long straight line transect between Kukulla and Lugozi recording the precise location of the samples by GPS.

During the hunt, professional hunters collected samples (0.2 to 0.3 kg) from 40 known locations from red deer rumens for us and from which we also determined the presence of natural (apple seed, only available at the feeding stations) and artificial (rubber) markers, indicating the consumption of supplemented apple pomace or maize silage, respectively. Hunters shot the deer individuals from stands within an approx. 5×5 km area around the transect between Kukulla and Lugozi, but never in the close proximity of the feeding plots.

Our laboratory approach was to simultaneously use two different methods (macro- and microscopic analysis). We used the macroscopic method, a thorough laboratory analysis under a stereo microscope, for the detection of natural (apple seed) and artificial (rubber) markers. Thus, our approach here is a conservative one where we determine the frequency of supplementary food consumption (samples with markers/all samples), but not the proportion of supplementary food in these individual samples (we could only say 'consumed to some extent' or 'not consumed at all', depending on the presence/absence of apple seed and rubber markers in the sample).

Before the macroscopic analysis, the collected and frozen deer faeces and rumen samples were defrosted and washed through by clean water through a tea filter with 0.1 mm diameter pores until the effluent water was clean. Afterwards we spread the samples in petri dishes and dried them for 24 h at room temperature, then used a stereo microscope to detect the apple seeds and rubber pieces. We macroscopically

Table 2. Total wet weight of different supplementary feed types provided at different feeders and the winter feeding period covered in different areas.

Area	Feeder	Feed type	Total wet weight of provided feed (kg)	Feeding period; feeding interval
Hajósszentgyörgy	Lugozi	apple pomace	20 000 (5×4000)	From beginning of November 2007 until the beginning of February 2008;
	Kukulla		20 000 (5×4000)	7–14 days intervals
	Kismajor	maize silage	5320 ($10 \times 532 \pm 55$)	From 6 November 2007 to 31 January 2008;
	Tinósi		4970 ($9 \times 552 \pm 50$)	7–14 days intervals
Valkó	whole area		400000	From 22 December 2007 to middle of February 2008; even everyday

analysed 40 red deer rumen samples (n = 40 for apple pomace, n = 19 for maize with rubber scrapings), as well as 10 faeces samples collected at feeding plots and 53 faeces samples collected in the forest.

Simultaneously, we carried out microhistological analyses (Katona and Altbäcker 2002) using our own reference collection (Mátrai and Katona 2004). With this parallel technique we were able to determine both the frequency and the proportion of supplemented feed in the collected individual droppings and rumen contents. The method is based on the microscopic identification of the residues of undigested plant dermal tissues according to the diagnostic anatomical characters specific of different plant species under binocular microscope. In Hajósszentgyörgy only apple pomace but not maize was examined in the microscopic analysis as maize was cultivated in some game fields, consequently only the rubber marker was useful indicator of consumption of supplementary maize food. We microscopically analysed 30 red deer faeces samples collected around the feeding plots, 20 collected in the forest, and 24 deer rumen contents. In each sample 100 epidermis fragments were identified.

Investigations in Valkó

In the Valkó forestry area, the feeding of maize silage was started when the first snow fell on 22 and 23 December 2007 and continued until the middle of February 2008. During this time 400 000 kg of silage were supplied in the area (Table 2) providing a continuous opportunity to feed on supplementary food to ungulates (Table 1) at feeding stations. In addition, permanent baiting plots operated in the area throughout the year, but provided only small amounts of food to attract game to shooting places. We had no information about the total number and spatial arrangement of temporary feeding and permanent baiting plots, but in the area we studied (approx. 600 ha) there was at least one known feeding site per 100 ha.

In this area we investigated the occurrence of the supplied food (maize silage) in the red deer faeces samples collected at the feeding plot at three sites (Gólyás, Szentpáli, Simonles; 1.5 to 2.7 km away from each other). Faecal samples were collected around the feeding plots (to a maximum distance of 100 m) seven times, on 31 January, 13, 15, 18, 21, 25 February and 4 March 2008. At the time of the last collection there was practically no silage left at the feeding plots. The frequency of food consumption (proportion of the individuals consuming maize silage) and the proportion of silage in the individual diet were evaluated only by microhistological means described above. Analysis was carried out in three periods (the end of January, mid-February and the end of February), and of five faecal samples at each feeding site (altogether 45 samples; 100 epidermis fragments identified from each of them).

