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Etologické projevy skotu na pastvě
(Cattle behaviour on pasture)

Doktorská dizertační práce

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Prohlášení

Prohlašuji, že jsem předloženou dizertační práci na téma **Etologické projevy skotu na pastvě** vypracovala samostatně, pod vedením doc. RNDr. Pavly Hejcmanové, Ph.D. a použila pouze pramenů, které uvádím v seznamu použité literatury.

V Praze dne

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1. Úvod

Přežvýkavci jsou nejvýznamnějšími konzumenty primární produkce na Zemi. Konvertují živiny do produktů využívaných lidmi, jako je maso, mléko, vlna, kůže a další. Abychom získali nejlepší podmínky pro chov a zároveň nejvyšší produkci, je velmi důležité porozumět požadavkům zvířat. Konečným cílem chovatelů hospodářských zvířat je tedy dosáhnout ekologicky a ekonomicky udržitelné živočišné výroby a zachovat produkci píce z travních porostů. Pastviny však mají multifunkční roli spočívající nejen v zajištění živočišné výroby, ale jsou také důležité jako regulace ekosystémových služeb. Též mají vysokou svou vlastní vnitřní hodnotu, mimo jiné pro budoucí údržbu kulturního dědictví a jako ohniska biologické rozmanitosti (Hart 2001, Pavlů *et al.* 2006, Smit *et al.* 2008). Chovatelé hospodářských zvířat proto musí vytvořit vhodnou strategii a management pastvy pro udržení všech těchto funkcí spolu s ekonomicky udržitelnými mezemi.

2. Cíle práce a hypotézy

Hlavním cílem dizertační práce bylo prostudovat různé faktory ovlivňující pastevní chování skotu na polopřirozených pastevních porostech a její konkrétní cíle jsou:

1. Porovnat chování skotu při různých systémech pastvy.
2. Stanovit vliv různé intenzity pastvy na pastevní chování skotu.
3. Stanovit vliv různé intenzity na selektivitu pastvy.
4. Porovnat obsah živin v listí vybraných druhů dřevin využívaných pro krmení skotu.
5. Porovnat obsah živin v biomase (letorostech, listí) vybraných druhů dřevin v zimním období.

ad1) Srovnání pastvy při kontinuální a rotační pastvě

Cílem bylo porovnat chování jalovic při různém systému pastvy (rotační, kontinuální) a stanovit, které parametry porostu ovlivňují pastevní chování jalovic;

Hypotézy:

H1: V chování jalovic mezi rotačním a kontinuálním systémem pastvy je určitý rozdíl.

H2: Různé parametry porostu (například výška porostu, hustota trav a bylin, obsah dusíkatých látek či vlákniny) mohou ovlivnit celkové chování jalovic i počet skusů za jednotku času (tzv. biting rate).

H3: Systém pastvy a parametry porostu ovliňují užitkovost jalovic.

ad2) Pastevní chování na heterogenním porostu intenzivní a extenzivní pastvy

Cílem práce bylo stanovit vliv různé intenzity pastvy (intenzivní a extenzivní pastva), pastevní sezóny a ostatních vlivů (například počasí či teplotní rozdíly) na pastevní chování skotu při různé intenzitě kontinuální pastvy na druhově bohatém polopřirozeném travním porostu;

Hypotézy:

H1: Neexistuje žádný vliv intenzity pastvy na pastevní chování jalovic (pasení, žvýkání, přežvykování a ostatní chování) v rámci jednoho dne.

H2: Chování jalovic je ovlivněno různou intenzitou pastvy na základě příjmu potravy.

H3: Postupující sezónou se tendence pasení bude zvyšovat, naopak snižuje se tendence odpočinku.

H4: Počasí a teplota bude mít vliv na pastevní chování jalovic.

ad3) Selektivita pastvy na heterogenním porostu

Cílem této studie bylo zhodnotit vliv různé intenzity pastvy jalovic, postupující vegetační (pastevní) sezóny a dalších faktorů (klimatické vlivy) na selektivitu pastvy založenou na příjmu a vyhledávání preferovaných typů porostu podle jejich druhového složení a výšky na paseném druhově bohatém heterogenním porostu, za pomoci tzv. funkčních znaků rostlin:

Hypotézy:

H1: Selektivita jalovic na kontinuálním systému pastvy se liší v závislosti na různém typu porostu, stejně tak i různou intenzitou pastvy.

H2: Tzv. funkční znaky rostlin můžeme využít jako ukazatele selektivity jalovic.

H3: Chování jalovic vykazuje vývoj v průběhu jednotlivých sezón.

H4: Počasí a teplota vzduchu nijak neovlivňuje pastevní chování jalovic a výběr

ad4) Nutriční hodnota listí dřevin využívaných jako krmení skotu v pravěku

Cílem výzkumu bylo stanovit a porovnat obsah makroprvků a vlákniny z hlediska nutriční hodnoty pro výživu zvířat vybraných druhů listnatých dřevin (dub, lípa, jilm, javor, jasan a líška), které se využívaly jako zimní krmení (tzv. letnina) pro hospodářská zvířata a dřevin, které využívány nebyly (buk, topol, habr); dále porovnat vliv postupující sezony na nutriční hodnotu dřevin.

Hypotézy:

H1: Nutriční hodnota dřevin používaných jako zimní krmivo je vyšší než u dřevin, které se údajně nekrmily.

H2: Nutriční hodnota dřevin se liší s postupující sezónou.

ad5) Nutriční hodnota v zimě sbíraných letorostů dřevin využívaných jako zimní krmivo, a listí jmelí a břečťanu

Cílem výzkumu bylo stanovit obsah nutričních hodnot u 9 vybraných druhů listnatých dřevin (dub, lípa, jasan, líska, buk, topol, habr, vrba, bříza), 2 druhů jehličnatých dřevin (smrk, borovice) využívaných jako zimní krmivo pro hospodářská zvířata a 2 vždyzelených druhů rostlin (břečťan, jmelí), jakožto rostlin nalezených v archeologických nálezech výkalů hospodářských zvířat pomocí pylových analýz.

Hypotézy:

H1: Navzdory rozdílům v nutričních hodnotách listí mezi druhy se nutriční hodnota letorostů těchto druhů neliší.

H2: Nutriční hodnota jmelí je nízká, do krmiva bylo přimícháváno náhodou s jinými druhy (např. borovicí).

H3: Nutriční hodnota břečťanu popínavého v zimním období odpovídá požadavkům skotu na obsah živin a vlákniny, a představoval významnou složku dostupné zimní píce.

3. Literární rešerše

Trvalé travní porosty (louky a pastviny)

Travní porosty jsou komplexní a různorodá luční a pastevní rostlinná společenstva trav, jetelovin a dalších bylin (Klimeš 1997, Chytrý 2007). Z geografického hlediska travní porosty můžeme najít ve všech vegetačních pásmech, od tropů až po arktické oblasti, kde ze všech rostlinných formací, tvořených vyššími rostlinami, zasahuje nejdále na sever. Louky a pastviny se vyskytují roztroušeně po celém území ČR od nížin do hor (Chytrý *et al.* 2001) a většina jich je původních (Chytrý 2007). Ráz společenstev udávají vytrvalé trávy a dvouděložné bylinky, které tvoří obvykle hustě zapojené, často druhově bohaté porosty. Tyto porosty jsou schopny rychle vegetativně obnovovat svoji nadzemní biomasu, a tím se přizpůsobit hospodářskému využívání. Pro jejich vznik a udržení je víceméně pravidelná redukce nadzemní biomasy sečí nebo pastvou (Chytrý 2007).

Pastviny

Pastva je nejstarší způsob obhospodařování trvale travních porostů (Mládek *et al.* 2006). Hlavní funkcí pastvin je poskytování krmiva ať už divokým či domestikovaným býložravcům, jejich role jsou však i ekologické a krajinotvorné, redukují půdní erozi podporováním stability svahů, regulují vodní režim, zabraňují průniku hnojiv a pesticidů do povrchových a spodních vod a také jsou důležitým zdrojem biodiverzity a konzervace genetických zdrojů (Klimeš 1997).

Dle Katalogu biotopů ČR lze pastviny rozdělit do několika biotopů (Chytrý *et al.* 2001).

„pravé pastviny“

- X5 intenzivní kulturní pastviny
- T1.3 poháňkové pastviny
- T3.1 skalní vegetace s kostřavou sivou
- T3.2 pěchavové trávníky
- T3.3 úzkolisté suché trávníky
- T3.5 acidofilní suché trávníky
- T5 trávníky písčin a mělkých půd

- T7 slaniska

Louky „pastvou ovlivněny“

- T1.1 mezofilní ovsíkové louky
- T1.2 horské trojštětové louky
- T2 smilkové trávníky
- T3.4 širokolisté suché trávníky
- T1.10 porosty vlhkých narušovaných půd

X5 intenzivní kulturní pastviny

Tyto pastviny představují kulturní, nepřirozené porosty založené výsevem nebo vzniklé v minulosti intenzivním hnojením polopřirozených společenstev. Patří sem prostorové typy srhy říznačky, kostřavy luční, kostřavy rákosovité a jílku vytrvalého. Typické jsou velmi nízkým počtem přítomných druhů a v pozdním létě vysokým podílem jetel plazivého.

T1.3 poháňkové pastviny (*Cynosurion* Tüxen 1947)

Poháňkové pastviny jsou krátkostébelné pastviny, narušované trávníky a louky kosené vícekrát do roka. Porosty jsou nízké, ale zapojené, s dominancí trav (*Agrostis capillaris*, *Cynosurus cristatus*, *Dactylis glomerata*, *Festuca pratensis*, *Lolium perenn*, *Poa trivialis*) a pravidelným výskytem dvouděložných bylin snášejících časté narušování (*Bellis perennis*, *Plantago major*, *Taraxacum sect....*). Významné zastoupení mají vytrvalé růžicovité bylinky a bylinky snášející časté plazivými nadzemními výběžky. Pro vlastní pastviny jsou typické skupinky trnitých, jedovatých nebo pro dobytek nechutných rostlin, které výrazně přečnívají okolní nízký trávník (např. *Carduus* spp., *Cirsium* spp. a *Rumex* spp.). Mechové patro často chybí nebo je jen velmi chudé.

Pastviny se vyskytují na obdobných půdách jako mezofilní louky, liší se však četností odběrů nadzemní biomasy, takže vegetační kryt je odlišného charakteru. Nejvýznamnějšími faktory jsou selektivní spásání rostlin, odstraňování rostlinné biomasy během celého vegetačního období, narušování vegetace sešlapem a pravidelné hnojení. Vegetace travních porostů sečených několikrát do roka je často podobná vegetaci pastvin, ale chybějí v ní skupinky trnitých nebo nechutných rostlin. Pastviny se

nejčastěji vyskytují v oblastech s extenzivním zemědělským hospodařením, v blízkosti sídel, na vesnických záhumencích, v oborách, ale také na trávnících v obcích a městech.

T3.1 skalní vegetace s kostřavou sivou (*Festuca pallens*)

Jsou to otevřené trávníky skalnatých svahů suchých a teplých oblastí na různých typech tvrdých hornin s dominantní kostřavou sivou, česnekem chlumním horským nebo bez výrazných dominant. Jsou zde zastoupeny druhy suchých trávníků. Charakteristický je výskyt sukulentů, zejména tedy rozchodníků (*Sedum* spp.) a netřesku (*Jovibarba globifera*). Mechy a lišejníky jsou zastoupeny pravidelně.

T3.2 pěchavové trávníky

Pěchavové trávníky jsou zapojené trávníky s dominancí pěchavy vápnomilné (*Sesleria albicans*) a často s dalšími dealpínskými nebo perialpínskými druhy. Dále jsou pravidelně zastoupeny druhy suchých trávníků, ale i druhy lesní nebo druhy skalních štěrbin. Mechové patro je pravidelně vyvinuto. Nachází se převážně na strmých svazích nebo skalních ostrožnách na bázích bohatých horninách (vápencích převážně), například v Českém či Moravském krasu a okolí Prahy.

T3.3 úzkolisté suché trávníky

Více nebo méně zapojené nízké trávníky s dominancí trsnatých travin kostřavy valiské (*Festuca valesiaca*), ostřice nízké nebo pérovitých druhů kavylů. Nachází se v oblastech výslunných svahů o různém sklonu na basických horninách (vápence) například v okolí Slaného, Loun a Žatce, Českém středohoří či v Moravském krasu.

T3.5 acidofilní suché trávníky

Jsou nízké, víceméně zapojené trávníky s dominancí trav *Avenula pratensis*, *Festuca ovina*, *F.rupicola* nebo *Phleum phleoides*. Pravidelně bývají zastoupeny mechy. Nachází se na výslunných svazích jakéhokoli sklonu na kyselých silikátových horninách (žula, rula, pískovec,...). V minulosti byly využívány převážně jako pastva pro ovce.

T5 trávníky písčin a mělkých půd

Tyto trávníky se nacházejí na suchých písčinách v oblastech vátých písků kvádrových pískovců, jejichž přirozenou vegetací by byly acidofilní doubravy. Jsou to nízké mezernaté trávníky, kde převládají acidofilní trávy, buď statnější vytrvalé (*Agrostis capillaris*, *Avenella flexuosa*, *Festuca ovina*, *F. rubra*, ...) nebo drobné jednoleté trávy. Hlavní oblastí výskytu je Polabí, Třeboňsko či Opavsko.

T7 slaniska

Jsou to louky, pastviny a ruderální trávníky slaných půd, nacházející se například na Mostecku, Neratovicku a na jižní Moravě v okolí Mikulova. Porosty mohou být otevřené či uzavřené, s travinnou či bylinnou dominantou, mechové patro však zpravidla chybí. Škála rostlinných druhů je široká, druhy slaných půd (např. *Aster tripolium* subsp. *Panonicum*, *Carex secallina*), druhy mezofilních trávníků a luk (např. *Cirsium cant.*, *Festuca pratensis*,...) druhy těžších a střídavě vlhkých půd (*Carex distans*) či četné druhy ruderální (*Agrostis gigantea*, *Trifolium repens*,...).

T1.1 mezofilní ovsíkové louky (*Arhetanherion elatioris* Koch 1926)

Jsou to louky nížin a pahorkatin s dominantním ovsíkem vyvýšeným (*Arrhenatherum elatius*) nebo podhorské louky, ve kterých převažují trávy nižšího vzrůstu (např. *Agrostis capillaris*, *Anthoxanthum odoratum*, *Festuca rubra* s lat...). Z trav se dále vyskytuje například *Poa pratensis*, hojně jsou i širokolisté, na živiny náročné bylinky. Porost může být vysoký až 1m a je zpravidla 2x ročně kosen.

Ovsíkové louky se vyskytují na vyšších stupních aluviálních teras a na svazích, nejčastěji v blízkosti sídel. Na živinami dobře zásobených půdách převládá ovsík, na půdách chudších na živiny převládá kostřava červená (*Festuca rubra* s lat.). Roztrošené jsem po celém území ČR.

T1.2 horské trojštětové louky (sv. *Polygono-Trisetion* Br.-Bl. et Tüxen ex Marschall 1947)

Jsou středně vysoké louky s dominantními trávami (*Agrostis capillaris*, *Anthoxanthum odoratum* s lat., *Festuca rubra* s lat....) a montánními bylinami (např. *Cirsium*

heterophyllum, *Silene dioica*). Porosty jsou zapojené, mechové patro však má z pravidla jen malou pokryvnost.

Vyskytuje se v horských oblastech od nadmořských výšek kolem 600 m až po horní hranici lesa, výjimečně i nad ní. Půdy jsou vlhčí, středně zásobené živinami. Porosty jsou kosené jednou až dvakrát ročně a příležitostně přepásány.

T2 smilkové trávníky

Smilkové trávníky se nachází ve všech podhorských, horských a subalpínských polohách na kyselých substrátech, jako náhrada vegetace po různých typech acidofilních lesů, vzácněji klečových porostů. Jsou to nízkoproduktivní trávníky o výšce 40 cm a převažují v nich především nižší, často trsnaté traviny jako je smilka tuhá (*Nardus stricta*) a dále *Agrostis capillaris*, *Carex Pallescens*, *Festuca ovina*, aj. Jsou také přítomny různé druhy oligotrofních dvouděložných bylin.

T3.4 širokolisté suché trávníky

Jsou to zapojené až mezernaté trávníky, kde převažuje válečka prapořitá (*rychypodium pinnatum*), sveřepu vzpřímeného nebo kostřavy žlábkaté. Jsou poměrně druhově bohaté s větším množstvím širokolistých vytrvalých bylin. Nachází se na mírnějších svazích například Českého středohoří.

T1.10 porosty vlhkých narušovaných půd

Převládají středně vysoké travinobylinné porosty s dominujícím sítinami (*Juncus conglomeratus*, *J. effusus* a *J. inflexus*), ostřicemi (*Carex flava*, *C. hirta*, *C. nigra*) doprovodnými bylinami vlhkých půd, které snázejí mechanické narušování. Spíše maloplošné porosty se nacházejí na vlhkých až střídavě vlhkých oglejených až glejových půdách se silně kolísající hladinou podzemní vody, na kyselých i karbonátových podkladech a často na prameništích a podmáčených vazích.

Historie pastvy skotu

Pastva dobytka je jedním z významných faktorů, které utvářely středoevropskou krajину a daly jí i dnešní podobu. Ke změnám začalo docházet v mladší době kamenné čili neolitu (5300-4300 př. Kr.), kdy byl lov a sběr potravy postupně nahrazen zemědělstvím (Buček 2000, Mládek *et al.* 2006). Neolitický způsob života má tak za následek první zásahy člověka do prostředí, které bylo doposud přirozené. Chov hospodářských zvířat byl založen výhradně na pastvě až do starší doby železné (750 – 500 př. Kr.). K chovaným hospodářským zvířatům této doby patřil nejvíce skot, dále ovce, kozy a nejméně prasata (Beranová 1980, Mládek *et al.* 2006). Od jara do podzimu dobytek spásal travní porosty v okolí obydlí, v zimě dobytek okusoval větve stromů a keřů v pastevních lesích. Dle písemných záznamů z pozdějších dob lze předpokládat, že dobytek byl příkrmován větvemi, výhonky a listím dřevin, tzv. letninou (Rasmussen 1990, Halstead *et al.* 1998). Využívalo se zejména listí a větvičky dubu, lípy, jasanu, jilmu, vrby, olše, lísky javoru a jedle (Pokorný 2011). Teprve v mladší době železné (500-0 př. Kr.) se v archeologických nálezech objevují nejstarší kosy a mohou tedy vznikat louky, umožňující přípravu píce na zimní období (Buček 2000, Mládek *et al.* 2006, Beranová *et al.* 2010). Kosy však nevypadaly jako dnes, ale byly krátké. Biomasa se musela sklízet výše nad povrchem země a tím vznikalo poměrně velké strniště. Dlouhá kosa se u nás začala používat až ve 14. století (Hejman *et al.* 2006). Pastva se velmi rozrostla na témař všech místech a samozřejmě i v lesích (tzv. **lesní pastva**). Les byl nejen jistou potravní rezervou na období, kdy na bezlesích již nebyl dostatek potravy, ale byl i zdrojem potravy, kterou běžná pastvina neposkytovala, například plody lesních dřevin, zejména žaludy a bukvice. Zvířata si ale oblíbila i výmladky dřevin, pupeny nebo mladou kůru. Významné rozšíření plochy pastvin a luk nastalo se středověkou kolonizací výše položených oblastí, přesto však po celý středověk a ještě značnou část novověku převládalo extenzivní obhospodařování bez přihnojování. Jsou využívány tzv. obecní pastviny, na kterých se dobytek pase pospolu (Chytrý 2007). Vzrůstající potřeba dřeva však vyvolala v 16. století snahu po ochraně lesů před škodlivými vlivy pastvy a postupně byla zakázána úplně (18. století) (Buček 2000). Od konce 18. století jsou zvířata zavírána celoročně do stájí. V 19. století se velká rozloha bývalých obecních pastvin přeměnila na ornou půdu nebo na sečně využívané louky, ve větší míře se začínala používat minerální hnojiva (Mládek *et al.*

2006, Chytrý 2007). Poslední obecní pastviny se udržely zhruba do poloviny 20. století, ale úplně vymizely až po kolektivizaci zemědělství. Od padesátých let do roku 1990 docházelo k poklesu rozlohy trvalých travních porostů, zejména pak po odsunu německého obyvatelstva. Plochy, udržované pastvou, se převáděly na pole, louky a především kulturní lesy. V devadesátých letech 20. století se opět zavádí pastva masného skotu (tzv. bez tržní produkce mléka). Pastva začala být vyhledávaným způsobem obhospodařování trvalých porostů, avšak klesají jak stavy hovězího dobytka, tak i ovcí (Beranová *et al.* Kubačák 2010, Mládek *et al.* 2006, Hejcmán *et al.* 2006).

