

# Similarities in foraging patterns of wisent, red deer and various breeds of European primitive horses

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**Abstract:** The aim of this paper was an attempt to analyse similarities in foraging patterns of three herbivorous species: wisent, red deer and primitive horse, occupying similar habitats in Europe. Regarding foraging patterns, the wisent presents many similarities to both compared species. Main similarities with the red deer are related to the structure and physiology of alimentary tract, foraging activity, requirements regarding food quality (better digestible), and habitat selection, as well as in diet composition (woody plants content and plant species composition in the diet) and debarking patterns. Primitive horses on the other side present similar feeding type, diet contents and debarking activity. Possibilities of wisent's population development are high however potential conflicts over the use of food resources may occur, involving other species, such as the red deer and primitive horses. Lower body mass of red deer and horses and specific features of digestive tract of horses give them some advantages in the competition between them and the wisent.

**Key words:** diet, bark stripping, foraging activity, habitat selection, competition

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## Introduction

The population numbers of free-living wisent (*Bison bonasus*) increased considerably since the initiation of their restitution and conservation. After the decline in 1990s, the current population trend is increasing (Pucek *et al.* 2004; Olech 2008; Krasieńska *et al.* 2014). Possibilities of wisent's population development are high, since only about 1% of its original range is now occupied, and there are a number of potentially suitable habitats in Europe (Kuemerle *et al.* 2011). However, following an increase of population numbers, potential conflicts may occur, involving other species, such as the red deer which is considered the most important competitor regarding foraging relations (Pucek *et al.* 2004). Red deer (*Cervus elaphus*) is also among the most numerous herbivorous mammals of Europe, occurring in various landscapes and inhabiting now similar area to original range of wisent in Europe (see: Pucek 1991; Lovari *et al.* 2008). Primitive horses (*Equus caballus*) on the other hand, ceased to belong to the native fauna of Europe long time ago, but nowadays they, or rather their hybrids, are frequently used in free grazing programs in grass-

land-type and meadow-forested mosaic areas, oriented towards the prevention of biodiversity loss in Europe (Josten 2002; Vera 2009; Navvaro and Pereira 2012; Kugler and Broxham 2014; Merckx and Pereira 2014). Current trends suggest that free ranging primitive horses may in time develop a feral metapopulation of this species. The aim of this paper was an attempt to analyse similarities in foraging patterns and possible competition among the three species: wisent, red deer and primitive horse, occupying similar habitats in Europe.

## Diet

Diet composition of those three species differs according to various studies, and depends on many factors like: season, age, sex and habitat. Red deer is mostly regarded as an intermediate feeder, and the woody plants content in its diet ranges between 40% to over 90% (e.g Gebert and Verheyden-Tixier 2001). The European bison is recognized as a grazer, and woody plants compose much lower percentage of its diet (7–33%) (Pucek *et al.* 2004). Primitive horses as typical grazers only marginally forage upon the woody plants (Cosyns *et al.* 2001). Much higher percentage of woody plants in the diet of both ruminants may be connected with ability for detoxification of plant secondary metabolites in the rumen (Carlson and Breeze 1984). Gramineous species on the other hand often lack such secondary metabolites, and generally grasses contain less defence chemicals than other types of herbivores' forage, especially the browse (Searle and Shipley 2010). Browse though, contains less of cell-wall fraction, and lower percentage of neutral detergent fiber than grasses (30–50 and 50–70%, respectively). Its mastication leads to small polygonous particles that are more susceptible to digestion than long and fibrous particles of grasses (Duncan and Poppi 2010).

The ability for detoxification of secondary metabolites of plants, may contribute to diversification of foraging niches among ruminants. Although there is no strong evidence on such differences, some plant species with high ability for chemical defence are consumed mainly by specific browsers (Vehviläinen and Koricheva 2006; Koster 2012). Also interspecific differences in functions of digestive tract, like mean retention time or saliva flow rate, may create specific conditions for resident microbial populations and influence food selection patterns (Duncan and Poppi 2010).