In Valkó no artificial food marker was used, consequently no macroscopic analyses were conducted.

Statistical analyses

The normal distribution of datasets was evaluated by Kolmogorov–Smirnov normality tests. The Pearson-correlation test and the Mann–Whitney U-test were performed to determine if the proportion of supplementary feed in the dietary samples was related to the distance from the feeding place. The proportion of the supplementary feed in the dietary samples collected around feeding places was compared to that of all the other items by paired t-tests or Wilcoxon matched-pairs signed-ranks test.

Results

Hajósszentgyörgy

Table 3 summarises the results from Hajósszentgyörgy. Based on our analyses in this area, 20 to 90% of the red deer (among different dates and measures) had eaten the supplementary food (see aggregate data on Fig. 1). However, the proportion of supplementary food in the samples was always very low (< 10%) (Fig. 2).

Based on the macroscopic analysis of faeces samples collected in the immediate surroundings (< 100 m) of the Tinósi feeding plot offering maize silage on 12 February 2008, the majority of samples did not contain the marker mixed into the maize silage (20%; n = 10 contained rubber).

Microscopic analysis of faeces collected at the Lugozi feeding plot offering apple pomace, on 22 November, 13 and 29 December 2007 revealed a greater consumption of supplementary food. There, the frequency of apple pomace consumption in the faeces reached 80 to 90% ($n_{1,2,3} = 10$). However, the proportion of apple pomace in the diet was low; it always stayed under 10%. Therefore, the proportion of apple pomace was significantly lower than that of all the other items; it was not the dominant food component (Paired t-test: $t = 95.59$, $DF = 29$, $p < 0.0001$).

Based on the macroscopic analysis of faeces samples collected along the 5 km long forest line connecting the apple pomace feeders of Lugozi and Kukulla on 14 January and 12 February 2008 the majority of samples did not contain apple pomace or the marker of maize silage (23%; n = 53 contained rubber scrapings).

Nevertheless, according to the results of microscopic analysis, 70% of deer faeces (n = 20) collected along the above mentioned line on 13 and 29 December 2007 contained residues of apple pomace, but the proportion of apple pomace was less than 10% in each sample.

On the basis of the macroscopic analysis of red deer rumens 20% (n = 40) of samples contained apple seed, which indicated the use of apple pomace feeders. However, no rubber scrapings were found in these samples (n = 19).

During the microscopic analysis of deer rumens apple pomace was found in 62.5% (n = 24) of samples (64%; n = 14 in November and 60%; n = 10 in December). The proportion of apple pomace in the rumen samples was always less than 10%.

There was a weak negative correlation between the proportion of supplementary feed in the diet and the distance between the feeder and the location of a given faecal or rumen sample (Pearson-correlation: $n = 69$, $r = -0.31$, $p < 0.01$). Although the proportion of apple pomace was very low, samples collected in the vicinity (between 0 and 500 m) of the feeding sites contained more supplementary food

Table 3. Summary of the results in Hajósszentgyörgy. Proportion of faecal and rumen samples containing supplementary feed (frequency) and proportion of supplementary feed in the individual diet are detailed according to different investigations.

Date of collection	Type of collection	Type of analysis	Feeder	Frequency (present/all) of supplementary feed	Proportion (%) of supplementary feed
12 Feb 2008	around the feeder	macroscopic from faeces	Tinósi, maize silage	2/10	–
22 Nov 2007		microscopic from faeces	Lugozi, apple pomace	9/10	always < 10%
13 Dec 2007				8/10	always < 10%
29 Dec 2007				9/10	always < 10%
14 Jan and 12 Feb 2008	in the forest	macroscopic from faeces	Tinósi, Kismajor, maize silage	12/53	–
13 and 29 Dec 2007		microscopic from faeces	Lugozi, Kukulla, apple pomace	14/20	always < 10%
2007–2008 autumn – winter	hunting	macroscopic from rumen	Tinósi, Kismajor, maize silage	0/19	–
			Lugozi, Kukulla, apple pomace	8/40	–
		microscopic from rumen	Lugozi, Kukulla, apple pomace	15/24	always < 10%

than samples found farther from the feeders (3.57 ± 2.77 vs 1.85 ± 1.84; Mann–Whitney U-test: $n_1 = 30$, $n_2 = 39$, $U = 374.5$, $p = 0.01$) (Fig. 2).