Pastevní systémy

Do poloviny 20. století byla pastva většinou neřízená, tzn. zcela volná nebo se omezovala na pastvu příležitostnou (například v okolí chlívů). Rozvoj pastveních systémů a jejich uplatňování ve větším měřítku nastal ve druhé polovině 20. století, kdy po druhé světové válce nastala potřeba zvýšení zemědělské produkce. Z hlediska obhospodařování pastviny je důležité vybrat vhodný systém pastvy. Používané pastevní systémy lze rozdělit na dvě základní skupiny, tzv. řízené (kontrolované) a neřízené (nekontrolované) (Brundage *et al.* Petersen 1952) neboli na rotační a kontinuální (Mládek *et al.* 2006, Pavlů *et al.* 2002, Mrkvička 1998).

Tab. 1: Srovnání porostu při rotační a kontinuální a pastvě (Hrabě et Buchgraber 2004)

Rotační pastva	Kontinuální pastva
větší asimilační plocha (LAI)	menší asimilační plocha (LAI)
vyšší produkce píce	nižší produkce píce
průměrná až vyšší kvalita	vysoká kvalita píce
méně jetelovin více trav	více jetelovin, "méně plevelů"
řidší dm	hustejší dm
vyšší zatižení pastviny	nižší zatižení pastviny
nižší denní přírůstek zvířat	vyšší denní přírůstek zvířat

Rotační a kontinuální pastva

Rotační pastva (rotational grazing, intermittent grazing) je definována jako spásání dvou a více pastvin (oplùtků), kde se střídá doba pasení s dobou obrùstání oplùtku. Počet zvířat na pastvině může být stálý nebo variabilní (Brundage *et al.* Petersen 1952, Bertelsen

et al. 1993, Frame 1992, Mrkvička 1998, Pavlů *et al.* 2006, Pavlů *et al.* 2002). Nejjednodušší formou pastvy rotační je tzv. **týdrování**, kde zvíře vypase plochu v dosahu řetězu či provazu, na kterém je uvázáno. Dalším typem je **pastva honová**, při které je pastva rozdělena na 4-6 částí, tzv. honů, které se spásají 10-20 dnů (Mládek *et al.* 2006).

Dalším systémem pastvy je **oplútková pastva**, což je systém pastvy, který byl rozpracován v západoevropských zemích již koncem 18. století (Mrkvička 1998). Její princip spočívá v tom, že je pastvina rozdělena na určitý počet většinou stabilně oplocených oplútků (zpravidla 6-24), jejichž velikost je volena s ohledem na výnos a velikost stáda. Oplútky zvířata vypásají po dobu 2-5 dnů. Tato pastevní forma tvoří přechod mezi extenzivní a intenzivní pastvou se

zatížením 1,5-3 DJ.ha-1 (Pavlů *et al.* 2003). Do oplútkové pastvy lze zařadit i postupnou a postupnou bariérovou pastvu, které se nejvíce využívají v USA (Mrkvička 1998).

- **Postupná pastva** – do oplútka mají jako první přístup zvířata s nejvyššími nároky na kvalitu píce (dojnice, telata, jehňata aj.). Po spasení nejkvalitnější píce je tato skupina přehnána do dalšího oplútku. Další skupina zvířat (tzv. „druzí spásaci“) s nižší nutriční potřebou dopase zbytky v oplútku po první skupině.
- **Postupná bariérová pastva** – představuje modifikaci postupné pastvy, kdy se zvířata s vyšší nutriční potřebou pasou s ostatními, avšak mají přístup do následujícího oplútku

Dalšími typy pastvy je pastva dávkovaná a pásová. Principem **dávková pastva** je přidělování dávek pastevní píce a plochy porostu, odpovídající denní nebo polodenní spotřebě stáda pomocí elektrického oplocení. **Pásová pastva** je taková pastva, která zvířatům se elektrickým ohradníkem přiděluje pás porostu („pohyblivý žlab“) o šířce 0,5 – 1 m a délce odpovídající 1,5 m na 1 DJ (tj. 3 m na 1 t živé hmotnosti stáda) s dobou vypasení asi 2-3 hodiny. Šířka přiděleného pásu závisí na výšce porostu, pravidlem je, že čím je vegetace vyšší, tím užší má být vymezený pás. Variantou pásové pastvy je tzv. **bloková pastva**, kdy spásaný oplútek má mít nejlépe čtvercový tvar. Tím se zabránuje chůzi podél delších částí oplocení, jako je tomu v případě dlouhých úzkých pásů u pásové pastvy. Bloková pastva se používá zvláště při pasení

skotu a ovcí v pomalé rotaci hlavně v zimě v Austrálii a Novém Zélandu (Pavlů *et al.* 2003, Pavlů *et al.* 2002).

Další formou rotační pastvy je tzv. **začišťovací pastva**, která se používá v situacích, kdy je k dispozici velké množství zvířat. Ta jsou přeháněna z oplútka po jeho úplném vypasení, které trvá různě dlouhou dobu v závislosti na fenologickém stádiu vegetace (např. 2 hodiny na mladé jarní trávě a 2 a více týdnů při vrcholu růstové periody). Začišťovací pastva se většinou používá při pastvě ovcí v období mezi bahněním a připouštěním ke spasení přestárlého porostu.

Velmi intenzivní rotační je pastva je používána mnoha farmáři na Novém Zélandu, kde jsou zvířata přeháněna 2x až 3x za 24 hodin. Tato pastva je vysoce produktivní pastvou (Brundage *et Petersen* 1952).

Kontinuální pastva (set stocking, continuous stocking) je definovaná jako nepřetržité pasení zvířat na jedné pastvině (oplútku) během roku nebo pastevní sezóny, při přerušení pastvy maximálně na tři dny (Brundage *et Petersen* 1952, Hodgson 1979, Mrkvička 1998, Pavlů *et al.* 2006). Výhodou tohoto způsobu pastvy jsou nízké finanční nároky (nižší pořadavky na oplocení, nižší potřeba manipulace se zvířaty) (Hejcmán *et al.* 2002).

Intenzita pastvy

Intenzita pastvy je zatížení pastviny zvířaty ve vztahu k produkci rostlinné biomasy na jednotku plochy. Intenzita neboli zatížení pastviny je dáno počtem nebo hmotností zvířat na jednotku plochy, tzn. počtem dobytčích jednotek (DJ) na 1 ha pastviny.

Stanovení intenzity pastvy

1) Výpočtem zatížení pastviny, kdy získáme odhad maximálního počtu zvířat, která mohou být na pastvině pasena celou pastevní sezónu (Mládek *et al.* 2006, Pavlů *et al.* 2002).

Do vzorce k vypočítání zatížení pastviny dosazujeme tyto proměnné:

- Celková plocha travních porostů na celou pastevní sezónu (PP)
- Odhadovaný průměrný výnos sušiny pastviny z 1 ha (PV)

- Odhadnutá délka pastevní sezóny ve dnech (DP)
 - Odhad průměrné živé hmotnosti paseného zvířete (ŽH) (počáteční hmotnost + konečná hmotnost/2)
- $$[(\text{PP}) \times (\text{PV})] / [(0,04) \times (\check{\text{Z}}\text{H}) \times (\text{DP})] = (\text{MP})$$

Číslo 0,4 znamená, že zvířata mají denní potřebu píce v průměru 4 % jejich živé hmotnosti. Výsledek (MP) se pak jednoduchým výpočtem převede do tvaru Dj.ha-1 za rok nebo pastevní období:

$$[(\text{MP}) \times (\check{\text{Z}}\text{H}) / 500] / (\text{PP}) = \text{zatížení pastviny v DJ.ha-1}$$

2) Podle cílových výšek porostu

Cílové výšky porostu se měří pomocí talířového měřidla (rising plate meter) v pravidelné vzdálenosti podél předem vytýčeného transektu, vedoucího přes pastvinu (tzv. stlačená výška porostu). Průměrná hodnota pak charakterizuje intenzitu pastvy (Correl *et al.* 2003, Dumont *et al.* 1995)

Kontinuální pastva extenzivní (volná) – představuje neregulované využití pastviny. Zvířata se pohybují volně na jedné pastvině (oplútku) během celé pastevní sezóny (Pavlů *et al.* 2003). Volná pastva má negativní vliv na snižování výnosového efektu pastvin v důsledku selektivního spásání porostu zvířaty (zvířata si vybírají nejhodnotnější rostliny), zbylý porost tedy není řádně využit a je znehodnocován pošlapáním a kálením. U nás byla tato neorganizovaná pastva příčinou znehodnocení velkého množství travních porostů (Mrkvička 1998). Nehodí se pro zvířata, která mají (Pavlů *et al.* 2003) vysoké nároky na kvalitu porostů (např. telata, dojnice). Obvykle je tato pastva uplatňovaná na horských pastvinách se zatížením 0,5-1,0 DJ.ha-1 (Mrkvička 1998; Pavlů *et al.* 2003).

Kontinuální pastva intenzivní – zastupuje vysoce produktivní využívání pastviny se zatížením pastviny 1,5-3 DJ.ha-1. Podle nárůstu biomasy se mění buď plocha pastvin, nebo počet zvířat. Intenzivní pastva se používá na kvalitních výnosných pastvinách (Mrkvička 1998, Pavlů *et al.* 2003).

Kontinuální pastva 1.2.3. – jedná se o modifikovaný systém, kdy na začátku pastevního období je spásána 1/3 plochy a zbylé 2/3 jsou posečeny k výrobě konzervované píce, například sena nebo siláže. Po nárůstu posečeného porostu jsou zvířata přesunuta na tuto plochu a za 5-6 týdnů plocha, která byla dříve jen spásaná, je pokosena. Dále se celá plocha pastviny využívá jen pasením. Kombinované využití pastvin (střídání pastvy a sečení) podporuje vytrvalost porostů. Používá se především pro výkrm skotu a při chovu mladých dojnic (Mrkvička 1998, Pavlů *et al.* 2003).

Pastevní chování

Pastevní chování skotu se projevuje střídáním několika typů chování. Hlavní aktivita na pastvě je rozdělena na periody pasení, žvýkání, přežvykování, odpočinku a sociálního chování (Mrkvička 1998, Hauptman 1972). Dalšími projevy jsou napájení, kálení či močení, pohyb a komfortní chování. Skot na pastvě stráví přibližně 95% času hlavními typy chování (Kilgour *et al.* 2012), ačkoli Hall (1989) uvádí pouze 74% až 85%. Pastevním chováním se v minulosti zaobírala mnoha autorů (např. Hejcmanová *et al.* 2009, Hull *et al.* 1960, Dumont *et al.* 1995, a mnoho dalších). Mnozí z nich se ovšem soustředili na hlavní projevy chování – pastvu, přežvykování a odpočinek a málo z nich se zaměřovalo na komfortní chování či sociální interakce, jak uvádí Kilgour *et al.* (2012).

Pasení

Skot je pastevní generalista, tzn., že spásá porost výrazně výběrově. Skot nemůže spásat porost nižší než 4 cm. Souvisí to se způsobem příjmu potravy, využívá totiž svého dlouhého pohyblivého jazyka k obtočení rostlin, vtáhnutí do tlamy a utrhnutí.

Délka pastvy u skotu se během dne liší u jednotlivých kategorií, plemen a vykazuje velké rozdíly i mezi jednotlivci. U skotu se udává široké rozhraní délky pastvy a to 4,33 hodin až 13,2 hodin (Hrouz *et al.* 2000). Kilgour *et al.* (2012) uvádí průměrně 6,1 hodin pastvy za den, tj. 5,0 – 7,3 hodiny na jednotlivá stáda. Při průměrné kvalitě pastevního porostu by neměla být celková doba pastvy jalovic během dne kratší než 7 hodin. Na podřadné píci se mladý skot pase více než 10 hodin, převážně v pohybu (Mrkvička 1998). Skot se pase téměř výlučně ve dne, jak také potvrzuje Kilgour (2012). Z celkové doby pasení v délce 7-8 hodin zabírá denní pastva 80-90 % a pouze 10-20 % připadá na noční pastvu (Mrkvička, 1998). K častějšímu pasení v noci dochází v případě vysokých

denních teplot (Hrouz *et al.* 2000). Pastva je rozdělena do 3-4 period během dne. První hlavní perioda začíná těsně před svítáním a trvá 2-3 hodiny. Druhá hlavní perioda začíná po poledni a končí se západem slunce. Mezi těmito periodami se vyskytuje kratší doby pasení, jak v dopoledních tak i v odpoledních hodinách, to je však závislé na teplotě a vydatnosti pastvy (Voříšková *et al.* 2001).

Přežvykování

U zvířat s vícekomorovým (4 komory - bachor, kniha čepec, slez) žaludkem je vyvinuto opakované přežvykování, které umožňuje vysokou efektivnost využití rostlinné potravy (Zahrádková *et al.* 2009). Přežvykování začíná zhruba 15 – 70 min po příjmu potravy. Přežvykování se skládá ze tří fází: rejekce, přežvykování a proslinění a polykání. Během rejekce dochází k vyvrhnutí obsahu předžaludků do dutiny ústní, kde se tento obsah formuje do podoby sousta prosliňováním a pohyby čelistí při přežvykování (Hrouz *et al.* 2000, Voříšková *et al.* 2001). Délka přežvykování se výrazně liší (Kilgour *et al.* 2012 uvádí 4,7 až 10,2 hodin za den), a to obsahem vlákniny, množstvím porostu a velikostí sousta. Jak se shoduje většina studií, během přežvykování skot obvykle leží a je zde větší tendence ruminace během noci (Kilgour *et al.* 2012).

Odpočinek

Odpočinek je definován jako ležení nebo stání, při kterém zvíře nevyvíjí žádnou aktivitu. Převážná část odpočinku probíhá vleže. U přežvýkavců se doba odpočinku spojuje s přežvykováním (Hrouz *et al.* 2000, Kilgour *et al.* 2012). Skot odpočívá během 24 hodin v několika periodách, z nichž nejdelší je noční, která trvá od 22 hodin do 4 hodin, kdy začíná ranní pastva. Druhá nejdelší perioda nastává v odpoledních hodinách a trvá 2-3 hodiny.

Sociální chování

Sociální chování je ovlivněno hierarchii ve stádě. Vysoko postavená zvířata jsou obvykle vůdci a zvířata na nízkém hierarchickém stupni jsou nezávislá a nenásledují skupinu. Pohyb stáda tedy může být chápán jako kumulativní reakce vysoko postavených zvířat, ostatní zvířata je následují (Bailey *et al.* 1998, Voříšková *et al.* 2001).

Další pastevní aktivity

Mezi další pastevní aktivity patří napájení, pohyb či komfortní chování.

Pití neboli příjem vody závisí na hmotnosti, věku, teplotě a vlhkosti prostředí, obsahu sušiny v krmné dávce, stádiu laktace a březosti. Při vyšších teplotách prostředí se zvyšuje spotřeba vody, protože se zvyšuje odpar vody kůží. Potřeba vody za 24 hodin se u skotu při zeleném krmení pohybuje v rozmezí od 25 do 40 litrů (Hrouz *et al.* 2000). Dalším projevem aktivity skotu na pastvě je chůze. Pohyb představuje aktivitu, při níž dochází k přesunu zvířete (Voříšková *et al.* 2001). Vzdálenost, kterou zvířata při pastvě urazí, záleží na produkci pastevních porostů, příkrmu, klimatických podmínkách a reliéfu terénu (Hrouz *et al.* 2000). Během dne se doba chůze pohybovala od 0,2 hodin do 1,4 hodin, zatím co během celých 24 hodin to bylo v průměru od 0,2 až 2,9 hodin (Kilgour *et al.* 2012). Dalším projevem chování je komfortní chování, to představuje péči o povrch těla. Patří sem olizování, drbání, tření, slunění, válení na zemi, ale i protahování a zívání apod. (Veselovský 2008, Hrouz *et al.* 2000, Voříšková *et al.* 2001).

Vliv pastevního porostu na chování a produkci zvířat

Typ pastviny, systém nebo intenzita pastvy určují základní charakteristiky porostu a sociálního prostředí, což jsou důležité faktory, které ovlivňují pastevní chování a užitkovost zvířat. Například, intenzivně obhospodařované pastviny oseté vysokoprodukčními rostlinami („improved“ pastures), kde dominují jílek vytrvalý (*Lolium perenne L.*) a jetel plazivý (*Trifolium repens L.*) nabízí zvířatům porost s vyšší nutriční hodnotou než druhově bohaté přirozené nebo polopřirozené travní porosty a výsledkem jsou i vyšší váhové přírůstky (Fraser *et al.* 2009). Na druhou stranu, pastva na přirozených travních porostech má pozitivní vliv na kvalitu masa (Fraser *et al.* 2009) a mléka (Priebe 1988). Denní přírůstky hospodářských zvířat jsou pozitivně ovlivněny výškou porostu (Realini *et al.* 1999). Porost při nízké a střední intenzitě pastvy je vyšší (Pavlů *et al.* 2006), proto nabízí více dostupné píce a tím zvyšuje velikost sousta a čas strávený pastvou (Hejcmánková *et al.* 2009). Podle Sharrawa (1983) pastevní systémy nevykazují žádný významný vliv na pastevní chování či příjem potravy, a je-li intenzita pastvy mezi systémy podobná, i rotační a kontinuální systém pastvy umožňuje dosáhnout podobného výstupu z hlediska denního hmotnostního přírůstku hospodářských zvířat (Bertelsen *et al.* 1993, Hepworth *et al.* 1991, Hart *et al.* 1993,

Kitessa *et al.* 2001) nebo produkce mléka (Pulido *et al.* 2003), i když některé studie uvádějí opak (Walton *et al.* 1981).

Druhově bohaté pastviny mohou také ovlivnit rozhodování a chování pasoucích se zvířat. Domestikovaní býložravci na pastvinách jsou vystaveni sérii rozhodnutí dělaných v různých prostorově-časových škálách (Roguet *et al.* 1998). Jsou především kontinuálně vystaveni sérii krátkodobých rozhodnutí, co selektovat a kde se pást. Tohle je základní rozhodnutí kompromisu mezi kvalitou píce a přijatou kvantitou (Griffiths *et al.* 2003, Sharow *et al.* 1979, Dumont 1997, Dumont *et al.* 2007). Bylo zjištěno, že velcí býložravci jsou schopni vracet se na místa s vyšší nutriční hodnotou častěji, než na místa s nižší nutriční hodnotou (Bailey *et al.* 1995, Dumont *et al.* 2002). Podobný pokus provedl Dumont a Petit (1998) na ovcích. Rozhodnutí, jaký management pastvy použít na druhově bohatých porostech tudíž vyžaduje základní znalosti vzájemných vztahů rostlin a býložravců.

Ale nejen struktura porostu, ale i jiné faktory pastevního prostředí mohou ovlivnit chování zvířat a jejich užitkovost. Jsou to faktory abiotické, například klimatické faktory, terénní podmínky či vzdálenost od vodního zdroje (Senft *et al.* 1987, Bailey *et al.* 1996). Při pastvě dobytka se z klimatických faktorů uplatňují teplota vzduchu, srážky, sluneční záření a povětrnostní podmínky (Roquet *et al.* 1998, Harris *et al.* 2002, Hejcmanová *et al.* 2009).

Vliv zvířat na strukturu a kvalitu pastevního porostu

Také zvířata ale dokáží svou pastvou ovlivnit strukturu pastevního porostu (Frame 1992, Watkinson *et al.* 2001, Rook *et al.* 2004). Hlavním mechanismem, který ovlivňuje pasoucí se zvířata, je heterogenita neboli různorodost porostu. Pastva stimuluje obrůstání rostlin, protože staré a mrtvé listy nestíní listům mladým (Begon *et al.* 1997). Pastviny, které jsou vystaveny přiměřenému pastevnímu tlaku, vykazují vysokou druhovou biodiverzitu jak flory, tak i fauny. Heterogenita porostu je způsobena převážně selektivním vypásáním porostů, tzv. odlistěním (defoliací) a dochází tak ke změně světelních podmínek a tudíž ke konkurenci rostlinných druhů (Rook *et al.* 2004). Pouze některé rostliny jsou dobře přizpůsobeny neustálému spásání (např. *Trifolium repens*, *Lolium perenne*), právě proto se vyskytují na kontinuálně pasených porostech. Rostliny uplatňované při pastvě rotační, potřebují pro zdarný vývoj klidové

období bez pastvy. Výnos biomasy (Paine *et al.* 1999) nebo kvalita píce (Walton *et al.* 1981, Walker *et al.* 1989, Pulido *et Leaver* 2003) se můžou v různých pastveních systémech lišit.