All three compared species use a wide variety of plant species, but the ranking of components of their diet is determined by environmental factors like habitat and season. According to available data, the red deer should be the most selective towards available food resources. While comparing the red deer, wisent and primitive horses, main three factors should be taken into account: the feeding pattern, characteristics of digestive tract and body mass. Both red deer and wisent are ruminants but vary regarding feeding patterns and body mass. Mean body mass of adult red deer male reach approximately 200 kg (Okarma and Tomek 2008), while a wisent

may be 2–3 times heavier (Kraśńska and Kraśński 2002), therefore their requirements of food intake per unit of body mass will be different. The ability for food selection depends also from the width of a jaw, which in turn is connected with body mass of an animal (Hanley 1982). Primitive horses' body mass is comparable to that of red deer, but both species differ regarding their feeding patterns. Grazers (horse and wisent) usually have to deal with different plant composition (forbs and grasses) on a meadow than browsers (shrubs and trees) in woodland. A woodland patch usually represents much lower plant numbers than a patch at a meadow, so grazers tend to have lower level of food selectivity than browsers (Searle and Shipley 2010). Horses, as hind gut fermenters, have a faster passage rate of food through the digestive system, and their food intake per unit of body mass is higher than in ruminants, but their requirements towards the quality of food are not so high (Duncan *et al.* 1990). Despite differences in food selectivity patterns typical for each species, there are considerable differences within the same species depending on characteristics of a site. Therefore, a comparison of diet composition of various herbivores foraging within the same site allows for more precise assessment of their overlap. Among three compared species, the wisent seems to have a highly overlapping range of consumed plants with deer and horses. In Białowieża Forest, a diet overlap between wisent and red deer was assessed at about 40%. Thus the red deer is regarded as a main natural competitor for the wisent (Pucek *et al.* 2004). On the other hand, the wisent diet contains high proportion of grasses and herbaceous plants, which suggest possible high diet overlap with primitive horses. Various studies conducted in temperate ecosystems on grazing equids and bovids, demonstrated a high overlap of their diet (between 65 to 95%) (Menard *et al.* 2002). Simultaneous use of an open area by bovids and equids may create good quality pasture however characterized by a lower sward height, where horses (and red deer) may get an advantage over the wisent (Duncan 1992). Shetland ponies, that diet highly overlaps with Highland cattle (0.92–0.98), spend comparatively more time grazing at grasslands with lower sward height (Lamoot *et al.* 2005), where their grazing efficiency was higher comparing to the cattle. Hence, in a consequence of strong competition between horses and cattle, horses may appear to be more competitive. It has been shown at Camargue pastures, where cattle changed their diet composition towards the more intensive use of dicotyledonous plants that were avoided by horses (Menard *et al.* 2002). Although cattle belong to a different genus than a wisent, they characterise in similar body mass and digestive tract. We may also expect similarities in the diet of primitive horses and a wisent. Grasses and sedges compose 80–99% of polish koniks' diet (depending on site and a season), over 90% of Shetland ponies' diet (Cosyns *et al.* 2001; Lamoot *et al.* 2005; Chodkiewicz and Stypiński 2011) and at least 65% of wisent's diet (Gębczyńska *et al.* 1991). Those data suggest then, that primitive horses introduced to wisent ranges may successfully compete with them for food resources at the pasture.