Valkó

The occurrence of maize silage in the red deer faeces samples collected around the feeding plots at Valkó was also low. In 42% of the cases ($n = 45$) no maize remains were found. Even where the presence of maize was detected, its proportion was usually under 10% and it reached 15 to 20% only in a couple of cases. Therefore, the proportion of maize silage was significantly lower than that of all the other items; it was not the dominant food component (Wilcoxon matched pairs signed-ranks test: $n = 45$, $W = -1035$, $p < 0.0001$) (Fig. 3).

Discussion

Our results indicate that red deer certainly use the feeding plots, as is also verified by the large amount of droppings found there. However, this does not automatically mean that the role of supplementary food would be significant in the diet. Sahlsten et al. (2010) also concluded in moose that the increased faecal pellet density in the vicinity of feeding sites reflected only the usage by a small portion of the population. They also found that many individuals just walked around the provided grass silage without feeding on it.

According to our results, the occurrence of supplementary food in the winter diet of the red deer, based on a large sample size of both rumen content and faeces analysis, is low. From 10 to 80% of the animals (varying among different dates and measures) had not eaten the supplementary food.

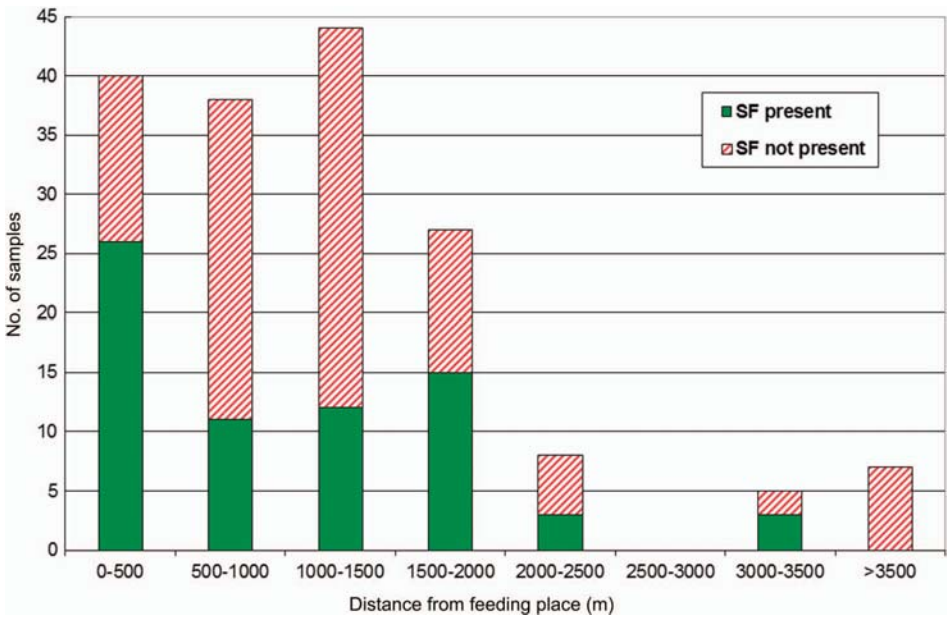

Figure 1. Presence of supplementary feed (SF; apple pomace or maize silage) in the winter diet of red deer determined from faeces and rumen contents of red deer shot at different distances from the feeding place in Hajósszentgyörgy and determined by micro- or macroscopic analyses. The total sample size in this area was $n = 177$, but in the case of eight samples (four with and four without SF) we did not obtain precise information about the distance from the feeding place.