Selektivním vypásáním, sešlapem a obohacováním porostu o exkrementy se struktura porostu velmi rychle mění, ať již změnou světelních podmínek, diferenciací fenologického vývoje či redistribucí živin. Odstraněním starých, odumřelých částí rostlin se zvyšuje nejen čistý výnos píce, ale také půdní vlhkost, a to zvyšováním hustoty přízemní vrstvy (Mládek *et al.* 2006). Dalším faktorem ovlivňujícím hlavně kvalitu porostu je vylučování tuhých a tekutých výkalů. Množství závisí na frekvenci močení a kálení. Na místě tuhých výkalů pak vznikají tzv. nedopasky, místa, kterým se zvířata záměrně vyhýbají. Nedopasky vznikají i na extenzivně využívaných porostech, kde čerstvě obrůstající plošky jsou skotem preferovány před ploškami s vyzrálejší vegetací (Adler *et al.* 2001, Pavlů *et al.* 2003). Mezi další mechanismy lze zařadit například zhutňování půdy, šíření semen či pastevní preferencí.

Ale nejen pastva sama o sobě, ale i typ pastevního systému mění složení vegetace v travních porostech. Například intenzita pastvy má nesporný vliv na vegetaci. Extrémy v intenzitě pastvy redukují druhovou diverzitu (Watkinson & Ormerod 2001) a mění kvalitu porostu. Hofman *et al.* (2001) prokázal výrazně nižší nutriční hodnotu u porostu z extenzivní pastvy, nežli u porostu z pastvy intenzivní. Také Pavlů *et al.* (2006) uvedl významné rozdíly v parametrech kvality porostu (dusíkaté látky, vláknina, organický materiál). Oba uvedli, že celková produkce biomasy byla u intenzivní pastvy vyšší, než u pastvy extenzivní.

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5. Výsledky dizertační práce

- I. **Stejskalová M.**, Hejmanová P., Pavlů V., Hejman M. 2013. Grazing behavior and performance of beef cattle as a function of sward structure and herbage quality under rotational and continuous stocking on species-rich upland pasture. *Animal Science Journal.* 84, 622–629.
- II. Hejmanová P., **Stejskalová M.**, Pavlů V., Hejman M., 2009. Behavioural patterns of heifers under intensive and extensive continuous grazing on species-rich pasture in the Czech Republic. *Applied Animal Behaviour Science* 117. 137-143.
- III. **Stejskalová M.**, Hejmanová P., Ludvíková V., Pavlů V., Hejman M. Plant functional traits as drivers of heifers' selectivity for a patch on heterogeneous pasture. *Animal* (submitted).
- IV. Hejmanová P., **Stejskalová, M.**, Hejman, M. 2013. Forage quality of leaf-fodder from main broad-leaved woody species and its possible consequences for the Holocene development of forest vegetation in Central Europe. *Vegetation History and Archeobotany.* 007/s00334-013-0414-2.ljk
- V. Hejman M., Hejmanová P., **Stejskalová M.**, Pavlů V. 2014. Nutritive value of winter collected annual twigs of main European woody species, mistletoe and ivy and its possible consequences for winter foddering of livestock in prehistory. *The Holocene* (Accepted).

5.1 Článek I.

Stejskalová M., Hejmanová P., Pavlů V., Hejman M. 2013.

Grazing behavior and performance of beef cattle as a function of sward structure and herbage quality under rotational and continuous stocking on species-rich upland pasture.

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**ORIGINAL ARTICLE**

Grazing behavior and performance of beef cattle as a function of sward structure and herbage quality under rotational and continuous stocking on species-rich upland pasture

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ABSTRACT

An experiment to reveal functional response and heifers' performance to sward characteristics and forage chemical composition was conducted for 5 years in rotational (RSS) and continuous (CSS) stocking systems on native species-rich upland grassland. We measured sward characteristics, forage chemical composition, heifers' grazing behavior and live-weight gains from July to September. Mean sward surface height was lower on CSS than on RSS; grass and forb density, and white clover stolon length, were similar. Herbage on CSS had higher crude protein content and lower crude fiber content than on RSS. No difference existed in time budgets of grazing, ruminating and resting between stocking systems and season, while grazing rates were higher on CSS. Stocking rate was 1671 and 1332 kg per ha on CSS and RSS, individual daily live-weight gain 683 and 652 g on CSS and RSS. Gain per ha was 20 kg higher on CSS. Results suggested stocking systems on native species-rich grassland had no effect on activity time budgets or animal performance. Both RSS and CSS allow similar outputs for stocking rates in terms of individual daily live-weight gain. Key parameters determining heifers' behavior and performance were sward height, grass and forb density in the sward, and content of crude fiber and protein in forage.

Key words: animal performance, grazing behavior, semi natural grasslands.

INTRODUCTION

Management systems relate directly to key components of animal performance. Pasture type, applied stocking system or grazing intensities determine basic sward characteristics and social environment, which in turn are important determinants of grazing behavior and animal performance. Improved pastures offer swards of high nutritive value to animals, resulting in better outcomes, whereas grazing on species-rich grasslands may not bring the highest levels of animal performance but may have positive effects on meat quality (Fraser *et al.* 2009). Livestock forage intake and performance are responsive to sward characteristics (Realini *et al.* 1999; Pavlů *et al.* 2006; Hejcmanová *et al.* 2009), while inconsistent effects are reported for rotational and continuous stocking systems (e.g. Kitessa & Nicol, 2001; Derner *et al.* 2008). However, most of the studies were conducted in intensive production systems with few highly productive plant species. On species-rich pastures, animals' foraging decisions

become more complex because of spatially heterogeneous sward and more variability in food resources of diverse quantity and quality. Consequently, the functional response of animal behavior and performance may become composite without obvious relationships to particular herbage components.

The overall aim of this research was focused therefore on exploring the functional response of heifers' behavior and performance on species-rich sward in two contrasting stocking systems on native mountain grassland. The objectives were: (i) to determine which sward characteristics and herbage quality parameters are the principle drivers of activity time budgets and grazing behavior of heifers; (ii) to determine which

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sward characteristics and herbage quality parameters are the principle determinants of heifers' performance; (iii) to figure out the overall functional relationships among sward parameters, cattle behavior and live-weight gains.

MATERIALS AND METHODS

Study area

The experiment was carried out on experimental pasture in the Jizera Mountains ($50^{\circ}49'N$, $15^{\circ}02'E$), 10 km north of Liberec, Czech Republic. Average precipitation for the area is 803 mm and the mean annual temperature is $7.2^{\circ}C$. The experimental pasture was established at an altitude of 420 m asl (above sea level). Vegetation on the pasture was classified as *Cynosurion*, with some elements of *Arrhenatherion* (Pavlů *et al.* 2003). Pasture sward had a high species diversity, ranging from 11 to 17 plant species per m^2 , dominated by grasses: couch grass (*Agropyron repens*), ryegrass (*Lolium perenne*), meadow foxtail (*Alopecurus pratensis*), orchardgrass (*Dactylis glomerata*), meadow fescue (*Festuca pratensis*), rough bluegrass (*Poa trivialis*), colonial bentgrass (*Agrostis capillaris*), Kentucky bluegrass (*Poa pratensis*) and forbs: white clover (*Trifolium repens*), dandelion (*Taraxacum officinale*) and fall dandelion (*Leontodon autumnalis*). Pasture productivity ranged from 5 to 7 tons/ha of dry matter biomass per year (Pavlů *et al.* 2003).

Management and experiment design

The experiment was conducted for 5 years, from 1993 to 1997. Rotational (RSS) and continuous (CSS) stocking systems (synonymous with short-duration rotational grazing and season-long grazing systems for RSS and CSS, respectively) were applied to the pasture, each of them on an area of 1 ha (Fig. 1). The RSS area was divided into six 0.166 ha paddocks. Heifers grazed paddocks consecutively, for a period ranging 2–7 days. The CSS consisted of one 1 ha paddock. Heifers grazed this paddock continuously throughout the grazing season. The average sward surface height of 5–7.5 cm was maintained by varying the number of animals, continuously for the whole grazing season on CSS and as residual sward surface height at the end of grazing on RSS. Both stocking systems were grazed by four to six heifers (Czech Pied, Friesian or crossbreeds Friesian \times Czech Pied, Czech Pied \times Charollais) of 131–206 kg in initial live weight. The animals were of the same age and came from the same breeding conditions. The grazing season started in early May and ended in September or mid-October. Sward in paddocks was partially cut in May before the start of grazing: two-thirds of CSS paddock sward and the three last-grazed paddocks in the six-paddock system on RSS.

Sward measurements

Data on sward characteristics (sward surface height, grass density, forb density and white clover *Trifolium repens* stolon length) and sward biomass for determining forage chemical composition were collected once a month at regular intervals (at the beginning of each of July, August and September) for each of the 5 years from 1993 to 1997.

Sward surface height was measured regularly for the whole grazing season using the 'first contact method' (modified point-quadrat method) (Mueller-Dombois & Ellenberg, 1974). In CSS, sward height was recorded twice a week at

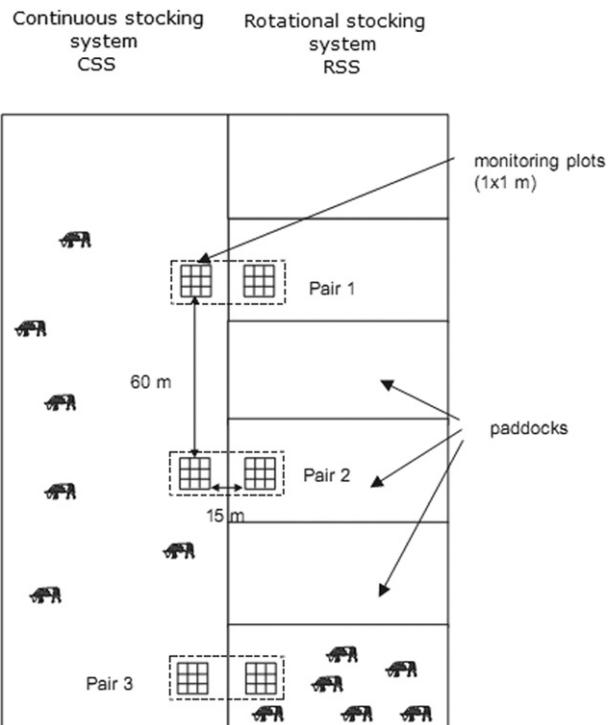


Figure 1 Design of the experiment with spatial arrangement of paddocks and plots monitoring the sward characteristics and forage chemical composition in two stocking systems.

100 points on a 20-m transect. In RSS, sward height was measured before and after plots were grazed and consisted of 50 records per plot on 10-m transects. For analyses, we used the latest measurements taken before observation of animal behavior began for CSS, and the measurement before grazing on RSS to compare actual sward surface height as much as possible. In order to determine other sward characteristics, three paired plots (1×1 m) were established on the pasture (Fig. 1). Grass density (number of grass tillers), forb density (number of forb stems), white clover stolon length (length of the stolon between growing point and leaf) were counted in 20×5 cm quadrats inside these plots before each animal observation during the grazing season, and recalculated to an area of $1 m^2$. To determine forage chemical composition as an indicator of forage quality, fresh biomass was hand-plucked before each animal observation and dried for 48 h at $70^{\circ}C$. Dry organic matter (OM) content, crude protein (CP), crude fiber (CF) and ash contents were analyzed by the methods of AOAC (1984).

Animal measurements

Data on animal behavior and performance were collected after sward measurements were accomplished, once a month at regular intervals (at the beginning of each July, August and September) for each of the 5 years from 1993 to 1997.

Animal behavior was recorded in 24-h direct observation sessions by three trained observers using the herd scan sampling method (Lehner 1996), at intervals of 15 min during

daylight hours (according to sunrise and sunset times in season from 04.00 or 06.00 hours to 19.00 or 21.00 hours) and 1 h during the night time (from 19.00 or 21.00 hours to 04.00 or 06.00 hours). The principal activities of heifers grazing on pasture were grazing (defined as biting, chewing or swallowing herbage, or walking with muzzle close to the sward), ruminating (chewing the cud), resting (defined as lying or standing without any activity), and 'other behavior', including activities such as drinking, salt-licking, comfort behavior and social interaction. In addition, the biting rates (number of bites per min) were recorded as three types of jaw movements (hereafter as bite): grazing, chewing and ruminating. Grazing bite was defined as a wrenching of the vegetation sward, chewing bite as jaw movements while grinding the forage in the muzzle before swallowing and ruminating bite as jaw movements while chewing the cud. There were 10 records for each type of biting rate in both stocking systems during each observation session.

All heifers were weighed, and live-weight gains (LWG) calculated, for both stocking systems once a month during the whole grazing season for each year.

Data analyses

To compare individual sward characteristics and forage chemical composition between RSS and CSS, and its development in the season, we used repeated measures analysis of variance (ANOVA) (using data from paired plots) separately for each parameter. In all analyses, the categorical predictors were date of observation session (July, August, September), stocking system (RSS, CSS) and the interaction 'date × stocking system'. Tested parameters were sward height, grass density, forb density and white clover length as sward characteristics, and CP, CF, OM and ash as indicators of forage quality.

To test the effect of the season, year, stocking system and their interactions on animal behavior in terms of total time spent on each defined behavior, we used repeated measures ANOVA, with data from paired herd observation sessions separately for each activity. To determine which parameters of sward characteristics and forage chemical composition are (separately) the best predictors of the total daily grazing time of animals, we used multiple forward stepwise regression.

To test the effect of season, stocking system and their interactions, on biting rates, we used factorial ANOVA for grazing, chewing and ruminating rates, separately. To determine which parameters of sward characteristics and forage

quality are (separately) the best predictors of grazing rate, we used multiple forward stepwise regression.

To evaluate animal performance, two separate two-way ANOVAs were used: (i) to test the effect of year, stocking system and their interactions, on daily weight gain during the whole grazing season from May to the end of September; and (ii) to test the effect of intra-seasonal period, stocking system and their interactions, on the daily weight gain in each period. The relationship of daily grazing time separately to weight of animals and daily weight gain was tested using correlation matrices. To determine which parameters of sward characteristics and forage quality are (separately) the best predictors of daily weight gain, we used multiple forward stepwise regression. All analyses were performed using STATISTICA 7.0 software (Statsoft, Tulsa, OK, USA).

Unconstrained principal components analysis (PCA) was used to visualize relationships among all sward characteristics, forage chemical composition, all recorded animal behavior and animal performance, using the CANOCO for Windows 4.5 package; and the ordination diagram was constructed by the CANODRAW program (ter Braak & Šmilauer 2002).

RESULTS

Sward characteristics

The results for sward characteristics and forage chemical composition are set out in Table 1. For the 5 years of the experiment, sward characteristics varied only in sward height (before grazing on RSS) between stocking systems ($F_{(1,10)} = 63.63$, $P < 0.001$), whereas there was no difference between stocking systems for grass tiller density, forb density and white clover stolon length (in all analyses $P > 0.05$). Sward height was higher in RSS before grazing each paddock than in CSS, whereas after grazing the RSS paddock, the sward height was not significantly different from CSS ($F_{(1,10)} = 1.48$, $P = 0.81$). Sward characteristics did not show any significant difference among periods as the season progressed, nor was there any significant difference in the interaction between stocking system and period (in all analyses $P > 0.05$). Forage chemical composition differed between stocking systems in the content of CP ($F_{(1,10)} = 21.45$, $P = 0.0012$) and CF

Table 1 Sward characteristics and forage chemical composition in continuous and rotational stocking systems (RSS)

Sward characteristics	Continuous stocking system		Rotational stocking system		Significance		
	Mean	SE	Mean	SE	SS	Period	SS × period
Sward surface height, cm	5.9	0.3	—	—			
- For RSS before grazing the paddock	—	—	12.8	0.8	**	n.s.	n.s.
- For RSS after grazing the paddock	—	—	7.2	0.9	n.s.	n.s.	n.s.
Grass density/m ²	4131	375	4267	399	n.s.	n.s.	n.s.
Forb density/m ²	667	66	577	101	n.s.	n.s.	n.s.
Clover length, cm	25.8	2.8	22.9	2.7	n.s.	n.s.	n.s.
Crude protein, g/kg	212.0	6.6	198.2	6.9	**	n.s.	n.s.
Crude fiber, g/kg	185.6	7.29	201.09	7.7	**	n.s.	n.s.
Ash, g/kg	97.2	2.4	96.5	2.5	n.s.	n.s.	n.s.
Organic matter, g/kg	902.7	2.4	903.5	2.5	n.s.	n.s.	n.s.

n.s. $P > 0.05$; ** $P < 0.01$; SS, stocking system.

($F_{(1,10)} = 28.44$, $P < 0.001$), but not for OM and ash (both analyses $P > 0.05$). The sward on CSS had higher CP content and lower CF content in the biomass than on RSS. Both stocking systems developed similarly during the season; the CP content in the sward increased ($F_{(2,10)} = 4.00$, $P = 0.05$) and the CF content showed a decreasing trend ($F_{(2,10)} = 3.41$, $P = 0.07$). None of the sward structure characteristics showed any development during the 5 years of the experiment (all analyses $P > 0.05$).

Activity time budget and biting rates

Results for daily activity time budget and biting rates are set out in Table 2. Stocking system, period of season, and their interaction, had no significant effects on the total time spent grazing, ruminating or resting (in all analyses $P > 0.05$). We found the only difference was in the time which heifers devoted to other activities per day, which was lower in RSS than in CSS ($F_{(1,1090)} = 4.69$, $P = 0.01$). Total grazing time had no

relation to sward structure in terms of actual sward height, grass tiller density or white clover length (in all analyses $P > 0.05$), but was positively correlated to forb density (Table 3). There was no relationship between the total grazing time and individual parameters of the forage quality. The best predictor, although non-significant, was determined to be the CF content in biomass and showed a positive relationship trend to total grazing time (Table 3).

Grazing rate and chewing rate were significantly higher on CSS than on RSS (grazing rate: $F_{(1,295)} = 6.10$, $P = 0.014$; chewing rate: $F_{(1,295)} = 4.29$, $P = 0.039$) and both increased as the season progressed (CSS: $F_{(2,295)} = 6.12$, $P = 0.002$; RSS: $F_{(2,295)} = 3.55$, $P = 0.029$). There was no difference in ruminating rate between stocking systems, and it was constant within the season (in all analyses $P > 0.05$). Grazing rate was positively correlated with grass and forb density and negatively correlated with sward height and white clover stolon length (Table 3). Grazing rate was positively

Table 2 Time budgets for animal activities and biting rates in continuous and rotational stocking systems

Type of behavior	Continuous stocking system		Rotational stocking system		Significance		
	Mean	SE	Mean	SE	SS	Period	SS × period
Grazing, in hours	9.7	0.3	9.8	0.4	n.s.	n.s.	n.s.
Ruminating, in hours	5.4	0.4	5.6	0.4	n.s.	n.s.	n.s.
Resting, in hours	8.3	0.4	8.2	0.4	n.s.	n.s.	*
Other behavior, in hours	0.7	0.2	0.4	0.1	*	n.s.	n.s.
Grazing rate, per min	69.7	1.4	64.9	1.3	**	**	n.s.
Chewing rate, per min	81.1	2.7	73.9	2.3	*	*	n.s.
Ruminating rate, per min	71.8	1.7	69.9	1.3	n.s.	n.s.	n.s.

n.s. $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; SS, stocking system.