## Bark stripping

All three species exert impact upon trees by stripping the bark. Although the red deer is regarded as a main debarking agent in the European forests, the wisent and primitive horses may also cause similar, significant damages (Kuiters *et al.* 2006; Paszkiewicz and Januszczak 2010). Red deer eat the bark from more than 20 species, of which the most frequently debarked are: pine, spruce, willow, poplar, rowan and ash (Gill 1992; Borkowski and Ukalski 2012). Most of them, especially pine, are debarked in young stage of tree growth. There is not much known so far, regarding horses' foraging patterns upon woody vegetation, but some studies indicate quite similar to red deer set of debarked tree species: rowan, willow, spruce, poplar and alder (Klich 2009). Debarking by wisents is generally more oriented towards hardwood species, i.e. mainly: hornbeam, ash, spruce, lime, hazel and even oak (Okarma and Tomek 2008). Some tree species like fir and ash are debarked by both wisent and the red deer, which may be significant for forest economy. Such tree damages may be thus mistakenly attributed to wisents although actually they were done by red deer and vice versa (Paszkiewicz and Januszczak 2010). All three compared species mainly debark during spring, when the bark is more easily removable and the demand for nutrients cannot be sufficiently covered from other food sources (Okarma and Tomek 2008). Nevertheless some data from Bieszczady indicate, that debarking by wisents occurred also in sites abundant in natural food (Paszkiewicz and Januszczak 2010). Debarking during other seasons is rare in case of horses and wisents, but red deer debark trees even in the middle of the summer (Saint-Andrieux *et al.* 2009). For red deer and primitive horses, some typical patterns were found regarding debarking characteristics: tree age, roughness of the bark, tree distribution (Gill 1992; Kuiters *et al.* 2006). However, the intensity of debarking upon particular tree species depends on site characteristics, including the composition of a stand or tree species that are dominating in the area, which makes difficult to determine general patterns for the preference of woody species by particular ungulates.

## Foraging activity

A polyphase rhythm of daily activity is typical for ruminants, due to physiology of their complex stomach forcing them to forage in time intervals alternate with rumination. However the length of consecutive phases is not stable, and duration of a single foraging bout (e.g. in case of a wisent) may vary between 15' to 5h15' (Caboń-Raczyńska *et al.* 1987). Time spend on foraging and ruminating changes during the year. From spring to autumn, a mean length of foraging bout may increase from 1–2 h in April to 5–6 h in September. The length of phases increased during the winter, when only two peaks of activity are observed daily (Caboń-Raczyńska *et al.* 1983). Total percentage of daily time budget spent on foraging during the vegetative season was approximately 60%, while in winter only 30%, which was connected with supplementary feeding with hay (Caboń-Raczyńska *et al.* 1983).

The red deer is commonly regarded as a species of bimodal peaks of activity, and many studies reported its high activity during dawn and dusk (Georgii and Schröder 1983; Jeppesen 1987; Hester *et al.* 1996). Nevertheless, the activity of red deer is interrupted mainly by human activity. In fact, other peaks of activity appear, but during a daytime, red deer tends to forage rather in more hidden places within the forest habitat, where it searches for meadows or clearings surrounded by the forest (Bobek *et al.* 1992). In natural ecosystems of Białowieża Forest, the polyphase rhythm of red deer's activity is clear and differs from anthropogenically disturbed ecosystems (Kamler *et al.* 2007). Other studies on this species report various length of a feeding bout from 0.5 to even 5h, and the number of bouts from 3 to 12 (e.g. Georgii and Schröder 1983; Jeppesen 1987; Kamler *et al.* 2007). Differences in activity patterns originate from many factors, like: temperature, rainfall and snowfall, but first of all depend on habitat characteristics, in particular on available food resources (Bobek *et al.* 1992; Hester *et al.* 1996; Kamler *et al.* 2007). The activity rhythm of red deer in Białowieża Forest show essential differences comparing to that of the wisent. Its bout length was much shorter and did not exceed 1 hour with mean about 42', that gave an average number of bouts of about 12 per day. In case of this species, no statistical differences were found between seasons (Kamler *et al.* 2007). The higher number of bouts per day and shorter bout duration is related to smaller body size in red deer, but is not connected with physiology of foraging (Gordon and Illius 1994). A volume of red deer's rumen approximately equals to 25% of wisent's rumen (Kraśńska and Kraśński 2007). A smaller rumen of red deer needs less time to be filled, and thus shorter foraging bouts are sufficient. This makes a difference, when foraging is interrupted by human (or predators) activity or within resource-poor areas, where smaller patches of high quality food are more profitable for red deer than for wisent. Moreover, shorter bouts give more possibilities for shifts between habitats, which may be also favourable in a heterogeneous landscape.