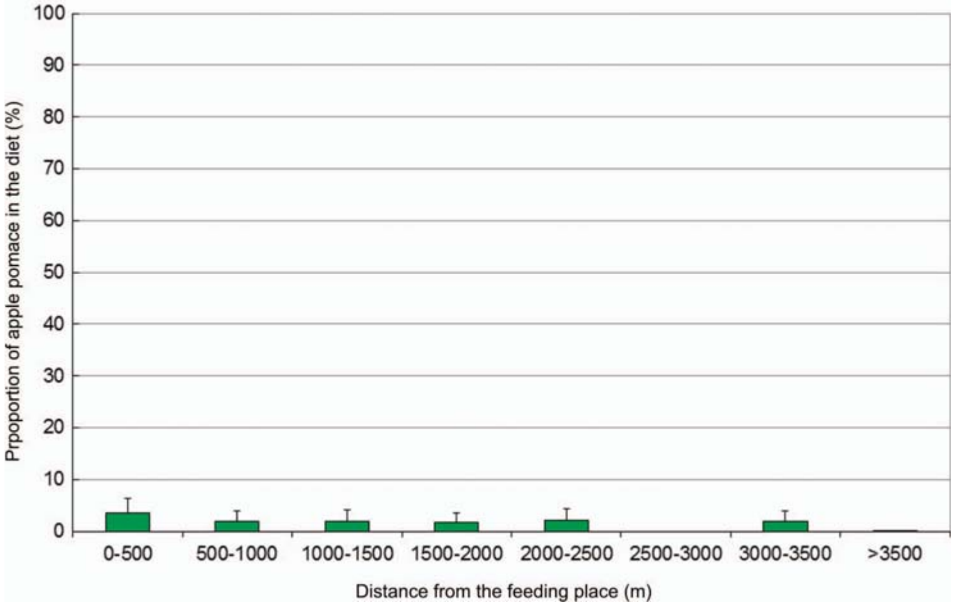

Figure 2. Proportion of supplementary apple pomace (mean + SD) in red deer faeces, and rumen content of red deer shot at different distances from the feeding place in Hajósszentgyörgy (aggregate data according to the microscopic analyses) during winter. The y-axis was left at 100% to better indicate the low proportion of supplementary feed in the diet. (n = 30; 5; 8; 17; 5; 0; 3 and 1, respectively).

Those specimens that had eaten from the food ate only a small proportion (less than 10% of their diet). This indicates that not every individual of the red deer population visits the feeders, or if does, eats a rather small amount of the provided food. It is important to note that we did not find any individual in which the supplementary food dominated the diet. Newey et al. (2009) found similar results for mountain hares *Lepus timidus.* They reported that over the course of one winter only 50% of the target hare population used supplementary feed and there was considerable individual variation in the time spent feeding among those individuals that did feed on it. Potentially, lower than expected consumption of supplementary feed by red deer could be partly explained by adaptive physiological mechanisms contributing significantly to lower energy expenditure during winter. Red deer could achieve a substantial reduction in metabolism by reducing core body temperature (Turbill et al. 2011) and allowing a nocturnal hypometabolism associated with peripheral cooling (Arnold et al. 2004) during winter food shortage.

According to the data collected at Hajósszentgyörgy by various methods, it seems that apple pomace may be preferred there to maize silage, as the frequency of its consumption was higher. In the case of faeces and rumen contents collected in the forest, apple pomace was detected more frequently microscopically than by a macroscopic analysis, so the former method seems to be more accurate, but