Table 3 Results of multiple regressions testing separately the effects of sward characteristics and forage quality on total grazing time, grazing rate and daily LWG (live-weight gain). Only significant parameters are displayed

Tested variable	Effect	Regression coefficient	P-value
Total grazing time	Forb density	0.52	$P = 0.024$; $F_{(2,23)} = 4.35$
	White clover length	0.40 -0.28	$P = 0.03$ $P > 0.05$
	Crude fiber	0.37 0.38	$P = 0.068$; $F_{(1,22)} = 3.66$ $P = 0.06$
Grazing rate	Crude fiber	0.50	$P < 0.001$; $F_{(4,257)} = 21.16$
	Sward height	-0.13	$P = 0.02$
	Grass tiller density	0.35	$P < 0.001$
	Forb density	0.12	$P = 0.03$
	White clover length	-0.15 0.25	$P = 0.01$ $P = 0.001$; $F_{(3,233)} = 5.29$
	Crude protein	0.34	$P = 0.02$
Daily LWG	Crude fiber	0.48	$P = 0.001$
	Ash	0.16 0.28	$P = 0.01$ $P = 0.001$; $F_{(1,129)} = 10.42$
	Grass tiller density	-0.28 0.39	$P = 0.001$ $P < 0.001$; $F_{(2,121)} = 10.63$
	Crude protein	0.39	$P < 0.001$
	Crude fiber	-0.30	$P < 0.001$
	Ash	-0.17	$P = 0.047$

Table 4 Stocking rate and animal performance in continuous and rotational stocking systems

	Continuous stocking system		Rotational stocking system		Significance
	Mean	SE	Mean	SE	
Stocking rate, kg/ha	1671	29	1332	49	***
Initial live-weight of heifers, kg	156.4	7.7	162.6	7.6	n.s.
Final live-weight of heifers, kg	265.3	12.9	266.4	14.8	n.s.
Live-weight gain per ha, kg	418.5	39.2	397.7	38.0	**
Daily live-weight gain per individual, kg	0.683	0.0419	0.652	0.047	*

n.s. $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; SS, stocking system.

related to forage quality parameters, namely to CF content, CP and ash (Table 3).

Animal performance

Stocking rate, animal live-weights, daily LWG for each period and the whole grazing season per individual and per hectare are set out in Table 4. Stocking rate was on average 339 kg per ha higher on CSS than on RSS ($t = 9.03$, $df = 4$, $P < 0.001$). Individual daily LWGs for the whole grazing season were not significantly different between stocking systems ($F_{(1,36)} = 1.28$, $P > 0.05$). Conversely, daily LWGs were not consistent for the 5 years of the study period ($F_{(4,36)} = 0.20$, $P < 0.001$) and were lower in years 1994–1996, higher in 1993, with the highest daily LWG being in 1997. The daily LWG differed also between periods of the grazing season ($F_{(2,143)} = 7.57$, $P < 0.001$). The mean daily LWG was 0.82 kg per day in early July, decreasing to 0.59 kg per day in early August, and finally increasing, at a similar level to July, to 0.85 kg per day in September. The weight of the animal, as well as individual daily LWG, were negatively correlated to total daily grazing time ($r = -0.27$ for animal live-weight and $r = -0.26$ for individual daily LWG). Gain per hectare was consistently higher (on average 20 kg per hectare) on CSS than on RSS ($t = 8.66$, $df = 4$, $P = 0.003$).

The daily LWG had no relation to actual sward height, forb density or clover stolon length (in all analyses $P > 0.05$), but was negatively correlated to grass tiller density (Table 3). Concerning forage quality parameters, daily LWG was positively correlated with CP content and negatively correlated with content of CF and ash (Table 3).

Relationships among sward characteristics, behavior and grazing season

Relationships between sward characteristics, forage quality, animal behavior and performance in different periods and stocking systems are clear from the PCA ordination diagram in Figure 2. The first axis of the PCA explained 28%, and all axes 69.5%, of the data variability. There is overall variability in records according to stocking system, which indicated no dif-

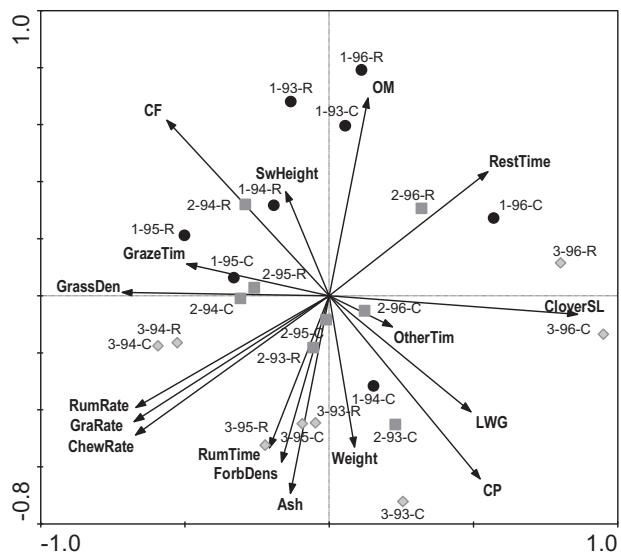


Figure 2 Ordination diagram showing results of principal components analysis of relationships among sward characteristics, forage chemical composition, animal behavior and performance. Abbreviations: ChewRate – chewing rate, CloverSL – white clover stolon length, CF – crude fiber, ForbDens – forb density, GraRate – grazing rate, GrassDen – grass tiller density, GrazeTim – total daily grazing time, CP – crude protein, OM – dry organic matter, OtherTime – total daily time spent by other activities than grazing, ruminating or resting, RestTime – total daily resting time, RumRate – ruminating rate, RumTime – total daily ruminating time, SwHeight – sward height, LWG – average individual daily live-weight gain, Weight – average live-weight of heifers. Plots are coded as follows: period (1 – July, 2 – August, 3 – September); year (1993–1997); stocking system (R – rotational, C – continuous). Records in each period are visualized to emphasize the pattern as ● – July, ■ – August, ◆ – September.

ference between them. There was a clear pattern shown by period of the season along the second (y) axis, but no pattern for year. Records from early July were positioned in the upper part of the diagram, records from early August in the centre, and those from September in the bottom section, on the margins of the diagram. Variability along the first axis was given by grass tiller density and white clover stolon length, with mutual negative correlation. Grass tiller density was positively correlated with sward height

and content of CF and OM. Sward height, OM and CF content were higher in early seasons whereas forb density, ash and CP content increased as the season progressed. Daily grazing time was positively correlated with grass tiller density, CF content and also slightly with sward height. Daily grazing time was negatively correlated with CP content and white clover stolon length. Time spent ruminating was positively correlated with forb density and ash content and negatively correlated with sward height, CF and OM content. Resting time was on the opposite side of the PCA diagram from daily grazing and ruminating time. The time spent on other activities was positioned in the centre of the diagram, which indicates that it is relatively independent of all other traits. All types of biting rate were mutually closely correlated, and showed some positive relationship to grass and forb density. Weight and daily LWG were positively correlated to CP content, forb density and white clover stolon length, while negatively correlated to sward height and CF content. Daily LWG was also negatively related to daily grazing time.

DISCUSSION

Experimental conditions were designed to correspond to current practice in cattle breeding management systems on semi-natural species-rich upland grasslands. During the 5 years of applied grazing management, there was no change in the measured sward characteristics, despite the considerable development of floristic composition and species diversity (Pavlů *et al.* 2003). Stocking systems had no effect on sward characteristics, except for the sward height, which was lower on CSS compared to each paddock on RSS before grazing, due to higher stocking rates and therefore higher grazing pressure on CSS. There was no evidence of development of sward structure during progression of the season on either CSS or RSS. The sward for both stocking systems was subjected to the same management in the early season (cutting). Consequent defoliation by heifers' grazing allowed grazing lawn to be maintained and did not allow the heterogeneity of the species-rich sward to be increased by ungrazed patches (Pavlů *et al.* 2006; Dumont *et al.* 2007), nor was there an effect of consecutive periods.

Most forage quality parameters were stable for all 5 years and during the grazing season, and did not differ between stocking systems. However, there was higher content of CP on CSS, increasing through progression of the season, and in turn higher content of CF in the forage on RSS, decreasing through the season. Sward on CSS was continually grazed, and so plant growth was maintained with high CP, and was not allowed to mature. Sward on RSS was cut once in spring and then grazed, but was higher than on CSS. Sward surface

height was correlated with CF content and represents therefore a direct link to forage quality. Furthermore, the higher the sward, the less digestible was CP and OM (Realini *et al.* 1999). However, studies comparing forage chemical composition between continuous and rotational stocking systems have produced inconsistent results. For instance, Pulido and Leaver (2003) found no difference in the CP and neutral detergent fiber concentrations between both stocking systems. Our results are in contradiction to those of Walton *et al.* (1981), Heitschmidt *et al.* (1982), Jung *et al.* (1985) and Lehmkuhler *et al.* (1999), who all report higher CP and lower CF concentrations on RSS, ascribing these results to lower levels of dead material in the sward and increased presence of legumes on RSS. Furthermore, in all these studies, higher grazing pressure was applied on RSS and higher rotation turnover in the grazing season. This indicates that the essential element determining the sward structure and quality is not the stocking system, but grazing intensity (e.g. Pavlů *et al.* 2006).

Sward structure and forage quality are crucial characteristics for determining grazing behavior of large herbivores on a species-rich pasture (Hejcmanová & Mládek 2012). Species-rich swards offer higher diversity and heterogeneity of food resources to animals, making foraging decisions more complex (Wang *et al.* 2010). In our study, heifers showed a weak response to sward characteristics and forage quality in terms of total grazing time, but were more responsive in terms of grazing and chewing rates. These reflect an instantaneous situation of sward options and animal choice of actual sward. The heifers displayed higher grazing rates on short swards, similar to results reported by Erlinger *et al.* (1990), Barrett *et al.* (2001) and Hejcmanová *et al.* (2009). Other characteristics of the sward are the grass tiller and forb density. Tillers and stems can act as structural foraging deterrents (Ginnett *et al.*, 1999; Drescher *et al.* 2006) decreasing the biting rate, namely by increasing the time spent manipulating the sward in order to select leaves between stems (Benvenutti *et al.* 2006, 2008; Drescher *et al.* 2006). Although we found a positive relationship of grazing rate to grass tiller and forb stem densities and, in turn, a negative effect of white clover stolon length on the grazing rate, we treated these relationships with caution. The natural species-rich pastures offer very complex swards with great structural contrasts for animals, and it is difficult to separate confounding effects between sward height and density, these being more pronounced in short swards (Bergman *et al.* 2000).

Among forage quality parameters, we found that the best predictor of grazing behavior was the CF content. We found a positive relationship between CF and grazing rate, which could seem contradictory because fiber is usually a limiting factor in forage

intake by saturating the rumen fill (Mertens & Ely 1979; McLeod & Smith 1989). However, the forage contained 14–21% of CF in biomass, and such a low content acts as a factor in activating chewing and rumen action. Both the continuously and rotationally grazed pasture may therefore maintain high-quality sward stimulating forage intake over the whole grazing season.

Time budgets of principal activities such as grazing, ruminating and resting of heifers, were not different between the two stocking systems. However, there were higher grazing and chewing rates on CSS than on RSS. Considering forage intake as a function of total grazing time, biting rate and bite size (Hodgson 1985; Forbes 1988; WallisDeVries *et al.* 1998; Griffiths *et al.* 2003), our results suggested that heifers should have higher forage intake on CSS and consequently higher daily LWG. However, there was no difference in LWG of heifers between the stocking systems, similar to the results reported for cattle by Kitessa and Nicol (2001) and Pulido and Leaver (2003). Pulido and Leaver (2003) recorded significantly lower grazing and ruminating time on RSS as the behavioral response of animal to an imposed short-term (24-h) rotation, without any effect on individual LWG. Another reason for maintenance of the performance at the same level could be the potentially higher energy expenditure needed for searching for forage or for travelling within a larger area on CCS than on RSS (Hepworth *et al.* 1991; Hart *et al.* 1993). Despite the similar performance of animals in both stocking systems, the gain per hectare was higher on CSS. However, higher gain per hectare on CSS was dependent principally on higher stocking rates and not directly on available biomass for animal feeding. Consequently, it appears that animals grazing on lower sward heights with higher quality give higher individual output (Pavlů *et al.* 2006; Derner *et al.* 2008).

Our results showed that the stocking system on species-rich grassland does not have any strong effect on grazing behavior patterns and animal performance. However, animal output in terms of LWG per ha and daily LWG was higher under higher stocking rates. The key parameters for grazing behavior and animal performance appear to be sward height, grass and forb density in the sward, and the CF and CP content in the forage.

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5.2 Článek II.

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Behavioural patterns of heifers under intensive and extensive continuous grazing on species-rich pasture in the Czech Republic

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ABSTRACT

This study examines the effects of season and of two grazing intensities, namely extensive grazing (EG) and intensive grazing (IG), on the grazing behaviour of heifers on species-rich upland pasture in the Czech Republic. Ten or eight (IG), and six or four (EG) heifers were continuously stocked in two completely randomized blocks from June to late September in 1998, 1999, 2000, 2006 and 2007. Swards were maintained at a target height of 5 and 10 cm, respectively. Grazing, ruminating, resting, and other activities were monitored during 24 h observations, and grazing, chewing and ruminating rates (per minute) were recorded. Daily behavioural patterns and the time budgets for particular activities were not significantly different between IG and EG heifers. However, IG heifers did spend more time grazing and slightly less time ruminating and resting than EG heifers. Other activity such as drinking, salt licking, comfort behaviour or social interaction was stable and there was no difference between the two treatments. Grazing rates were found significantly higher for IG heifers. Grazing was negatively affected by increase in air temperature at the expense of resting. Grazing time increased as the season progressed in the both IG and EG treatments, while resting showed a reverse trend. Concurrently, the ruminating time of IG heifers decreased and was variable for EG heifers. As the season progressed further, grazing rates then showed a decreasing trend. Considering that the differences in behavioural patterns between IG and EG were not conspicuous, our results indicate that the target sward of 5 cm commonly used in animal husbandry practices in the Czech Republic does offer enough forage to animals. Furthermore, the seasonal patterns of ingestive behaviour showed that the heifers under both grazing intensities balanced their intake by increase of grazing time along with decrease of grazing rates as the season progressed. These findings suggest that the herbage on species-rich pasture was sufficiently available to livestock at both the investigated grazing intensities.

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1. Introduction

A key aim of animal husbandry is to optimize the livestock production systems and grassland management

(Rook et al., 2004; Tallowin et al., 2005; Pavlů et al., 2007). The ingestive behaviour on which production closely depends has consistently remained at the centre of grassland management interest. Forage intake is determined as the function of bite size, biting rate and total grazing time (Allden and Whittaker, 1970; Hodgson, 1985; Forbes, 1988).

Cattle have a distinct diurnal grazing pattern with a grazing time which ranges from 6 h to nearly 13 h a day

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(Krysl and Hess, 1993). Fatigue limit was assumed to be 12 h (Stobbs, 1975). Total daily grazing time tends to be relatively stable in order to meet animals' nutritional requirements at the circadian level (Linnane et al., 2001). Grazing time can, however, be constrained by availability of time for grazing imposed by the management system or stocking rate. For instance, animals facing limited time for grazing may adapt by seeking forage of a higher quality (Ginane and Petit, 2005). Under moderate grazing pressure the total grazing time was longer than under lower pressure (Huber et al., 1995), while a heavy stocking rate reduced grazing time (Hepworth et al., 1991) because of time spent searching. Grazing intensity, as one of components determining availability of forage of particular quality, affects the trade-off animals make between forage quantity and quality (Wallis de Vries and Daleboudt, 1994; Newman et al., 1995). In fact, cattle retain their preference for more abundant forage regardless of its quality and compensate for fluctuations of forage accessibility by matching grazing time and biting rate. However, when accessibility of forage decreases under a certain limit, animals switch their dietary choice to better quality forage (Ginane et al., 2003). This behavioural adaptation is valid throughout the grazing season; animals increase their grazing time and biting rate in response to the changing parameters of the sward (e.g. Funston et al., 1991; Realini et al., 1999).

Time for grazing is limited by the performing of other, mutually exclusive, activities. The second most important activity after grazing in ruminants is chewing the cud (Arnold and Dudzinski, 1978; Realini et al., 1999). Ruminating time and ruminating rate vary according to the diet. Cattle ruminate for longer as fibre content increases in the forage and for less time with decreasing forage particle size (Albright, 1993).

Understanding livestock behaviour in relation to varying environmental conditions and forage dynamics is paramount in designing management strategies for livestock production (Demment et al., 1986). Management systems for livestock on pasture have increasingly become an important domain of livestock production as well as a tool for biodiversity conservation over the last decades (Watkinson and Ormerod, 2001). Therefore, we aim to evaluate heifers' behavioural pattern on species-rich semi-natural pasture under a continuous grazing regime as this is currently the most extensive management system employed in Central Europe (Isselstein et al., 2005).

Our objective was to investigate how heifers cope with various grazing intensities and the ongoing seasons in terms of grazing time and rate of biting. Specific questions addressed were: (1) is there any effect of grazing intensity on the daily activity pattern of heifers? (2) Is there any effect of grazing intensity on the biting rate of heifers? and (3) Is there any effect of grazing season on heifers' grazing behaviour?

2. Material and methods

The study was performed on an experimental upland pasture in the Jizerské Mountains ($50^{\circ} 49'N$, $15^{\circ} 02'E$). The altitude is 420 m.a.s.l., annual rainfall 803 mm, mean

annual temperature $7.2^{\circ}C$) The land belongs to the Crop Research Institute, Prague, the Czech Republic. The experiment was conducted for 5 years (1998, 1999, 2000, 2006, and 2007).

2.1. Design of the experiment and animals studied

The experiment was arranged in two treatments composed of two completely randomized blocks consisting of two paddocks of intensive grazing (IG1, IG2) and two paddocks of extensive grazing (EG1, EG2). Each grazed paddock was approximately 0.35 ha. The pasture was continuously stocked with growing heifers (1998, 2006—Czech Simmental × Charolais, 1999, 2000, and 2007—Holstein) of 150–220 kg in initial live weight. The animals were of the same age and came from the same breeding conditions. In 1998, 1999 and 2000, IG and EG paddocks were grazed by five and three heifers each, respectively, while in 2006 and 2007 they were grazed by four and two heifers each, respectively. The grazing season lasted from early May to the end of October. The stocking density during the grazing season in both of the groups was adapted to a target sward height of 5 cm (IG) or 10 cm (EG), respectively. This was maintained by manipulating areas of the respective paddocks according to biomass growth rate. Sward height was measured weekly using the first contact method (modified point quadrat method) between 1998 and 2000, and by the rising plate meter method between 2006 and 2007 (Pavlů et al., 2007). The mean sward heights were 5.10 ± 0.11 cm and 9.62 ± 0.23 cm (mean ± S.E.) for IG and EG treatments, respectively. Predominant species in the sward were *Aegopodium podagraria* L., *Agrostis capillaris* L., *Alopecurus pratensis* L., *Festuca rubra* agg. L., *Galium album* Mill., *Trifolium repens* L., and *Taraxacum* spp. Wigg. The mean forage yields were $3.57 (\pm S.E. 0.20) t\ ha^{-1}$ and $2.81 (\pm S.E. 0.17) t\ ha^{-1}$ under IG and EG, respectively. Total crude protein content and forage digestibility were both higher under IG, and the content of crude fibre consequently showed a reverse effect. Sward quality parameters showed seasonal changes, namely decrease of biomass growth rate and increase in crude fibre content as the season progressed (Pavlů et al., 2006).

2.2. Animal behaviour and bite rate recording

Behavioural pattern data were collected between June and September once a month at a regular interval for each year. Principal activities were recorded by scan-sampling each heifer at 15-min intervals from 06.00 h to 21.00 h and at 1-h intervals during the night (between 21.00 h and 06.00 h), all together making up 24 h of observation. The principle activities of heifers on pasture included grazing, ruminating, resting as well as other behaviour. Grazing was defined as biting, chewing or swallowing herbage, or walking with the muzzle close to the sward. Ruminating was defined as chewing the cud, resting as lying or standing without any activity and 'other behaviour' included activities such as drinking, salt licking, comfort behaviour and social interaction, etc. Actual weather conditions, air temperature and other circumstances (if any) were recorded at 1-h interval.

Table 1

Mean behaviour patterns of heifers expressed as percentage of the observation time per 24 h (in %) in the study years.

Month	Behavioural pattern							
	Percentage of observation time (in %)							
	Intensive grazing				Extensive grazing			
	Grazing	Ruminating	Resting	Other	Grazing	Ruminating	Resting	Other
June	49	22	26	3	50	18	30	2
July	49	20	28	3	47	22	28	3
August	58	18	22	2	53	23	23	1
September	61	18	19	2	58	18	21	3
Average	54	19.5	24	2.5	52	20	25	3

The biting rate was investigated by comparison of forage ingestion by heifers from both of the two grazing intensities (IG, EG). We recorded three types of bite: grazing, chewing, and ruminating. Grazing was defined as a wrenching of the vegetation sward, chewing as biting and grinding of forage in the muzzle (for better swallowing) and rumination as chewing the cud. All these type of bites were recorded in the form of biting rate (number of bites per minute). We made ten records for each type of biting behaviour (grazing, chewing, and rumination) in each paddock.