The ultradian rhythms of horses activity present considerable differences between seasons. During summer, factors that are important for determination of their foraging behaviour are: harassment by insects and high temperatures. This induces a bimodal daily activity, with two peaks at the sunrise and sunset, and other activities than grazing predominate during the midday time (Pluta *et al.* 2013). Summer time is also specific in shifting the grazing time to night hours, while during the rest of the year, horses mainly present a diurnal activity type (Mayes and Duncan 1986; Boyd *et al.* 1988; Berger *et al.* 1999). Primitive horses spent about 55–70% time for grazing, but in a landscape of lower forage quality, horses increase time spent on foraging (Cosyns *et al.* 2001; Lamoot *et al.* 2005). Much lower grazing activity show wild equids e.g.: Przewalski horse, at the level of about 29–46% (Boyd *et al.* 1988; Berger 1999), and donkeys (52%) due to their capability for consuming fibre at a high rate (Cosyns *et al.* 2001). Their time budget changes between seasons, the highest grazing activity occurs during spring and the autumn, and the lowest during

summer (Cosyns *et al.* 2001; Menard *et al.* 2002). Foraging activity of horses reflects their high flexibility, that is connected to specific morphology and physiology of their digestive tract.

## Habitat selection

A habitat selection is mainly connected with foraging activity, and depends on spatial and temporal variation in food quantity and quality, but also on availability of the shelter. Wisent's habitat selection highly depends on environmental factors, and reflects high plasticity of this species, that is connected to its historical range (Kuemmerle *et al.* 2010). An analysis from Bieszczady, indicates preference of wisent to forest interior but also to perforated forest connected to open areas within the forest habitat (Kuemmerle *et al.* 2010). A preference was also shown towards particular types of stand composition and structure. In summer, wisents mainly preferred beech and mixed coniferous stands with low stand density. Similar stands, and also ash-sycamore stands were mostly used during winter, but then higher density stands were preferred (Perzanowski *et al.* 2008). Wisents from Polish part of Białowieża forest used mainly deciduous forests and mixed coniferous forests (Kraśńska *et al.* 1987), but other studies indicate also use of other forest habitats and young plantations up to 10 years old (Dzięciołowski 1991). Open areas are indicated as important part of habitats inhabited by wisent population, but their importance differs strongly between studied sites. Some studies indicate marginal use of openings (Kraśńska *et al.* 1987; Perzanowski *et al.* 2011), but other suggest most of time spent on open area and only seasonal importance of forested habitat for wisents (Balčiauskas 1999). Among open areas cultivated meadows and crops are preferred (Balčiauskas 1999; Kuemmerle *et al.* 2010; Tracz and Tracz 2010). The use of open areas is thus a question of preference, but some factors (e.g. human activity) could force wisents to use forest habitat as Early Holocene bison used more open areas than current populations (Bocherens *et al.* 2015). A majority of introduced wisent populations change their home range from fully forested to forest-meadow landscape (Kerley *et al.* 2012).

The red deer tends to use more forested habitat than wisent, which may be an effect of human activity. The specific type of daily bimodal activity of red deer gives only few hours per day for foraging in better quality open habitats, but according to Clutton-Brock (1982), red deer naturally tend to use open habitats. Nowadays generally, red deer prefers similarly like wisent broadleaved and mixed forests, but may also exist in poor coniferous forests (Bobek *et al.* 1992; Okarma and Tomek 2008). Although the highest red deer density in Carpathians was recorded in hunting grounds with 75% forest cover (Bobek *et al.* 1992), the vast range of this species in the Europe indicates its ability to live in various habitats. Even in highly forested habitats, red deer search for gaps exposed to the light, i.e. with higher biomass and faster regeneration of forage (Kuijper *et al.* 2009). This suggests high

similarity with habitat selection patterns of wisents, oriented towards perforated forests (Okarma and Tomek 2008). The use of open habitats by red deer in mosaic landscapes of Europe vary strongly, and may reach 100% of home range in Scotland (Clutton-Brock *et al.* 1982). Available resources condition the use of each habitat type, and in more forested areas utilization of meadows may be less intensive than in patchy forest-agricultural mosaics (Náhlik *et al.* 2009). Similarly to wisent, among open habitats cultivated meadows in young and medium stage of development are mostly preferred by red deer (Náhlik *et al.* 2009; Lande *et al.* 2014).