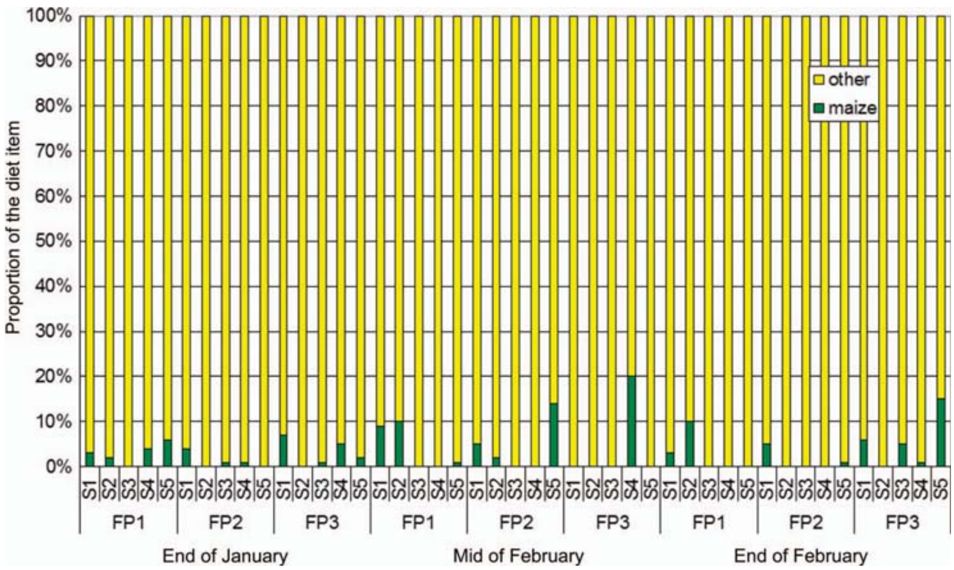

Figure 3. Proportion of supplementary maize silage in the faecal samples of red deer in Valkó (five faeces for each of the three feeding places in three different periods of wintertime). S1..S5: faecal samples, FP1..FP3: feeding places, dark column area: proportion of maize, light column area: proportion of everything else. The y-axis was left at 100% (i.e. the entire diet) to show the low proportion of supplementary feed.

it is too labour-intensive to become an everyday practice. Therefore, the microhistological method is recommended first of all for research objectives, while in the field the game manager can examine the consumption of the provided food by macroscopic marking with a tracer like rubber scrapings and macroscopic analysis of the food. Naturally, in the case of suitable financial resources and sufficient motivation in improving the management of a given area, game managers should spend money for information gained by state-of-the-art methodologies, such as stable isotope analysis (Robb et al. 2011) or NIRS (Walker et al. 2002). In the laboratory, rubber scrapings were not affected by the simulated conditions of digestion, and they were detected in both stomach and faeces contents, suggesting that rubber scrapings are a suitable marker for deer. Furthermore, our analysis of various samples indicated a similarly low proportion of supplementary food regardless of whether it was marked with rubber scrapings, or identifiable by other means (rubber scrapings were mixed only into the maize silage and only in Hajósszentgyörgy), so it seems unlikely to affect food selection.

We suggest that the low consumption of supplementary feed we report is unlikely to be misleading due to methodological factors. In our microhistological analyses we did not establish correction factors for differential digestibility of plant species (Leslie et al. 1983), but epidermis fragments of maize leaves or apple fruit are not easily digestible; consequently the proportion of supplementary food is unlikely to be strongly underestimated in our study. Our experiences during macroscopic analyses confirmed us that we were able to detect even a single rubber item by a thorough looking through the samples under stereo microscope. The probability of missing markers in the samples from the individuals that consumed the marker was relatively low due to the mixing ratio of marker (10 to 20 kg to 5000 kg maize feed; 0.3%) we used. Even if the proportion of supplementary food in the entire sample was only 10%, this concentration would still result in approximately 0.09 g of rubber scrapings in a 300 g rumen sample. This is about 90 particles between 1 and 3 mm in size, and thus easily detected.

Overall, our analyses indicate that supplementary feed was not the primary diet component of red deer during winter. This is in agreement with a previous study at Hajósszentgyörgy (Mátrai et al. 2002), which reported the role of both supplementary food and game field crops negligible in the forest diet of the red deer, with only the consumption of alfalfa reaching 20% in some cases. Thus, in spite of frequent observations of the rapid disappearance of the supplementary food from feeding plots, we should be careful about concluding that this diet component would surely be important for red deer. Its importance in the diet could be rather low compared to natural food sources (especially woody understory species). According to our biomass estimations carried out in the forests of Hajósszentgyörgy, the natural food supply of the forest understory can offer 2000 to 3000 kg of woody shoots per hectare during the vegetation season and it is still above 500 kg per ha in winter (Katona et al. 2007). In theory, supplementary winter feeding could be performed at a scale comparable to this amount, but only at huge expense. However, we suggest a more appropriate goal for supplementary feeding should be to provide food which complement nutrients or compounds which are of limited availability in natural foods in the area. Low consumption of apple pomace and maize silage could be an indication that they had a reasonable high attractive value, but low nutritive value. Vegetation surveys and thorough planning of qualitative feeding programs could be the base of this kind of management measure.