2.3. Statistical analyses

All of the data were analyzed using the STATISTICA 8.0 package (StatSoft, 1995).

We used General Linear Model (GLM) procedures for repeated (within-subject) measures. The behavioural variables were time spent grazing, ruminating, resting, and other behaviour as a percentage of the observed 24-h cycle. All these variables showed normal distribution (all tested by Kolmogorov-Smirnov test had $P > 0.2$). We tested the effects and interactions of the treatment (IG/EG) (categorical predictor) and year, month and temperature (continuous variables) on behavioural variables. For statistical analyses of intensity of biting (grazing, chewing, and ruminating rates), the same General Linear Models procedures were carried out for categorical predictor treatment (IG/EG) and continuous variables for year, month, and sward height. We performed linear regressions to reveal relations between temperature and grazing time and relations between sward height and grazing rate.

3. Results

3.1. General activity pattern

The time budget for particular activities of heifers during the 24-h cycle was not different between IG and EG treatments (Table 1). Results revealed that the grazing intensity had no significant effect on any activity (Table 2). However, heifers on intensively grazed pasture spent generally more time grazing than heifers on extensively grazed pasture (Fig. 1a). In addition, grazing time became significantly longer as the vegetation season progressed (effect of month) for both treatments (Table 2). Furthermore, grazing behaviour was a negative function of

temperature (Fig. 2); in the range of 11–28 °C, time spent grazing decreased at the rate of 1.2% per 1 °C.

Treatment and month had no effect on rumination but the effect of treatment was affected by month ($P = 0.06$). There were some variations in the time budget allotted to ruminating activity between IG and EG treatments with the ongoing season, and only heifers on intensively grazed pasture showed a continuously decreasing trend in time spent ruminating (Fig. 1b). Ruminating activity also tended to be affected ($P = 0.077$) by temperature.

Resting was affected by season, temperature and year (Table 2). The differences between IG and EG were not significant. However, on average heifers from EG spent more time resting than heifers from IG (Fig. 1c). In both treatments the animals showed a decreasing trend in resting in the course of season (Fig. 1c).

Other activities such as drinking, salt licking, comfort behaviour or social interactions were affected neither by the season, nor by temperature (Table 2). The time allotted to these activities was stable for the IG as well as EG treatment (Fig. 1d).

Table 2
Results of GLM analyses of different effects on behaviour during 24-h cycle.

Behaviour	Effect	DF	F	P-value
Grazing	Year	1	1.21	0.277
	Temperature	1	16.84	<0.001
	Month	3	5.96	0.001
	Treatment	1	2.15	0.148
	Month × treatment	3	0.66	0.577
Ruminating	Year	1	1.227	0.273
	Temperature	1	3.248	0.077
	Month	3	0.342	0.795
	Treatment	1	0.687	0.411
	Month × treatment	3	2.604	0.060
Resting	Year	1	5.43	0.023
	Temperature	1	10.16	0.002
	Month	3	4.16	0.010
	Treatment	1	1.47	0.230
	Month × treatment	3	0.37	0.777
Other	Year	1	0.118	0.733
	Temperature	1	0.254	0.616
	Month	3	0.091	0.965
	Treatment	1	0.232	0.632
	Month × treatment	3	0.365	0.779

DF: degree of freedom; F: F-statistics.

Effects in bold characters were significant at the level $p < 0.05$.

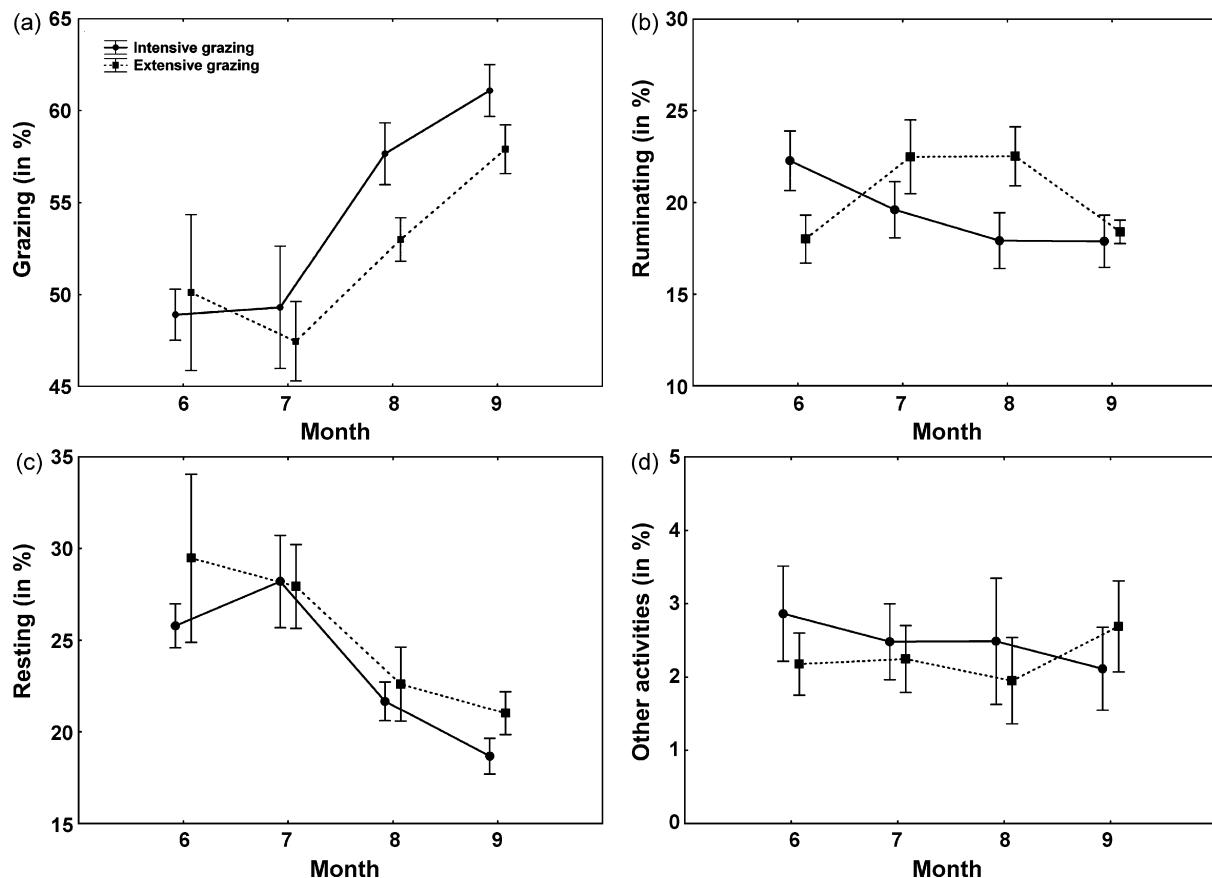


Fig. 1. Development of time budget for grazing (a), ruminating (b), resting (c), and other activities (d) of heifers with the progressing season on intensively and extensively grazed pasture (S.E. are indicated by vertical lines).

3.2. Biting rates

Biting rates significantly differed between IG and EG treatments and showed dependence upon the ongoing season (Table 3). In both treatments the animals showed a decreasing trend in grazing rate (Fig. 3a). The grazing rate increased by two bites per minute for each 1 cm decrease in sward height (Fig. 4). On the other hand, ruminating rate was affected by the ongoing season with only a slight

difference in trend between the treatments (Table 3 and Fig. 3c).

4. Discussion

4.1. Effect of grazing intensity

The present study did not reveal significant differences in the daily activity patterns of heifers between two

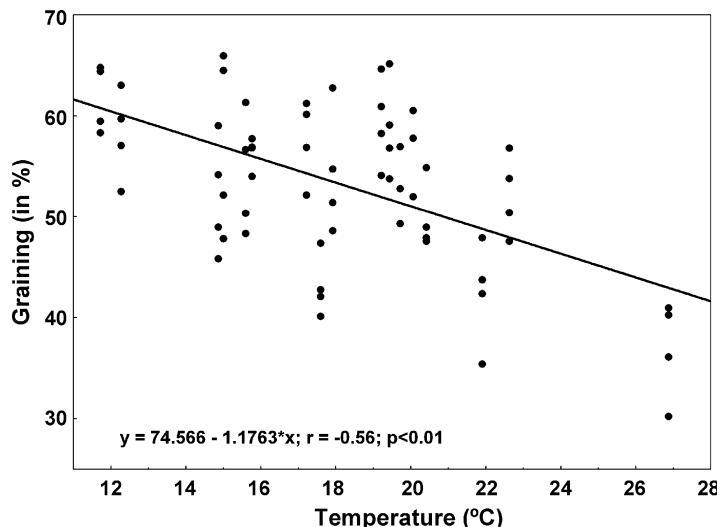


Fig. 2. Effect of actual daily temperature on grazing activity of heifers (in percentage of 24-h cycle).

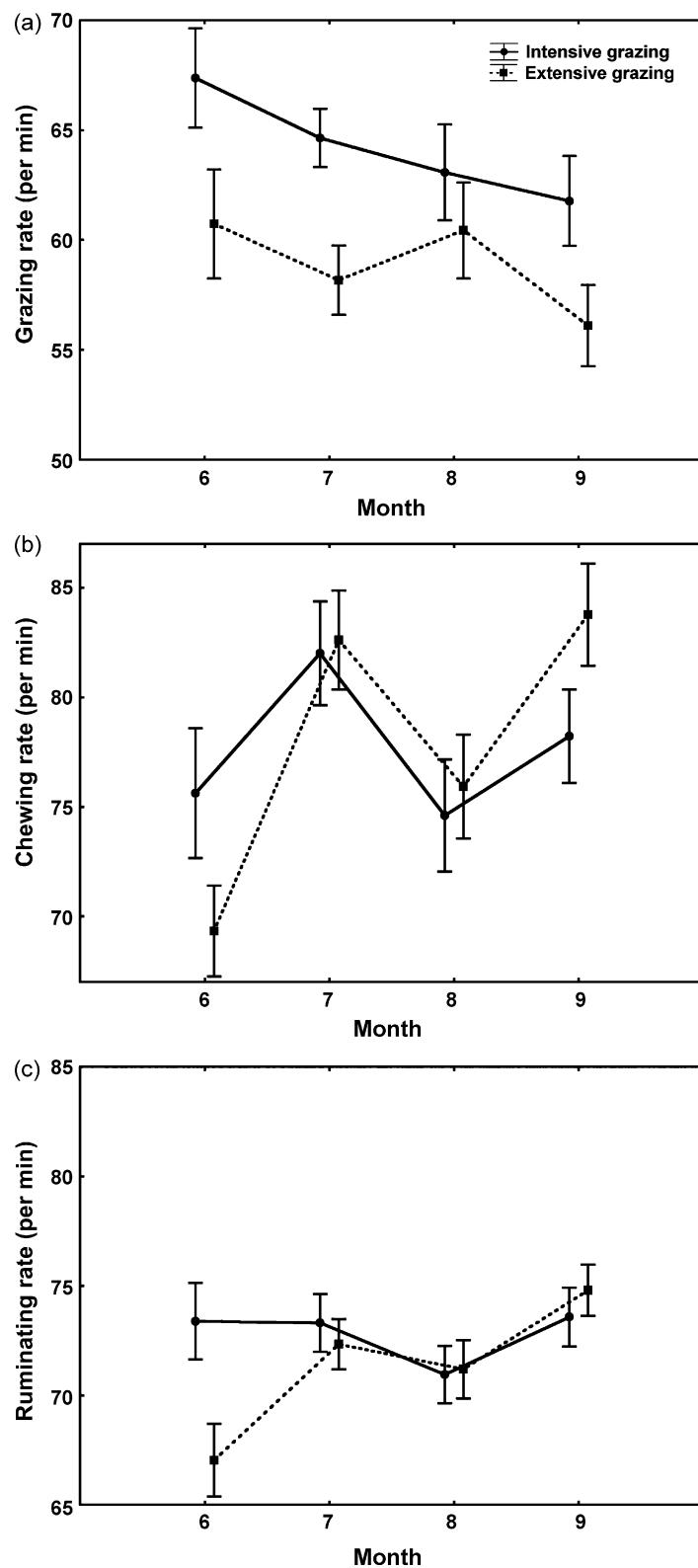


Fig. 3. Grazing rate (a), chewing rate (b), and ruminating rate (c) of heifers with the ongoing season on intensively and extensively grazed pasture (S.E. are indicated by vertical lines).

grazing intensities which were similar to species-rich natural pastures (Huber et al., 1995; Dumont et al., 2007). However, animals did display some differences in their behaviour that were more likely to consist of the frequencies of particular activities during the day. The

major grazing periods persisted (described also by Linnane et al., 2001), but EG heifers often interrupted their grazing by ruminating, whilst IG heifers grazed for longer and more continuously, which corresponds with Arnold and Dudzinski (1978). As daily intake is to be maintained (Penning

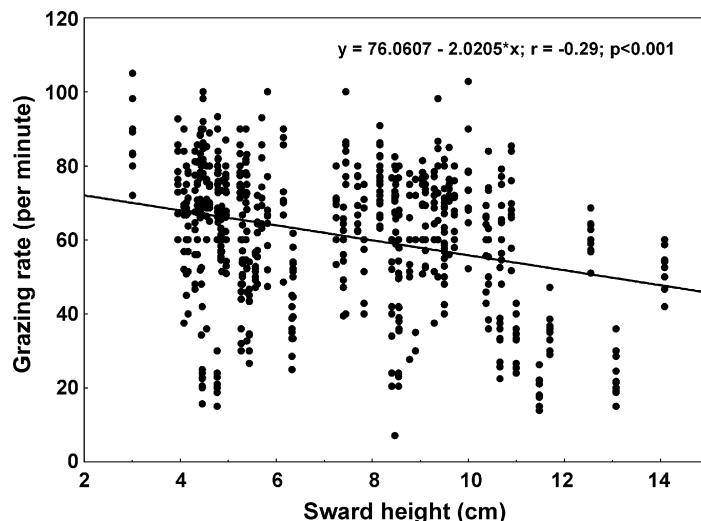


Fig. 4. Effect of the actual sward height on grazing rate (per minute) of heifers.

et al., 1991; Morris et al., 1993; Rutter et al., 2002) and the heifers in the IG treatment were exposed to a shorter sward, the IG heifers compensated for less available forage by increasing their grazing time (Jamieson and Hodgson, 1979; Allison, 1985; Penning et al., 1991; Ginane et al., 2003). However, the total length of time spent grazing per day may have a relatively small impact upon daily herbage intake (Wade and Carvalho, 2000). Thus, it was in order to meet a necessary daily forage quantity that this additional increase of grazing rate in the IG treatment occurred, which is consistent with the findings of Forbes (1988). It is in accordance with the fact that on lower sward, the quantity of herbage per bite is lower (Allden and Whitaker, 1970; Forbes, 1988). Hence, the chewing rate was higher for the EG treatment where longer particles of herbage probably caused longer periods of mastication before swallowing.

Longer ruminating time (except in June) of EG heifers, and variations in ruminating rate as consequence of higher fibre and lower crude protein content in the EG sward were consistent with the findings of Albright (1993) or Realini

et al. (1999). However, the differences were not significant and this is probably due to more variable sward heights encountered by the EG treatment: the EG heifers fed on the both taller and shorter patches with both quality parameters. Consequently, the effect of grazing intensity diminished.

4.2. Effect of season

The grazing season on our upland semi-natural pasture lasted from May to the end of September. Seasonal changes in forage quality parameters were reflected in adaptations of behavioural processes. Time budget of principle activities changed as the season progressed in the both IG and EG treatments, with more or less the same trends. Grazing time increased with the month as expected, following the consistently decreasing biomass growth rate. The same findings were noted e.g. by Stricklin et al. (1976), Funston et al. (1991), Huber et al. (1995), or Realini et al. (1999). Resting exhibited a reverse trend, whereas ruminating varied in relation to treatment and month, and other activities did not show any important trends. At the same time, grazing rate showed a clear decreasing trend although parameters of forage quality, namely crude protein and crude fibre content, did not display any continuous trend (Pavlu et al., 2006). This is in contrast with the results of, for instance, Realini et al. (1999) or Ginane and Petit (2005) who recorded an increase in biting rate over the investigated periods. The increase in grazing time together with the increase in biting rate usually occurs under conditions of less available forage (e.g. Chacon and Stobbs, 1976; Penning et al., 1991; Linnane et al., 2004). In our study, however, maintaining the target sward height across the whole vegetation season had the effect of providing an adequate availability of forage on both of the treatments. Consequently, there was no restriction of forage accessibility and the heifers could balance their daily intake through a decrease in grazing rate, similarly to as described by Funston et al. (1991).

The only point when the seasonal trend in grazing and resting time was interrupted appeared in July when high

Table 3
Results of GLM analyses of different effects on different types of bite.

Type of intake	Effect	DF	F	P-value
Grazing per minute	Year	1	1.34	0.247
	Sward height	1	98.43	<0.001
	Month	3	4.28	0.005
	Treatment	1	48.84	<0.001
	Month × treatment	3	2.86	0.036
Chewing per minute	Year	1	12.39	<0.001
	Sward height	1	8.28	0.004
	Month	3	7.43	<0.001
	Treatment	1	6.96	0.008
	Month × treatment	3	2.20	0.086
Ruminating per minute	Year	1	2.92	0.087
	Sward height	1	1.87	0.171
	Month	3	3.04	0.028
	Treatment	1	3.60	0.058
	Month × treatment	3	2.03	0.10

DF: degree of freedom; F: F-statistics.

Effects in bold characters were significant at the level $p < 0.05$.

temperatures (particularly excessive in July 2006) caused a sharp decline in grazing and ruminating activities in favour of resting. Changes in temperature induce changes in behavioural patterns (Seath and Miller, 1946; Arnold and Dudzinski, 1978; Beverlin et al., 1989). Particularly hot weather imposed a long rest period on the heifers during a great part of the day which can be perceived as a constraint of shorter time for grazing (Ginane and Petit, 2005).

5. Conclusion

There was a clear trend towards longer grazing time and higher grazing rate, and less time for ruminating and resting found among heifers under higher grazing intensity, and hence with less availability of forage on the shorter sward. On the other hand, inconspicuous differences could be caused under conditions of sufficient forage availability to both groups during the course of grazing season. In fact, stocking rates as well as other grazing management conditions of pasture in our experiment were designed to correspond to the conditions of animal husbandry practices in the Czech Republic. This affected, furthermore, the seasonal patterns of ingestive behaviour. As the season progressed, the heifers under both grazing intensities increased their grazing time along with the decrease in their grazing rates. This suggests that the herbage on species-rich pasture was sufficiently available to livestock at both the investigated grazing intensities.

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5.3 Článek III.

Stejskalová M., Hejčmanová P., Ludvíková V., Pavlů V., Hejčman M. 2014.

Plant functional traits as drivers of heifers' selectivity for a patch on heterogeneous pasture.

Animal (submitted)

Plant functional traits as drivers of heifers' selectivity for a patch on heterogeneous pasture

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Abstract

The aim of our study was to investigate heifers' diet selection on two continuous grazing systems (intensive and extensive) on species-rich heterogeneous pasture. We expected that cattle will graze selectively for specific patches of the sward on pastures and that the selectivity will differ according to grazing intensity. We aimed at determining principle drivers of selectivity for particular patches using plant functional traits of plant community on the sward patches. The experiment was carried out on the experimental pasture Betlem in the Jizerske Mountains in the Czech Republic. Heifers were continuously stocked in two blocks in 2 seasons (2008 and 2009) from April to October. We measured height and plant species composition of sward patches on both intensive and extensive grazing intensities, distinguished three types of patches (short, medium and tall), then we calculated their plant functional traits using LEDA plant traitbase. We observed grazing frequency on sward patches of two to four heifers (Friesian) on extensive and intensive grazing intensity, respectively. We collected the data on actual sward and animal behaviour twice a month in a regular interval (from July to September) for

each year. Finally, we calculated the selectivity for particular patches and analysed the effect of functional traits of plants in sward patches on heifers' selectivity for patches.

Heifers selectively grazed on the short swards and the selectivity for the short sward was higher on extensive grazing. Medium swards were avoided by heifers on intensively grazed pastures, while on extensively grazed pasture, they were grazed in the balance with their availability. No difference between selectivity for the tall sward patches on intensive and extensive grazing pastures were recorded. Most of plants functional traits of patches were closely positively correlated among one another and had higher values on intensive grazing system, with the exception of LDMC which was negatively correlated with all of them and was higher on the extensive grazing system. Heifers' selectivity was positively correlated with particularly with foraging value and LDMC of patches and negatively correlated with the sward height of patches. We can therefore conclude that for cattle grazing on pasture, the grazing intensity is the principle determinant of grazing behaviour and diet selection because it determines further drivers of selection such as occurrence of particular sward patches with given forage quality (foraging value) and quantity (LDMC).