Primitive horses as typical grazers mostly use open areas, nevertheless the partial use of forest is common (Klich and Grudzień 2013; Popp and Scheibe 2014). Their grazing time is mostly spent at grasslands, but also on rough vegetation (Putman *et al.* 1987; Menard *et al.* 2002), that differs horses from both compared ruminants, due to an ability to utilize low quality herbage (Gudmundsson and Dyrmondsson 1994). The use of the forest for foraging purposes is marginal, and increases mainly during spring, when horses tend to use more of woody vegetation (Lamoot *et al.* 2005). The forest habitat is used by horses marginally, since the majority of horses' grazing pressure occurs close to the edge to the forest, and depending on forest habitat features, their grazing pressure decreases substantially along first 100 m from the forest edge (Klich and Grudzień 2013). Foraging intensity of horses within forest habitat is also influenced by canopy openness and the abundance of available forage (Skiwski and Klich 2012; Klich and Grudzień 2013). Although the habitat use by primitive horses is not generally disturbed by human activity or predation, the use of forest in other form than foraging also occurs, and is mainly related to temperature and insects' activity (Jezierski and Jaworski 1999; Popp and Scheibe 2014). Thus the use of forest habitat generally increases during summer, where horses may spent almost 50% of the daytime under tree canopy (Szaj 2011).

## Conclusions

Regarding foraging patterns, the wisent present many similarities to both compared species. Main similarities with the red deer are related to alimentary tract, foraging activity, requirements regarding food quality (better digestible), and habitat selection, as well as in general diet composition and debarking. Primitive horses on the other side present similar feeding type, diet and debarking activity. Lower body mass of red deer and horses, and specific features of digestive tract of horses give some advantages to these species in competition between them and the wisent. Red deer needs less time and thus smaller patches of vegetation to fill the rumen, horses may successfully graze on lower quality food and is more flexible in foraging activity, both species may graze on a lower sward height. In a direct confrontation, we may expect an avoidance behaviour of wisents, weakening food and habitat competition. Nevertheless, a wisent may be outcompeted by both species from a part of feeding grounds.

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### Podobieństwa w schemacie żerowanie żubra, jelenia i koni ras prymitywnych

**Streszczenie:** Trend wzrostowy populacji żubra oraz występowanie rozległych potencjalnych siedlisk dla tego gatunku, wskazują na duże możliwości dalszego jego rozwoju w najbliższym czasie w Europie. Wraz z rozwojem populacji żubra mogą wystąpić konflikty z innymi gatunkami kopytnych jak jeleni, który jest uważany za jego głównego konkurenta oraz końmi ras prymitywnych, których hodowla w obecnym czasie w Europie notuje wyraźny wzrost. Celem pracy była próba analizy podobieństw w schematach żerowania oraz możliwej konkurencji między wskazanymi gatunków, które zajmują zbliżone siedliska w Europie. Żubr posiada wiele podobieństw do jelenia oraz koni odnośnie parametrów żerowania i wykorzystania pokarmu. Główne podobieństwa z jeleniem są związane z budową układu pokarmowego, aktywnością żerowania, wymaganiami dotyczącymi jakości pokarmu oraz wybiórczością siedliskową, ale również ogólnym składem diety oraz niektórymi gatunkami spalowanych drzew. Konie ras prymitywnych wykazują podobieństwa z żubrem odnośnie składu diety, typu odżywiania się oraz aktywnością związaną ze spalowaniem. Mniejsza masa ciała jelenia oraz konia oraz specyficzna morfologia i fizjologia układu trawiennego konia dają tym gatunkom przewagę w sytuacji konkurencji pokarmowej z żubrem. Jeleń potrzebuje mniej czasu oraz mniejszych płatów roślinności aby napełnić żwacz, konie mogą z sukcesem pobierać pokarm o niższej jakości oraz są bardziej elastyczne w aktywności żerowania, obydwa gatunki mogą żerować na niższej runi. Możliwe jest zatem wyparcie żubra z części żerowisk przez te gatunki.

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