Where does the enormous amount of supplementary feed go, if it is not the main diet component of red deer? In our study areas, red deer composed about one third of the local ungulate population. Roe and fallow deer and wild boar also occur, and they are also consumers of supplementary food. There are also many other mammalian (badger *Meles meles*, red fox *Vulpes vulpes*, martens *Martes* spp., red squirrel *Sciurus vulgaris*, mice, voles etc.) and bird (small songbirds, corvids *Corvidae*, pheasant *Phasianus colchicus*, etc.) species certainly feeding on supplementary feed. In addition, a non-negligible part of the food put down on the ground is trampled into the soil while ungulates are feeding on them or simply it becomes rotten and mixed with soil. Moreover the calculations about the absolute amount of the potentially consumed supplementary food by the total ungulate populations could be strongly biased depending on the reliability of reported data on population densities and the provided amount of supplementary food. Population size of deer and other ungulates are reported every year by game management units, but are not scientific estimations but guesstimates (Csányi and Lehoczki 2010). According to scientific analyses, ungulate population densities in Hungary are commonly underestimated (Milner et al. 2006). All those things together may account for the discrepancy between the consumption potential of deer population and the huge amount of food which disappears.

In terms of the biological effect of game feeding, research data published so far are not consistent (Putman and Staines 2004). Our results suggest that supplementary feeding is unlikely to reach and be beneficial for all individuals of a population of red deer. In Hajósszentgyörgy our radiotelemetry studies also confirmed that the majority of red deer individuals could use the feeding sites only occasionally (Szemethy et al. 2013). Nevertheless, this does not mean that for those specimens who regularly eat the supplied food it cannot have physiological consequences (e.g. balancing the lack of quality food, increased survival or reproduction in the following year). Groot Bruinderink et al. (2000) stated that cessation of supplementary feeding resulted in problems in the mineral status of red deer and wild boar. Schmidt and Hoi (2002) reported that in their first year of life, supplemented red deer are under reduced natural selection pressure. Since measuring the local importance of these effects is not easy for the game manager, our results should be viewed with some caution. Nevertheless, we suggest that the observation that the supplied food regularly vanishes from the feeder does not necessarily mean that even one red deer has gained significant biological advantage which might be expressed as a later financial profit for the game manager. Put another way, the red deer population can have an obvious effect on supplementary feed; meanwhile that food may have little or no effect on deer individuals.

Conclusions

One should always consider the exact goals of supplementary feeding in a given area. The feeding program should take into consideration the natural dietary preferences and diet choice of the red deer about which much is known (Mátrai and Kabai 1989, Gebert and Verheyden-Tixier 2001, Szemethy et al. 2003). Finally, it is very important to evaluate the status of the entire forest area based on the availability and quality of food supply in the understory layer (Katona et al. 2013). We emphasise that the use of feeding plots is only partly determined by the supplementary food itself, as the natural food supply offered to red deer by other patches of the habitat should be much more important.

Acknowledgements – We are grateful to Nikolett Bak and Viktória Kiss for their participation in the microhistological faeces analyses. Our work was supported by the Natural Resources Dept of the Ministry of Agriculture and Rural Development (64396/2007), as well as the Forestry of the Gemenc Forest and Game Management J.S.C. at Hajósszentgyörgy and the Forestry of the Pilis Parkforest J.S.C. at Valkó. This paper was supported by the János Bolyai Research Scholarschip of the Hungarian Academy of Sciences (to KK) and the Research Centre of Excellence (8526-5/2014/TUDPOL). The investigations comply with the current Hungarian laws. The authors declare that they have no conflict of interest.

References

Arnold, W. et al. 2004. Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). – Am. J. Physiol. Regul. Integr. Comp. Physiol. 286: R174–R181.

Bella, Sz. and Kolláth, K. 2009. Beszámoló 2008. év éghajlatáról és szélsőséges időjárási eseményeiről. – OMSZ (in Hungarian).

Biró, Zs. et al. 2010. A kiegészítő takarmányozás jelentősége a nagyvadgazdálkodásban. – Vadbiológia 14: 55–64 (in Hungarian).