Key words: cattle, diet selection, foraging value, grazing behaviour, plant functional traits

Introduction

Grasslands often consist of a mosaic of patches of different vegetation structure, which vary in forage availability and nutritive value (Wallis De Vries and Daleboudt 1994). Heterogeneity of the sward brings to foraging ungulates new challenges for optimal diet selection. The selection between sward patches with various properties is the main tool by which animals may manipulate forage intake and quality. In turn, the sward structural heterogeneity is particularly result of these dietary choices of grazing animals (Rook et al. 2004). According to Dumont (1997), the selection is a function of preference, but it is clearly affected the abundance or the availability of preferred plant species and by their spatial distribution. Selection is influenced by some of the animals foraging abilities, for instance, their ability to sort dietary items one from another, to walk long distance to preferred forage resources or to learn and remember the location of food patches (Dumont 1997, Bailey et al. 1996). Another key point determining the structure and composition of pastures is the grazing management, particularly stocking rate and grazing intensity (Dumont et al. 2007a). Lower grazing intensity enable increase of heterogeneity by creating sward patches of different height and plant species composition (Correl et al. 2002) and offer to animals more variable resources which they may select for. But what exactly makes the animals to decide for a specific patch? Which sward or plant species properties drive animals to stay grazing or to go looking for another diet?

The aim of our study was therefore to investigate heifers' diet selection on intensively and extensively grazed pastures. We expected that cattle managed by continuous grazing system on species-rich heterogeneous pasture graze selectively for a specific patch of sward, and the selectivity will differ according to grazing intensity. We aimed at determining principle drivers of selectivity for particular patches using plant functional traits of plant community on the sward patches.

Materials and Methods

Study area

The experiment was carried out on the experimental pasture Betlem in the Jizerske Mountains ($50^{\circ} 49'N$, $15^{\circ} 02'E$), the Czech Republic. The pasture is situated in

uplands in the village Oldřichov v Hájích, approximately 10 km west from Liberec, at the altitude of 420 m a.s.l. The average precipitation for the area was 803 mm and the mean annual temperature was 7.2°C (Liberec meteorological station). The vegetation on the pasture was classified as *Cynosurion* with some elements of *Arrhenatherion* (Chytrý, 2007). The dominant species were common bent (*Agrostis capillaris*), perennial ryegrass (*Lolium perenne*), dandelion (*Taraxacum* spp.) and white clover (*Trifolium repens*) (Pavlů et al. 2007).

Management and experiment design

The experiment was arranged in two treatments composed of two completely randomized blocks consisting of two paddocks of intensive grazing (IG1, IG2) and two paddocks of extensive grazing (EG1, EG2) (Fig. 1). The area of paddocks railed between 0.38 and 0.71 ha. Both grazing intensities (IG and EG) were grazed from April to October 2008 and 2009 by two to four heifers (Friesian) from the same breeding conditions of initial life weight 208-339 kg. The stocking density during the grazing season in both of the groups was adapted to a target sward height of 5 cm (IG) or 10 cm (EG), respectively (Pavlů et al. 2007). We collected the data on actual sward and animal behavior twice a month in a regular interval (from July to September) for each year.

Sward measurements

For the sward, we measured sward height in order to identify the type of patch and plant species composition in order to identify plant functional traits and calculate them for each type of patch.

The compressed sward height was measured regularly one day before the observation of animal behaviour, it means twice a month during the grazing season using the rising plate meter method (Correl et al. 2003), in total six times. The sward height was recorded in 50 m transects in 1 meter distance. Patch types in both paddocks were classified according to the sward height into the three categories - short (0 – 5cm), medium (5.5 - 10cm) and tall (10.5 cm and more).

Plant species composition of patches was determined and measured at 40 fixed sampling points at 1 m intervals along the line transect. The percentage cover for

all vascular species was estimated up to 100% within circles of diameter 30 cm. Plant species nomenclature follows Kubát et al. (2002). The plant species composition and coverage data were collected in all paddocks twice during the grazing season each year. For all recorded plant species (60) we assigned a set of grassland utilization indicator values for vascular plant species (plant functional traits) from BIOFLOR and LEDA Traitbase: foraging value, grazing tolerance, trampling tolerance, specific leaf area (SLA) and leaf dry matter content (LDMC) (Briemle et al. 1996, Cornelissen *et al.* 2003.).

Foraging value is an oldest feeding value used for farm animals, especially for cattle, to evaluate the forage quality of individual plants in 10-point scale. The criteria for the feed value of the living plant are for example protein and mineral contents, palatability and popularity with the livestock, share valuable plant parts (leaves, stems, flowers, fruits), duration of the full value as a forage crop, harmfulness or toxicity and parasitism, permissible share in the stand (poisonous plants with a maximum of 3% by mass).

Grazing tolerance is a complex trait that encompasses many morphological and physiological plant characteristics (characteristics of plant height and form of life) and their interactions with the environment. It is one of the general plant defence strategies against herbivores.

Trampling tolerance is individual, morphologically eco physiological feature of green vascular plants. Particularly relevant for this feature are plant height, growth habit and life form. Basically, the higher herbaceous plant grows the more sensitive it is incurred from mechanical injuries by treading on (Briemle et al. 2002).

Specific leaf area (SLA) is the one-sided area of a fresh leaf divided by its oven-dry mass, expressed in $\text{m}^2 \text{ kg}^{-1}$ or in $\text{mm}^2 \text{ mg}^{-1}$ and it is positively correlated with its potential relative growth rate and mass-based maximum photosynthetic rate (Cornelissen *et al.* 2003). Leaf dry matter content (LDMC) is a measure for the tissues density and is associated with nutrient utilisation by plant and determines the rate of biomass turnover.

According to coverage of each plant species in each patch type, we calculated weighted average of plant functional types for whole patches in each paddock.

Animal behaviour measurements

Grazing data were collected between July and September twice a month at a regular interval for each year. The data were collected with a scan sampling method during 14 hours (from 6:00 a.m. to 8:00 p.m.) as a direct observation of each heifer every 5th minute. Grazing was defined as biting, chewing or swallowing herbage, even while walking with the muzzle close to the sward. Type of the patch grazed by the animal was recorded.

Selection for a type of patch (short, medium or tall), defined as the proportion of a patch type in the diet relative to its proportion in the paddock, was quantified by calculating selectivity indices (S_i) for each type of patch in each paddock separately using Jacobs' (1974) selectivity index: $S_i = \frac{c_i - a_i}{c_i + a_i - 2c_i a_i}$. c_i is the proportion (between 0 and 1) of each patch type where animals grazed and a_i is the proportion (between 0 and 1) of occurrence of each patch type in the paddock. To estimate a_i , we recorded the proportion of each patch type in each paddock from data collected on line transects. These data were averaged to estimate the relative abundance of each patch type separately in intensive and extensive grazing system. S_i varies from -1 (avoided and never used) to +1 (selectively searched for grazing, exclusively used), with negative and positive values indicating avoidance and preference, respectively, and 0 indicating that the type of patch is used in proportion to its availability (Dumont *et al.* 2007, Hejcmanová and Mládek 2012).

Data analyses

Data met assumptions for normal distribution (tested by Kolmogorov-Smirnov test). Factorial ANOVA was applied to test the effect of the 'grazing intensity' (IG, EG), 'sward height' (short, medium, tall) and interaction 'grazing intensity*sward height' on heifers' selectivity. Then, we tested effect of the grazing intensity on heifers' selectivity on each sward height separately. The effect of the ongoing season on heifers' selectivity was tested by one-way ANOVAs for each grazing intensity and for each sward height separately.

Unconstrained principal component analysis (PCA) in Canoco for Windows 4.5 program (ter Braak and Šmilauer 2002) was used to analyze relationships among

plant functional traits of patches, type of patch (in the form of sward height) and heifers' selectivity for a type of patch (in the form of Jacobs' selectivity index Si. Grazing intensity (IG x EG) were included in the analysis as supplementary explanatory environmental variables. Data were centred and standardized before the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram constructed by CanoDraw program (ter Braak and Šmilauer 2002).

The functional response of heifers' selectivity for a type of patch on the foraging value of each patch type separately was tested by simple linear regressions for intensive and extensive grazing system, respectively.

Results

Heifers grazed selectively on specific patches of the swards ($F_{(426, 2)}=211.2$, $p<0.001$) and this selectivity of heifers' grazing on specific patches was different on intensive and extensive grazing management ($F_{(426, 1)}=23.2$, $p<0.001$). Heifers selectively grazed on the short swards and the selectivity for the short sward was higher on extensive grazing (EG: $Si = 0.69 \pm SE 0.03$; IG: $Si = 0.54 \pm SE 0.03$; $F_{(142, 1)}=11$, $p=0.001$). Selectivity of grazing for the medium sward was different the both grazing intensities ($F_{(142, 1)}=90$, $p<0.001$). On intensive grazing pasture, heifers avoided the medium swards ($Si = -0.51 \pm 0.03$) while on extensive grazing pasture, heifers grazed on medium swards in the balance with the availability of this type of the sward ($Si = 0 \pm 0.05$). Finally, there was no difference between selectivity for the tall sward patches on intensive and extensive grazing pastures ($F_{(1,142)}=0.12$, $p=0.73$), on the both heifers avoided these sward patches (EG: $Si = -0.40 \pm SE 0.06$; IG: $Si = -0.36 \pm SE 0.07$). In the course of the season the selectivity remained stable on the intensive grazing system for the short and medium sward (both analyses $P > 0.05$) and rather variable for tall sward ($F_{(5,90)} = 10$, $P < 0.001$) whereas on the extensive grazing the selectivity for patch types in the course of season was highly variable for all three sward heights (all analyses $P < 0.05$) (Fig. 2).

Results of the PCA analysis are presented in the form of the ordination diagram on Fig. 3. The first ordination axis explained 61% and the first two axes together 81% of the variability of plant functional traits and heifers' selectivity data. Grazing

intensity in the form of supplementary variable increased substantially the explained variability to 82 % and 98% on the first and on first and second axes together, respectively. Most of plants functional traits of patches were closely positively correlated among one another and had higher values on intensive grazing system, with the exception of LDMC which was negatively correlated with all of them and was higher on the extensive grazing system. Heifers' selectivity was positively correlated with particularly with foraging value and LDMC of patches and negatively correlated with the sward height of patches.

On the intensive grazing system heifers' selectivity was not responsive for any patch in relation to foraging value of the plant community on the patch (Fig. 4a) whereas on the extensive grazing system foraging value affected heifers' selectivity for each patch differently (Fig. 4b).

Discussion

Differences between intensive and extensive grazing

The principal result of our study is that selectivity of heifers for their forage is highly responsive to the management, in particular to grazing intensity on pasture. Both grazing intensities, intensive and extensive, create specific conditions for sward development in the course of season and enable differentiation of swards according to the canopy height to specific patches (Pavlů et al. 2006). Heifers selectively grazed short swards because of their higher nutritive value in comparison to taller patches, similarly as reported by Dumont et al. (2007a), Wallis De Vries and Daleboudt (1994) or Cingolani et al. (2005). Short patches are quite widespread on intensively grazed pastures, hence the selectivity for these swards is not such strong as on extensively grazed pastures where they are relatively scarce. On extensively grazed pasture they are repeatedly sought out and grazed by animals, consequently they are continually being renewed and thus maintaining high nutritive value (Illius 1986), but at once low number of grazing animals does not allow spreading of this patch type.

The different selectivity of heifers appeared even for medium tall sward. Heifers on intensively grazed pastures directly avoided medium patches most of the time despite their high nutritive value, equal to short patches (see Fig. 4a). These

patches developed mostly on places of deposited excrements, because cattle avoid such places due to odour (Frame 1992, Pavlů et al. 2005). On extensively grazed pastures, medium tall patches were grazed by heifers in balance with their occurrence in the sward, developed from swards growing due to low grazing pressure. These medium patches had, however, lower nutritive value in comparison to intensively grazed pastures. Tall swards were similarly avoided in both grazing intensities, continually in the course of the season because they were older, hence with lower nutritive value and heifers had many other grazing opportunities.

Another question is which of the sward properties is a real driver for heifers to select a bite? Plant species within patches grow under similar conditions and grazing pressure, therefore mutually related and complementary functional traits are favoured to develop. For instance, plants with high SLA have due to higher metabolic rate also higher N concentrations and overall nutritive value (Cingolani et al. 2005), while they have lower LDMC (Louault et al. 2005). These plants with higher growth rate are also able to withstand biomass removal by grazing animals and to quickly regenerate, hence correlation with grazing and trampling tolerance. Functional traits of plants within a patch were therefore interlinked and heifers' selectivity could be regarded as driven by all plant properties together. However, as the best predictor could be assigned foraging value and LDMC. Swards on intensively grazed pastures were more homogeneous therefore foraging value did not differ among patches, whereas extensively grazed pastures offered more heterogeneous swards and the effect of foraging value on selectivity became conspicuous, similarly as recorded by Bailey (1995). LDMC, on the other hand, reflects the quantity of the biomass, which is also required by cattle, balancing thus trade-off between quantity and quality of the forage. Cattle need not only high nutrient content in the forage, but also to fulfil the rumen to a certain level for a good physiological digestion, particularly to stimulate the function of rumen and for creation of healthy environment for bacteria growth. Selectivity of a diet is only one of possible strategies to cope with trade-off between quality and quantity of forage, another can be to adjust grazing behaviour pattern. For instance, as the intensively grazed pastures do not offer too heterogeneous swards on comparison

to extensively grazed one, animals spend more time grazing and graze with higher biting rate (Hejcmanová et al. 2009) in order to compensate less available forage and maintain quantity of the daily intake (e.g. Penning et al., 1991, Ginane et al., 2003).

We can therefore conclude that for cattle grazing on pasture, the grazing intensity is the principle determinant of grazing behaviour and diet selection because it determines further drivers of selection such as occurrence of particular sward patches with given forage quality (foraging value) and quantity (LDMC).

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Figures

Figure 1. Experiment design: scheme of the paddocks location in Betlem, Jizerske Mountains, 2006. IG1, IG2 – 2 paddocks of intensive grazing, EG1, EG2 – 2 paddocks of extensive grazing.

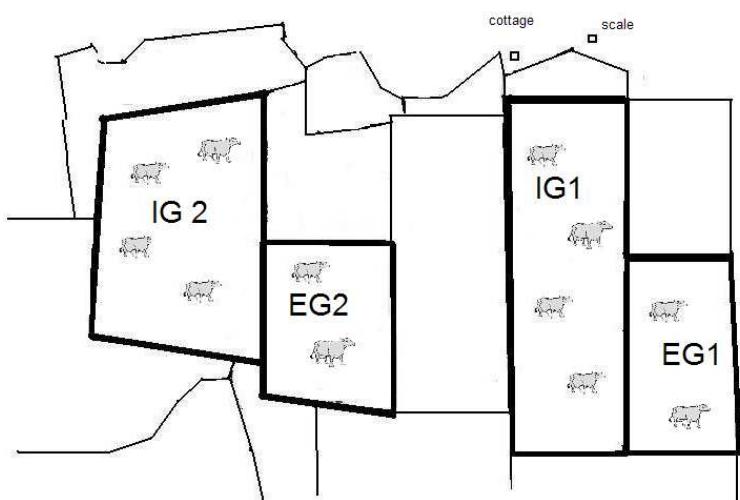


Figure 2. Heifers' selectivity for a type of patch in the course of the vegetation season for each patch separately on the intensive and extensive grazing system. On the x axis, dates of heifers' observations are indicated: July, Aug – August, Sep – September, 1 – the beginning of the month, 2 – the middle of the month.

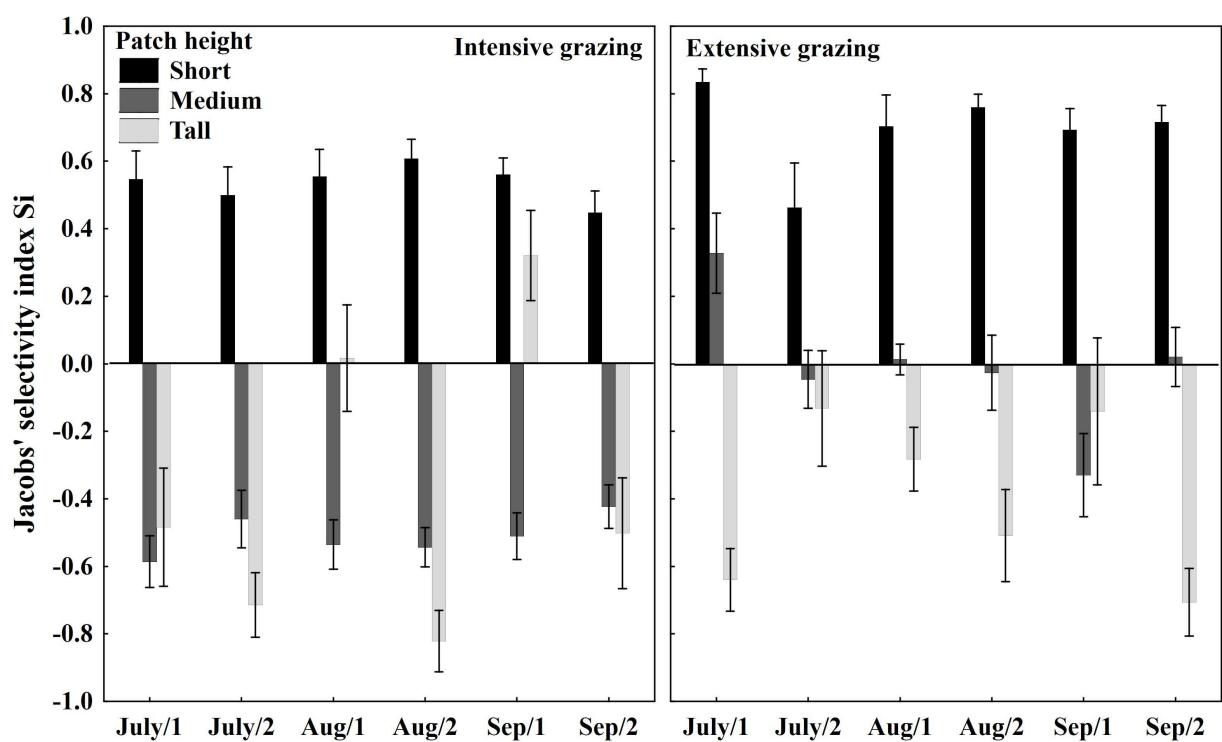


Figure 3. Ordination diagram showing results of PCA analysis of relationships among plant functional traits and heifers' selectivity for a type of patch on intensive (IG) and extensive (EG) grazing system (as supplementary environmental variable). Abbreviations: SLA – specific leaf area, LDMC – leaf dry matter content, N-Ellengerg – Ellenberg's value for nitrogen content, Si - Jacobs' selectivity index.

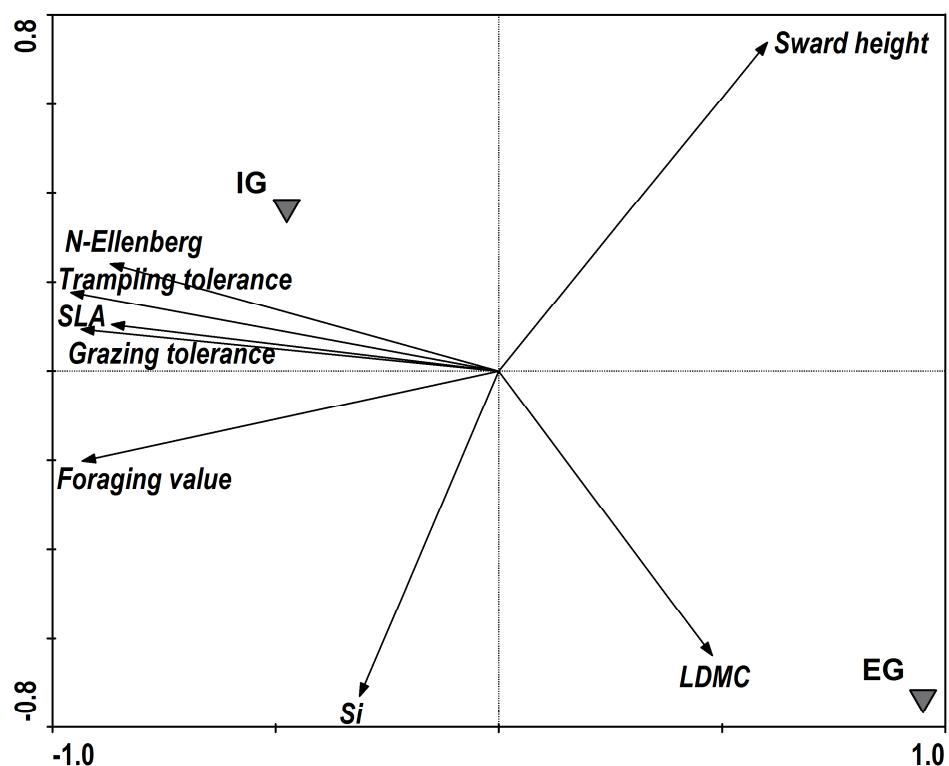
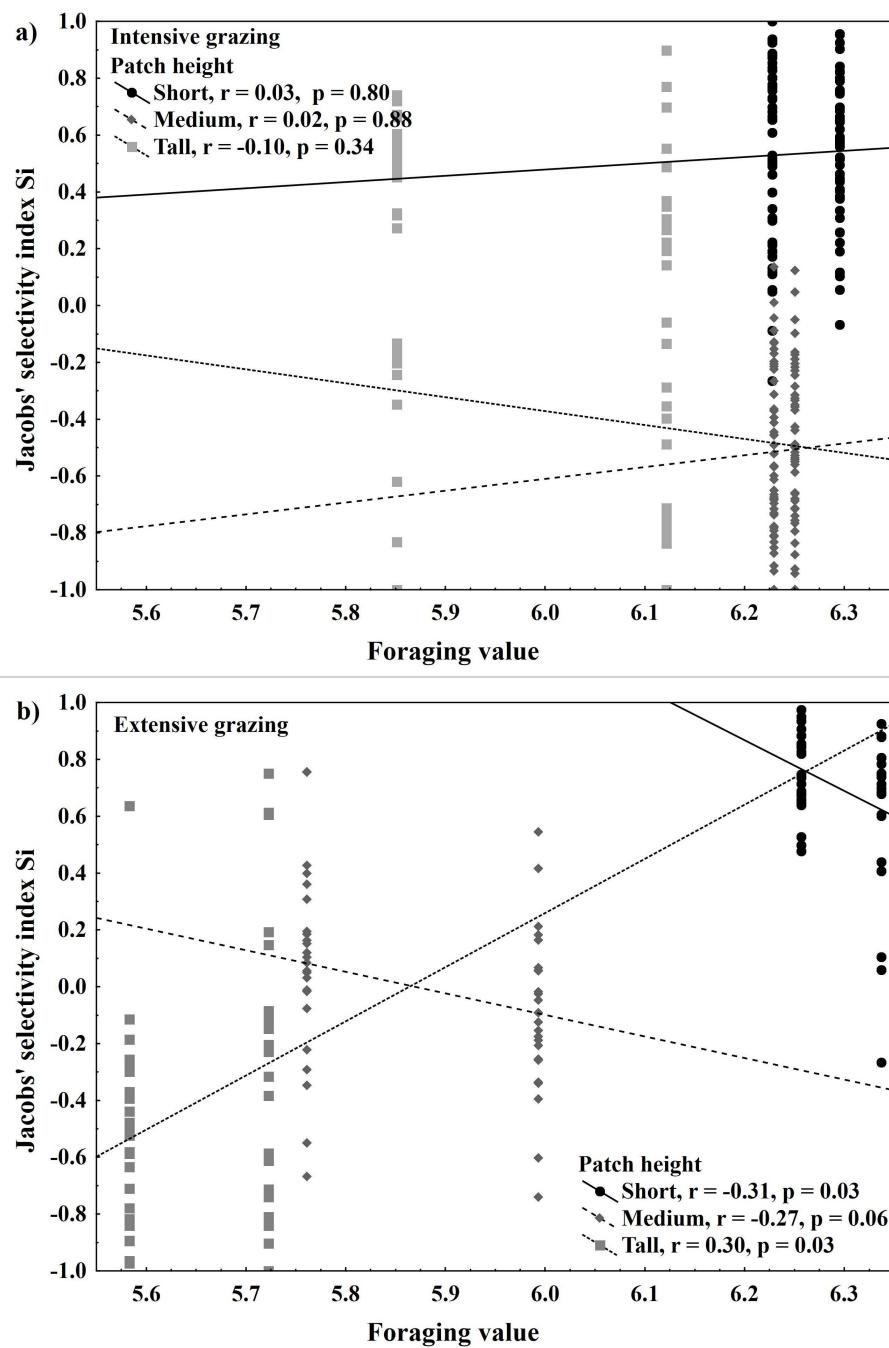


Figure 4. Response of heifers' selectivity for a type of patch on the foraging value of each patch separately on the a) intensive and b) extensive grazing system.



5.3 Článek IV.

Hejcmanová P., Stejskalová, M., Hejcmán, M. 2013.

Forage quality of leaf-fodder from main broad-leaved woody species and its possible consequences for the Holocene development of forest vegetation in Central Europe.

Vegetation History and Archeobotany. 007/s00334-013-0414-2.ljlk

Forage quality of leaf-fodder from the main broad-leaved woody species and its possible consequences for the Holocene development of forest vegetation in Central Europe

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Abstract Leaf-hay was the principal winter feed of livestock from the Neolithic until the first archaeological records of scythes dated to the Iron Age (700–0 b.c.). Despite the use of meadow hay, leaf-fodder remained an important winter supplement until the present. Archaeological evidence lists *Quercus*, *Tilia*, *Ulmus*, *Acer*, *Fraxinus* and *Corylus* as woody species harvested for leaf-fodder, while *Fagus*, *Populus* or *Carpinus* were rarely used. The aim of our study was to test whether the use of listed woody species followed the pattern of their forage quality (syn. nutritive value). In late May 2012, we collected leaf biomass at four localities in the Czech Republic and determined concentrations of N, P, K, Ca, Mg, neutral- and acid-detergent fibre and lignin. Species with leaves of low forage quality were *Carpinus betulus*, *Fagus sylvatica* and *Quercus robur*, species with leaves of intermediate quality were *Corylus avellana* and *Populus tremula* and species with leaves of high quality were *Ulmus glabra*, *Fraxinus excelsior*, *Tilia cordata* and *Acer platanoides*. Selective browsing and harvesting of high quality species *Acer*, *Fraxinus*, *Tilia* and *Ulmus* thus probably supported their decline in the Bronze and Iron ages and supported the expansion of *Carpinus* and *Fagus*. Our results indicate that

our ancestors' practice of exploiting woody species as leaf-hay for winter fodder followed their nutritive value.

Keywords Agricultural history · Leaf-fodder · Livestock feeding · Nutritive value · Prehistory

Introduction

The practice of collecting leaves and twigs for livestock feeding is probably the oldest method of fodder harvesting in Europe and is still widely practiced in tropical and subtropical regions of Asia and Africa (e.g. Roothaert and Paterson 1997; Le Houerou 2000; Cheema et al. 2011). Leaf-hay (syn. leaf-fodder) played a significant role in livestock feeding especially during the winter at least from the Late Neolithic (3000 b.c.) and was widely used over the course of time in Europe (Dreslerová 2012). The first written records about the use of leaf-fodder come from Roman authors, Marcus Porcius Cato (234–149 b.c., *De Agricultura*, Hooper and Ash 1935) or Lucius Junius Moderatus Columella (A.D. 4(?)–70 A.D., *De Re Rustica*, Ash 1941). Another valuable source of knowledge of prehistoric livestock foddering with twigs and leaves comes mainly from charcoal (Regnall 2003), and from analyses of plant macrofossils and pollen from sheep and goat coprolites found in the Neolithic lake-shore settlements in the Alps (Akeret and Jacomet 1997; Akeret et al. 1999) or from the Neolithic shepherd's shelter of la Grande Rivoire (Delhon et al. 2008; Martin 2011).

The advantage of leaf-hay is that it can be very efficiently collected without the use of any special tools such as sharp metal scythes or sickles. Based on recent analogies (Austad 1988) it is supposed that there have been three main techniques of leaf-hay collection since the Neolithic:

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- (1) Pollarding, which consists in cutting off the top of the tree and harvesting the shoots.
- (2) Shredding, which leaves the trunk and crown intact while the side branches are removed.
- (3) Coppicing, based on cutting suckers or young shoots directly from the tree base.

Leaf-hay was widely used across the whole of Europe, from Greece (Halstead 1998) to Great Britain (Smith 2010) and from Italy and France (Haas et al. 1998; Karg 1998) to Scandinavia (Slotte 2001). In each region, different woody species were used according to the regional vegetation and woody species availability, which latter could be ensured for instance by transhumance (Akeret and Jacomet 1997; Poschlod and WallisDeVries 2002). Many archaeological records have confirmed year-round leaf-hay foddering of sheep and goats in stables in the Alps, using ash (*Fraxinus excelsior*), lime (*Tilia* spp.) and hazel (*Corylus avellana*), or fir (*Abies alba*) (Rasmussen 1989; Rasmussen 1993; Delhon et al. 2008). In the northern part of Europe woody species exploited as fodder for cattle, horses, sheep and goats were ash, alder (*Alnus glutinosa*), birch (*Betula* spp.), lime, poplar (*Populus* spp.) and several coniferous species, primarily Scots pine (*Pinus sylvestris*) or juniper (*Juniperus communis*) (Austad 1988; Austad and Hauge 2006). However, the most important tree species for leaf-hay across Europe, considered of a high forage quality, was the elm (*Ulmus* spp.). Consequently the elm has been suggested as having been selectively harvested by Neolithic farmers. This could have resulted, according to pollen analysis, in the marked elm decline (Troels-Smith 1960; Iversen 1973; Magyari et al. 2012). On the other hand, hornbeam (*Carpinus betulus*) or beech (*Fagus sylvatica*) were not exploited to the same extent due to being considered of low forage quality (Halstead 1998).

Although it is supposed that different woody species were selected for leaf harvesting according to their quality, the forage qualities of common broad-leaved woody species in Central Europe has never been compared with each other. Forage quality can be evaluated according to concentration of macro-nutrients, N, P, K, Ca and Mg particularly, their ratios, Ca:P and K:(Ca+Mg) and by fibre content (cellulose, hemi-cellulose and lignin) which pre-determine organic matter digestibility (Hejman et al. 2006, 2010; Pavlů et al. 2006).

In this paper, we investigated whether the main European broad-leaved woody species *Acer platanoides*, *C. betulus*, *C. avellana*, *Fagus sylvatica*, *F. excelsior*, *Quercus robur*, *Populus tremula*, *Tilia cordata* and *Ulmus glabra* differ in their forage quality for livestock, and consequently whether their supposed use could follow the pattern of this. In addition, we discussed possible consequences of forage quality of different woody species for their selection by

livestock and for the woody species composition of agriculturally used forests in Central Europe.

Materials and methods

Biomass sampling

For the analysis, we selected nine broad-leaved woody species common in Central Europe at least since the Bronze Age (1900–800 b.c.). We collected the leaf biomass (fully expanded leaves, blades and petioles together) of selected woody species from at least three individuals of each species at each of four selected localities in late May 2012. These localities were broad-leaved forests and their margins in Bohemia, the western part of the Czech Republic:

- (1) Kozly (50° 15' N, 14° 32' E, 167 m a.s.l.);
- (2) Měsice (50° 11' N, 14° 31' E, 203 m a.s.l.);
- (3) Běstvina (49°50' N, 15°35'E, 338 m a.s.l.);
- (4) Mšec (50°12'N, 13°52'E, 435 m a.s.l.).

Mean annual precipitation and temperatures ranged at the sampling sites from 614 to 723 mm and from 8 to 9 °C, respectively. We collected in total 36 (nine species × four replicates) leaf biomass samples, which were then oven-dried at 60 °C for 48 h and ground to powder.

Leaf chemical properties

In the leaf samples, the concentrations of macro-elements (N, P, K, Ca, Mg) and the residual ash content (ash-(P+K+Ca+Mg)) neutral- (NDF) and acid-detergent fibre (ADF) and acid-detergent lignin (ADL) were determined. NDF represents cellulose, hemi-cellulose and lignin together, ADF represents cellulose and lignin. The N concentration in the plant samples was determined using an automated analyser TruSpec (LECO Corporation, USA) by combustion with oxygen in an oven at 950 °C. Combustion products were mixed with oxygen and the mixture passed through an infrared CO₂ detector and through a circuit for aliquot ratio where carbon is measured as CO₂. Gases in the aliquot circuit were transferred into helium as a carrying gas, conducted through hot copper and converted to N.

Biomass samples were burnt in a microwave oven at temperature of 550 °C and weighed in order to determine ash content. Biomass samples were mineralized using *aqua regia* and P, K, Ca and Mg concentrations were then determined in the solution using ICP-OES (Varian Vist-aPro, Mulgrave, Vic., Australia). Residual ash containing mostly Si was calculated as the ash content minus the sum of P, K, Ca and Mg concentrations. NDF, ADF and ADL

contents were determined by standard methods of AOAC (1984).

All analyses were performed in the accredited national laboratory Ekolab Žamberk (<http://www.ekolab.zamberk.cz>). N:P, Ca:P and K:(Ca+Mg) ratios were calculated from determined concentrations.

Data analyses

The data were tested by the Kolmogorov–Smirnov test of normality and met the assumption for the use of parametric tests. One-way ANOVA followed by post hoc comparison using the Tukey's multiple range tests in the STATISTICA 9.0 program (StatSoft, Tulsa, USA) were used to identify significant differences in concentrations of nutrients and NDF, ADF and ADL contents among species.

Unconstrained principal component analysis (PCA) in the CANOCO for Windows 4.5 program (Ter Braak and Šmilauer 2002) was used to analyze relationships among leaf chemical properties and similarity of 36 samples. Data were log-transformed before the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram constructed by the CanoDraw program (Ter Braak and Šmilauer 2002).

Results

No significant effect of species on N and Mg concentrations in leaves was recorded ($P > 0.05$, Table 1). Nitrogen concentration ranged from 28.2 to 36.0 g kg⁻¹ and Mg

from 2.6 to 4.1 g kg⁻¹, respectively. Effect of species on concentrations of other elements in leaves was significant (all $P < 0.01$).

Concentration of P ranged from 1.97 g kg⁻¹ in *Carpinus* to 3.22 g kg⁻¹ in *Fraxinus*, concentration of K ranged from 9.1 g kg⁻¹ in *Fagus* to 20.9 g kg⁻¹ in *Fraxinus* and concentration of Ca ranged from 9.3 g kg⁻¹ in *Quercus* to 17.2 g kg⁻¹ in *Fraxinus*.

There was a significant effect of species on N:P, Ca:P and K:(Ca+Mg) ratios (all $P < 0.001$) in leaves. N:P ratio ranged from 10.5 in *Fraxinus* to 15.5 in *Carpinus*, Ca:P ratio ranged from 3.8 in *Quercus* to 7.2 in *Corylus*, and K:(Ca+Mg) ratio ranged from 0.69 in *Carpinus* to 1.46 in *Tilia*.

There was a significant effect of species on content of NDF, ADF, ADL and residual ash in leaves (all $P < 0.001$, Table 2). Content of NDF ranged from 397 g kg⁻¹ in *Ulmus* to 663 g kg⁻¹ in *Fagus*, content of ADF ranged from 243 g kg⁻¹ in *Ulmus* to 480 g kg⁻¹ in *Fagus*, content of ADL ranged from 85 g kg⁻¹ in *Carpinus* to 236 g kg⁻¹ in *Fagus* and content of residual ash ranged from 24.8 g kg⁻¹ in *Quercus* to 51.8 g kg⁻¹ in *Ulmus*.

Results of the PCA analysis are presented in the form of the ordination diagram in Fig. 1. The first ordination axis explained 32 %, the first two axes together 56 % and the first four axes together 84 % variability of leaf chemical data. Concentrations of macro-elements were positively correlated one with another and generally bore no relation to the contents of NDF, ADF and ADL which were positively correlated with one another and negatively correlated with the K:(Ca+Mg) ratio. The first axis divided species

Table 1 Concentration (mean ± standard error of mean) of N, P, K, Ca, Mg and N:P, Ca:P and K:(Mg+Ca) ratios in leaf-fodder of the studied species

Species	N (g kg ⁻¹)	P (g kg ⁻¹)	K (g kg ⁻¹)	Ca (g kg ⁻¹)	Mg(g kg ⁻¹)	N:P ratio	Ca:P ratio	K:(Mg + Ca)
<i>Acer platanoides</i>	28.2 ± 1.2 ^a	2.7 ± 0.3 ^{a,b}	18.0 ± 0.6 ^{a,b}	12.3 ± 0.5 ^{a,b,c}	3.0 ± 0.2 ^a	10.8 ± 1.3 ^{a,b}	4.6 ± 0.4 ^{a,b}	1.18 ± 0.07 ^{a,b}
<i>Carpinus betulus</i>	30.7 ± 0.6 ^a	1.9 ± 0.1 ^a	10.6 ± 1.0 ^{c,d}	12.7 ± 1.7 ^{a,b,c}	2.7 ± 0.4 ^a	15.5 ± 0.4 ^c	6.4 ± 0.7 ^{a,b}	0.69 ± 0.04 ^a
<i>Corylus avellana</i>	31.5 ± 1.4 ^a	2.3 ± 0.1 ^{a,b}	16.0 ± 1.9 ^{a,b,d}	16.4 ± 1.3 ^{b,c}	3.6 ± 0.3 ^a	13.8 ± 1.2 ^{a,b,c}	7.2 ± 0.8 ^b	0.79 ± 0.06 ^a
<i>Fagus sylvatica</i>	31.4 ± 2.9 ^a	2.1 ± 0.2 ^a	9.1 ± 0.5 ^c	10.2 ± 0.4 ^{a,b}	2.6 ± 0.2 ^a	15.3 ± 0.3 ^{a,b,c}	5.1 ± 0.3 ^{a,b}	0.71 ± 0.05 ^a
<i>Fraxinus excelsior</i>	33.2 ± 2.1 ^a	3.2 ± 0.2 ^b	20.9 ± 0.9 ^a	17.2 ± 1.3 ^c	4.1 ± 0.7 ^a	10.5 ± 1.0 ^a	5.4 ± 0.6 ^{a,b}	0.99 ± 0.05 ^{a,b}
<i>Populus tremula</i>	28.9 ± 1.0 ^a	2.6 ± 0.2 ^{a,b}	18.3 ± 2.0 ^{a,b}	15.4 ± 1.1 ^{a,b,c}	2.8 ± 0.4 ^a	11.3 ± 0.7 ^{a,b,c}	6.1 ± 0.6 ^{a,b}	1.01 ± 0.09 ^{a,b}
<i>Quercus robur</i>	32.9 ± 0.9 ^a	2.5 ± 0.1 ^{a,b}	11.6 ± 0.7 ^{b,c,d}	9.3 ± 0.5 ^a	2.6 ± 0.2 ^a	13.5 ± 0.8 ^{a,b,c}	3.8 ± 0.1 ^a	0.97 ± 0.03 ^{a,b}
<i>Tilia cordata</i>	36.0 ± 1.2 ^a	3.0 ± 0.5 ^{a,b}	19.7 ± 0.4 ^a	12.1 ± 2.4 ^{a,b,c}	2.8 ± 0.6 ^a	12.6 ± 1.3 ^{a,b,c}	4.1 ± 0.7 ^a	1.46 ± 0.25 ^b
<i>Ulmus glabra</i>	34.3 ± 3.3 ^a	2.7 ± 0.1 ^{a,b}	19.9 ± 2.7 ^a	14.2 ± 1.9 ^{a,b,c}	2.7 ± 0.3 ^a	12.7 ± 0.7 ^{a,b,c}	5.2 ± 0.5 ^{a,b}	1.18 ± 0.08 ^{a,b}
Meadow hay	20.0–28.7	2.7–3.7	24.1–34.0	6.0–8.4	1.5–4	5–10	1.7–2.5	–
Optimum range	19.2–25.6	2.3–3.7	5–10	2.9–5.8	1.5–3.5	5–10	1–2	1–2.2

Using Tukey post hoc comparison test, differences among species indicated by the same superscripted letters were not significant

Chemical properties of good quality meadow hay follow Hejcmán et al. (2010, 2012), Hrevusová et al. (Hrevušová et al. 2009) and Tallowin and Jefferson (1999) and the optimum range for cattle follows Kudrna (1998) and Whitehead (1995)