Bleier, N. et al. 2006. A vadföldek, a kiegészítő takarmányozás, a sózók és a dagonyák jelentősége a nagyvadgazdálkodásban. – Vadbiológia 12: 29–39 (in Hungarian).

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and future. – Can. J. Zool. 68: 203–220.

Brown, R. D. and Cooper, S. M. 2006. The nutritional, ecological, and ethical arguments against baiting and feeding white-tailed deer. – Wildl. Soc. Bull. 34: 519–524.

Calenge, C. et al. 2004. Efficiency of spreading maize in the garrigues to reduce wild boar (*Sus scrofa*) damage to Mediterranean vineyards. – Eur. J. Wildl. Res. 50: 112–120.

Cooper, S. M. et al. 2006. Video-scale: a novel device to measure supplemental feed consumption by wildlife. – Wildl. Soc. Bull. 34: 1362–1367.

Csányi, S. and Lehoczki, R. 2010. Ungulates and their management in Hungary. – In: Apollonio, M. et al. (eds), European ungulates and their management in the 21st century. Cambridge Univ. Press, pp. 291–318.

Faragó, S. 2002. Vadászati állattan. – Mezőgazda Kiadó (in Hungarian).

Feuereisel, J. 2005. Practical verification of food supply to game in conditions of large-scale shelterwood system. – J. For. Sci. 51: 564–571.

Feuereisel, J. and Ernst, M. 2009. Verification of the food supply to game under conditions of the floodplain forest ecosystem. – J. For. Sci. 55: 81–88.

Gebert, C. and Verheyden-Tixier, H. 2001. Variations of diet composition of red deer (*Cervus elaphus* L.) in Europe. – Mammal Rev. 31: 189–201.

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). – J. Zool. 267: 89–96.

Gortázar, C. et al. 2006. Disease risks and overabundance of game species. – Eur. J. Wildl. Res. 52: 81–87.

Groot Bruinderink, G. W. T. A. et al. 1994. Diet and condition of wild boar, *Sus scrofa scrofa*, without supplementary feeding. – J. Zool. 233: 631–648.

Groot Bruinderink, G. W. T. A. et al. 2000. Effects of cessation of supplemental feeding on mineral status of red deer *Cervus elaphus* and wild boar *Sus scrofa* in the Netherlands. – Acta Theriol. 45: 71–85.

Haigh, P. M. 1997. Silage dry matter content and predicted effluent production in England and Wales 1984–1994. – J. Agric. Engin. Res. 66: 63–77.

Heltay, I. 2000. Vadásziskola. – Hubertus Kft. (in Hungarian).

Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. – Oecologia 78: 443–457.

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

Katona, K. and Altbäcker, V. 2002. Diet estimation by faeces analysis: sampling optimisation for the European hare. – Folia Zool. 51: 11–15.

Katona, K. et al. 2002. A gímszarvas napi aktivitásmintázatának biotelemetriás vizsgálata. – Vadbiológia 9: 27–35 (in Hungarian).

Katona, K. et al. 2007. A hazai erdők cserjeszintjének szerepe a nagyvad-erdő kapcsolatok alakulásában. – Természetvédelmi Közlemények 13: 119–126 (in Hungarian).

Katona, K. et al. 2013. Ungulate browsing shapes climate change impacts on forest biodiversity in Hungary. – Biodivers. Conserv. 22: 1167–1180.

Kim, K. H. et al. 1996. A comparison of oak browse (*Quercus* spp.) and silages of rye and maize with respect to voluntary intake, digestibility, nitrogen balance and rumination time in penned Korean sika deer. – Anim. Feed Sci. Tech. 61: 351–359.

Leslie, D. M. et al. 1983. Correcting for differential digestibility in microhistological analyses involving common coastal forages of the Pacific Northwest. – J. Range Manage. 36: 730–732.

Luccarini, S. et al. 2006. Red deer (*Cervus elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations, and effects of snow and winter feeding. – Ethol. Ecol. Evol. 18: 127–145.

Mátrai, K. and Kabai, P. 1989. Winter plant selection by red and roe deer in a forest habitat in Hungary. – Acta Theriol. 34: 227–234.

Mátrai, K. and Katona, K. 2004. Mikroszövettani határozókulcs növényevők táplálékvizsgálatához / Digital key for microhistological analysis of herbivore diet. – Hungarian – English bilingual CD content, ISBN 963 219 865 4.

Mátrai, K. et al. 2002. A szarvas táplálékának mennyiségi és minőségi jellemzői a vegetációs időszak alatt egy alföldi erdőben. – Vadbiológia 9: 1–10 (in Hungarian).

Milne, J. A. et al. 1978. A comparison of the voluntary intake and digestion of a range of forages at different times of the year by the sheep and the red deer. – Brit. J. Nutr. 40: 347–356.

Milner, J. M. et al. 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. – J. Appl. Ecol. 43: 721–734.

Newey, S. et al. 2009. Using PIT-tag technology to target supplementary feeding studies. – Wildl. Biol. 15: 405–411.

Osborn, R. G. and Jenks, J. A. 1998. Assessing dietary quality of white-tailed deer using fecal indices: effects of supplemental feeding and area. – J. Mammal. 79: 437–447.

Page, B. D. and Underwood, H. B. 2006. Comparing protein and energy status of winter-fed white-tailed deer. – Wildl. Soc. Bull. 34: 716–724.
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 Rev. 34: 285–306.
Rajský, M. et al. 2008. Influence supplementary feeding on bark browsing by red deer (*Cervus elaphus*) under experimental conditions. – Eur. J. Wildl. Res. 54: 701–708.
Reimoser, F. 2003. Steering the impacts of ungulates on temperate forests. – J. Nat. Conserv. 10: 243–252.
Robb, G. N. et al. 2011. Using stable-isotope analysis as a technique for determining consumption of supplementary foods by individual birds. – Condor 113: 475–482.
Ru, Y. J. et al. 2002. Predicting feed intake of fallow deer (*Dama dama*) using alkanes as a marker. – Asian Austral. J. Anim. 15: 209–212.
Sahlsten, J. et al. 2010. Can supplementary feeding be used to redistribute moose *Alces alces*? – Wildl. Biol. 16: 85–92.
Sanchez-Prieto, C. B. et al. 2004. Reproductive behavior in female Iberian red deer: effects of aggregation and dispersion of food. – J. Mammal. 85: 761–767.
Schlanger, V. and Kolláth, K. 2008. Beszámoló 2007. év éghajlatáról és szélsőséges időjárási eseményeiről. – OMSZ (in Hungarian).
Schmidt, K. T. and Hoi, H. 2002. Supplemental feeding reduces natural selection in juvenile red deer. – Ecography 25: 265–272.
Sibbald, A. M. and Milne, J. A. 1993. Physical characteristics of the alimentary tract in relation to seasonal changes in voluntary food intake by the red deer (*Cervus elaphus*). – J. Agr. Sci. 120: 99–102.
Szemethy, L. et al. 2003. Seasonal home range shift of red deer hinds *Cervus elaphus*: are there feeding reasons? – Folia Zool. 52: 249–258.
Szemethy, L. et al. 2013. A gímszarvasok őszi-téli vadföld használatának értékelése Hajósszentgyörgyön. – Vadbiológia 15: 53–62 (in Hungarian).
Taasoli, G. and Kafilzadeh, F. 2008. Effects of dried and ensiled apple pomace from puree making on performance of finishing lambs. – Pak. J. Biol. Sci. 11: 294–297.
Timmons, G. R. et al. 2010. Does supplemental feed increase selective foraging in a browsing ungulate? – J. Wildl. Manage. 74: 995–1002.
Točka, I. 1983. Study of the natural feeding capacity of field hunting grounds for small field game in conditions of intense large scale agricultural production in the south-western region of Slovakia. – Folia Venatoria 13: 95–105.
Tremblay, J.-P. et al. 2004. Choice and development of decision support tools for the sustainable management of deer-forest systems. – For. Ecol. Manage. 191: 1–16.
Turbill, C. et al. 2011. Regulation of heart rate and rumen temperature in red deer: effects of season and food intake. – J. Exp. Biol. 214: 963–970.
Walker, J. W. et al. 2002. Calibrating fecal NIRS equations for predicting botanical composition of diets. – J. Range Manage. 55: 374–382.