Calculated by one-way ANOVA, differences among species for all chemical properties were significant ($P < 0.01$)

Table 2 Concentration (mean \pm standard error of mean) of NDF neutral detergent fibre, ADF acid detergent fibre, ADL acid detergent lignin and residual ash in leaf-fodder of the studied species

Species	NDF (g kg ⁻¹)	ADF (g kg ⁻¹)	ADL (g kg ⁻¹)	Res. Ash (g kg ⁻¹)
<i>Acer platanoides</i>	400 \pm 24.3 ^a	313 \pm 6.3 ^{a,b}	102 \pm 3.2 ^{a,b}	37.0 \pm 1.9 ^{a,b,c}
<i>Carpinus betulus</i>	437 \pm 16.4 ^a	273 \pm 10.1 ^{a,d}	85 \pm 6.3 ^a	30.1 \pm 3.2 ^{a,b}
<i>Corylus avellana</i>	476 \pm 23.5 ^a	342 \pm 13.4 ^{b,c}	163 \pm 26.2 ^{b,c,d}	43.6 \pm 2.7 ^{b,c}
<i>Fagus sylvatica</i>	663 \pm 11.6 ^b	480 \pm 7.0 ^e	236 \pm 9.4 ^e	30.0 \pm 1.6 ^{a,b}
<i>Fraxinus excelsior</i>	512 \pm 77.8 ^{a,b}	401 \pm 13.9 ^c	207 \pm 14.3 ^{d,e}	47.7 \pm 2.2 ^c
<i>Populus tremula</i>	452 \pm 27.5 ^a	374 \pm 24.9 ^c	195 \pm 22.8 ^{c,d,e}	41.1 \pm 4.7 ^{b,c}
<i>Quercus robur</i>	450 \pm 10.9 ^a	306 \pm 5.3 ^{a,b}	135 \pm 9.6 ^{a,b,c}	24.8 \pm 2.8 ^a
<i>Tilia cordata</i>	409 \pm 21.4 ^a	305 \pm 7.0 ^{a,b}	116 \pm 4.6 ^{a,b}	37.3 \pm 3.7 ^{a,b,c}
<i>Ulmus glabra</i>	397 \pm 41.2 ^a	243 \pm 12.0 ^d	99 \pm 13.4 ^{a,b}	51.8 \pm 4.6 ^c
Meadow hay	500–680	340	40	
Optimum range	330–450	190–300	Max. 80	

Using Tukey post hoc comparison test, differences among species with the same superscripted letter were not significant

Chemical properties of good quality meadow hay follow Worrel et al. (Worrell et al. 1986) and Isselstein et al. (2007) and the optimum range for cattle follows Kudrna (1998) and Whitehead (1995)

Calculated by one-way ANOVA, differences among species for all chemical properties were significant ($P < 0.01$)

into groups with a low concentration of macro-elements and a high N:P ratio on the right hand side of the diagram (*Fagus*, *Quercus* and *Carpinus*), with an intermediate concentration of macro-elements in the middle of the diagram (*Corylus*, *Populus*) and with a high concentration of macro-elements and a low N:P ratio on the left hand side of the diagram (*Ulmus*, *Fraxinus*, *Tilia*, *Acer*). Species with a low variability of leaf chemical properties among the localities were *Acer*, *Fagus* and *Quercus* as for all four localities these species plotted close together in the diagram. Species plotting as similar in three localities while differing in the fourth were *Carpinus* and *Corylus* and finally species with high variability between all the localities were *Fraxinus*, *Populus*, *Tilia* and *Ulmus*.

Discussion

Forage quality of studied species

The main message of this paper is that there are large differences in forage quality among the main broad-leaved woody species in Central Europe. The species with leaves of low forage quality are *Carpinus*, *Fagus* and *Quercus*, species with leaves of intermediate forage quality are *Corylus* and *Populus*, and species with leaves of high forage quality are *Ulmus*, *Fraxinus*, *Tilia* and *Acer*. Concentrations of N in the leaves of all species are in the optimum range for cattle nutrition and comparable with meadow hay. Nitrogen requirements of cattle can thus be fully covered using the leaf hay of all the studied species. Concentrations of P in leaves of *Carpinus* and *Fagus*, in contrast to other species,

are below the optimum range for cattle. Insufficient P concentration in leaf-fodder represents the real problem for performance of livestock, especially for lactating cows and young, quickly growing stock. Although the range of optimum P concentrations in forage for cattle is relatively wide, lactating cows and young stock require high P concentrations in the upper part of this range, at least above 3 g P kg⁻¹ (Liebisch et al. 2013). Such high P requirements could be covered only by the leaf-fodder of *Fraxinus* and *Tilia* collected early in the spring. Relatively high N concentrations in the leaves of all species and also relatively high P concentrations in several species were given by collection of leaves shortly after their full flush, as N and P concentrations are high in young spring leaves and then decrease during the vegetation season as they senesce (Kobe et al. 2005). Low P concentrations in the leaves of *Carpinus* and *Fagus*, and therefore their low forage quality, was well reflected by the N:P ratio which was above 15. In grassland hay of good forage quality the N:P ratio is generally below 10 (Hejeman et al. 2012).

With the exception of *Fagus*, concentrations of K in leaves of the other species were too high for optimum cattle nutrition. K concentrations too high for livestock nutrition are also common in the forage from almost all meadow or crop species, and animals are well adapted to excrete accessible K through their urine (Kayser and Isselstein 2005). Accessible concentration of K in the forage, if not above 25 g kg⁻¹, does not represent the main problem in the use of leaf-fodder for cattle although the optimum concentration is up to 10 g kg⁻¹.

Concentrations of Ca were excessive in leaf-fodder from all the species and this may cause relatively severe health

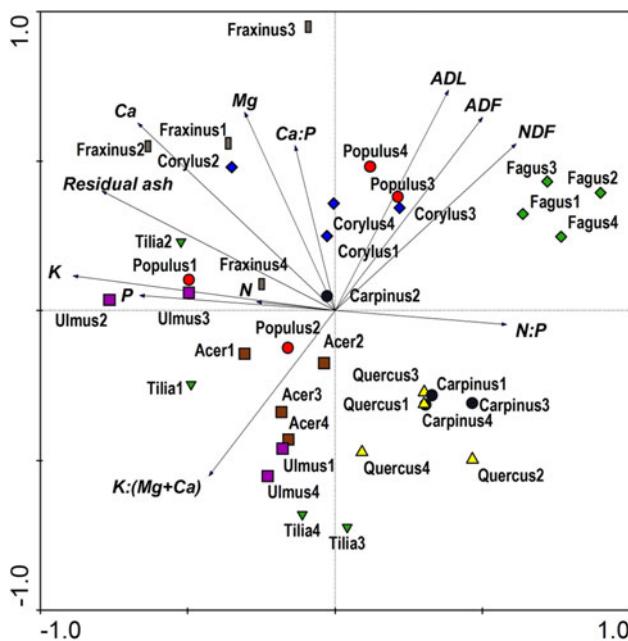


Fig. 1 Ordination diagram showing results of PCA analysis of relationships among woody species, N, P, K, Ca and Mg concentrations; N:P, Ca:P and K:(Ca+Mg) ratios, NDF neutral detergent fiber, ADF acid detergent fiber and ADL acid-detergent lignin. Numbers indicate the locality: 1 Kozly, 2 Měšice, 3 Běstvina and 4 Mšec

problems connected with decrease in cattle performance if combined with insufficient P supply. Although both elements are required by animals in large quantities for bone growth particularly, their supply must be balanced as accessible Ca supply decreases absorption of P, thus causing P deficiency. Excessive Ca concentrations are the main reason why the Ca:P ratio in the leaf-fodder of all the species was from two to three times higher than the optimum range for cattle nutrition. Taking into account the Ca:P ratio, the leaf-fodder from the studied species was of substantially lower quality than meadow hay with its optimum ratio.

Concentrations of Mg in leaf-fodder were, with the exception of slightly higher concentrations in *Corylus* and *Fraxinus*, in the optimum range for cattle nutrition similarly as in the case of meadow hay. Leaf-fodder can thus fulfill the Mg requirements of cattle.

High K concentration associated with low concentrations of Ca and Mg resulting in a K/(Ca+Mg) ratio higher than 2.2 (Butler 1963), together with excessive N in forage may induce grass tetany syndrome (Swerczek 2007). This is not however the case with leaf-hay forage as the K/(Ca+Mg) ratio was below the critical value of 2.2 in all species.

The content of NDF was within or below the range corresponding to meadow hay from semi-natural grasslands, or even lower. An appropriate content of NDF stimulates rumen activity. The important finding is that leaves of woody species have a very high content of fibre constituted by the lignin

fraction that represents an anti-nutritive, indigestible component in the forage. High amounts of leaf-fodder may restrain forage intake and inhibit digestive enzymes, and consequently induce adverse effects on animal performance. From this point of view, leaf-fodder probably only played a maintenance role enabling cattle to survive the winter but did not enable live-weight gain. Such fodder during the winter may also shift calving and lambing to a more favourable period in comparison to that of contemporary free ranging cattle and sheep (Balasse et al. 2012). In addition, leaf-fodder was probably used particularly as a supplement for cattle during the winter in addition to pasture forage, or as a by-product of timber harvesting for house construction, the latter consisting mostly in the use of fir, *Abies alba* (Akeret and Rentzel 2001). As we recorded in the Altai Mts., cattle can also graze senescent grassland biomass during the winter and can scrape out the biomass hidden under a 20 cm deep snow layer. Up to the Hallstatt period when the first iron scythes appeared in Central Europe and thus enabled hay-making (Hejcmán et al. 2013), leaf-fodder probably served as the main winter food for cattle especially in areas with deep snow layers. In areas with a snow layer less than 20 cm, leaf-fodder was probably a supplement to the winter grazing, or animals could graze on it on their own in the surroundings of the settlement (Akeret and Jacomet 1997).

Leaf-fodder was probably more widely used for sheep and goats as they feed naturally more on leaves of shrubs and trees than cattle and are physiologically adapted to this (Papachristou et al. 2005). In particular goats may have mechanisms to attenuate the undesirable effects of lignin and secondary metabolites (Howe et al. 1988) and their natural food can contain more than 50 % of leaves of woody species (Papachristou and Nastis 1993). On the other hand, the use of leaf-fodder has been widely recorded for sheep and goats in archaeological localities. This is because their dung is compact and easily recognisable (Akeret and Jacomet 1997; Akeret et al. 1999), compared with cattle dung which forms pats of typical form, but are usually mixed with the rest of the sediment (Akeret and Rentzel 2001; Shahack-Gross 2011).

Consequences of leaf-fodder quality for development of forest vegetation in Holocene

In many European regions, farmers preferred, if possible, to use *Acer*, *Fraxinus*, *Ulmus* and *Tilia* for leaf-fodder harvesting (Dreslerová 2012). We can conclude that this preference closely followed their better forage quality in comparison with other common broad-leaved woody species in Central Europe. Similar results, i.e. the substantially better forage quality of *Fraxinus ornus* than *Carpinus orientalis*, were also recorded in Mediterranean (Papachristou 1997). Nowadays, forage quality is analyzed by modern

analytical methods, but farmers were surely able to recognize the forage quality of different woody species without any analytical methods, but according to milk yield or live weight gain of their livestock (our personal experience). For example the use of *Ulmus* leaves as supplementary fodder for cattle in the time of forage shortage was recommended, for the first time, by Marcus Cato (234–149 b.c.) in his book *De Agricultura* (Hooper and Ash 1935). In Iceland in the 6–8th centuries A.D., *Ulmus* was highly valued as fodder for cows (Kelly 2000). Farmers were undoubtedly also aware of other qualities of tree fodder, in particular their medicinal properties which may, for instance, help to control parasite infestation of animals (Austad 1988; Musonda et al. 2009; Martin et al. 2011).

During grazing, livestock make up their diet with species of higher forage quality to fulfill their nutritional requirements. As lactating cows and calves require a high P supply, they frequently prefer to graze P rich biomass. Cattle were the most important animals from the first farmers up to modern times not only in the Czech Republic (Schibler and Chaix 1995; Kyselý 2012). Phosphorus-poor leaves of *Carpinus* and *Fagus* were thus probably avoided by cattle during grazing in forests if other woody species with higher P concentrations and lower lignin content in leaves were available. As the spread of both species has occurred since the Bronze Age in Bohemia, the western part of the Czech Republic (Pokorný and Kuneš 2005; Chytrý 2012), it is highly probable that this was at least partly connected to their avoidance by livestock in forests and also probably by farmers during leaf-fodder harvesting. Selective browsing and harvesting of *Acer*, *Fraxinus*, *Tilia* and *Ulmus* thus probably augmented their decline in the Bronze and Iron ages and supported the expansion of *Carpinus* and *Fagus*.

Conclusion

Our results suggest that our ancestors' practice of tree species exploitation for leaf-fodder in the past was not only governed by their availability, but also followed the forage quality of harvested woody species within the actual vegetation context. The forage quality of investigated woody species does not however reach the level of dietary requirements of contemporary dairy cattle for their satisfactory performance. Leaf-fodder was thus probably used as a supplement to biomass grazed during winter and enabled winter survival without substantial loss of the live weight of cattle. Species providing the best forage quality of leaf-fodder were *Acer*, *Fraxinus*, *Tilia* and *Ulmus*, species providing intermediate quality were *Corylus* and *Populus*, and finally species providing very low quality were *Quercus*, *Carpinus* and *Fagus*.

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5.4 Článek V.

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Nutritive value of winter collected annual twigs of main European woody species, mistletoe and ivy and its possible consequences for winter foddering of livestock in prehistory.

The Holocene

Nutritive value of winter collected annual twigs of main European woody species, mistletoe and ivy and its possible consequences for winter foddering of livestock in prehistory

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Abstract

In Central Europe, forest grazing was probably the main way of providing winter feeding for livestock in prehistory; the main components of this diet most likely included annual twigs of woody species (*Acer platanoides*, *Betula pendula*, *Carpinus betulus*, *Corylus avellana*, *Fagus sylvatica*, *Fraxinus excelsior*, *Picea abies*, *Pinus sylvestris*, *Populus tremula*, *Quercus robur*, *Salix caprea*, *Tilia cordata* and *Ulmus glabra*), *Hedera helix*, *Viscum album* and senescent grassland biomass, however, their nutritive value has never been compared.

Biomass samples were collected in the Czech Republic in February 2013 and analyzed for concentration of nitrogen, phosphorus, potassium, calcium, magnesium, fiber and lignin. With the help of a recent analogy from the Altai Mts. (Russia), possible consequences of winter grazing on the development of forest vegetation and cattle breeds in prehistory were assessed. *Hedera* and *Viscum* were the best forage available in winter and their nutritive value, according to the highest N and lowest fibre and lignin concentrations, was higher than the nutritive value of all winter collected annual twigs of woody species. Nutritive value of annual twigs of all woody species was very low, especially compared to the quality of meadow hay, leaf-fodder or senescent steppe grassland biomass. Therefore *Hedera* and *Viscum* might have been preferentially grazed by livestock and collected by ancient farmers for the supplementary feeding of privileged animals. According to recent analogy, annual twigs of woody species were browsed by livestock. Their insufficient quality could be one of the reasons for the low body size of cattle recorded in prehistory. The most realistic model of livestock breeding in prehistory seems to be year-round grazing opening forests and causing deforestation in the surroundings of prehistoric settlements.

Key words

agricultural history, forage quality, *Hedera helix*, livestock feeding, prehistory, *Viscum album*, year-round forest grazing

Introduction

It is generally accepted that the livestock of prehistoric farmers grazed on pastures, fallows, stubbles and in forests during the vegetation season, but it is still not clear how

livestock was fed during the winter time. In Central and Northern Europe, winter time is generally the bottle neck for livestock breeding as the carrying capacity of the landscape is substantially lower in winter than during the vegetation season. This problem was at least partly solved by transhumance in some mountain regions - seasonal movement of people with their livestock between summer and winter pastures (Moe *et al.*, 2007). According to many authors, the shortage of fodder during the winter time was solved by feeding livestock with leaf fodder from the main broad-leaved woody species, harvested and conserved by drying during the vegetation season (Dreslerová, 2012; Rasmussen, 1989). Livestock was probably also partly fed by winter collected twigs (Haas *et al.*, 1998). Leaf-foddering should thus have played the main role in winter feeding of livestock in Europe from the Neolithic and at least up to the Latene Period when the first scythes enabled cutting of grasslands and hay making (Hejcmán *et al.*, 2013). Therefore, hay making step by step replaced leaf-fodder harvesting, although leaf fodder was used as a supplement to winter hay feeding in some regions up to the present (Austad and Hauge, 2006; Halstead *et al.*, 1998; Slotte, 2001).

Although generally accepted, the theory of leaf foddering in the Neolithic is based on relatively weak archaeological evidences of several woody species recorded in coprolites of goats, sheep and cattle discovered in Switzerland, Germany (Akeret and Jacomet, 1997; Akeret and Rentzel, 2001; Akeret *et al.*, 1999; Rasmussen, 1993) and in France (Delhon *et al.*, 2008). However, sheep and particularly goats browse frequently on woody species even if they have non-limited access to high quality pasture forage (Kühn and Hadorn, 2004; Papachristou and Platis, 2011; Pokorná *et al.*, 2013). Leaves of woody species in coprolites of sheep and goats are thus not direct evidence for harvesting of leaf-fodder and analysis of coprolites must be supplemented by analysis of

charcoals and twigs on archaeological localities (Regnell, 2002). The second argument for large-scale leaf-foddering were declines of elm (*Ulmus* spp.) in different periods of agricultural prehistory, detected according to a marked fall of its pollen in pollen diagrams in many countries (Troels-Smith, 1960; Heybroek, 1963; Garbett, 1981; Peglar and Birks, 1993; Andersen and Rasmussen 1993). Elm is a species with a high forage value of leaves in comparison to other woody species (Hejčmanová *et al.*, 2013) and its decline was interpreted by some authors as resulting from Dutch disease transferred by the beetle *Scolytus scolytus*, although it could also be triggered by large-scale leaf-foddering together with climate and soil changes (Girling and Greig 1985; Moe and Rackham, 1992; Peglar, 1993; Parker *et al.*, 2002; Troels-Smith, 1960).

The importance of large scale leaf-foddering for winter feeding of livestock since the Neolithic can be thus deduced particularly from (sub) recent analogies. The question which remains open is thus whether cattle, sheep and, since the Bronze ages, also horses were mainly fed by leaf fodder during the winter time or whether they were able to obtain enough fodder by winter grazing. Unique information about a possible solution, in a European context, can be found in the memoirs of the farmer F. J. Vavák, who managed his small peasant farm in the Elbe lowland (190 – 210 m a.s.l.) 50 km east of Prague in the last third of the 18th century (Klír, 2008). In moderate winters, livestock (cattle, sheep, goats and pigs) were grazed year-round on communal pastures and in forests without housing. Storage of conserved forage for winter use was insufficient and areas of pasture substantially exceeded areas of hay meadow. Year-round livestock grazing without any or with a very limited amount of supplementary feeding was thus most probably the dominant means of livestock breeding in Central Europe from the Neolithic up to the 18th century. Year-round cattle grazing was also documented by

medieval written resources from the Czech Republic (Szabó and Hédl, 2013). According to Zimmermann (1999), replacement of year-round livestock grazing on pastures and in forests with livestock housing and winter feeding was the result of an increase in human population density and the necessity of using all natural resources with maximum effectiveness. This is also the reason why the first cow houses were used after the Bronze age in western Europe (Netherlands and NW Germany, in particular) where human density was substantially higher than in the Czech Republic where livestock was not definitively closed into barns until the 19th century (Petrášek, 1972).

This leads us to question which plant species could be eaten by livestock during winter forest grazing and ask how this winter forage could fulfil the nutritive requirements of livestock. In the lowlands of Central Europe where the climate borders the oceanic and continental, winter grass biomass is generally senescent (yellow). There are, however, some winter green understory species such as ivy (*Hedera helix*) and hemiparasitic species such as mistletoe (*Viscum album*), which were, according to several authors (Akeret and Rentzel, 2001; Bottema, 2001; Deforce *et al.*, 2013; Kühn and Hadorn, 2004; Kühn *et al.*, 2013; Troels-Smith, 1960), also used for winter feeding of livestock. Thus the main role in winter feeding of livestock was probably played by annual twigs of woody species since the Neolithic up to the 18th century, but their nutritive value (syn. forage quality) has never been studied. Nutritive value of forage can be evaluated according to the concentration of macro-nutrients, N, P, K, Ca and Mg, particularly their ratios, Ca:P and K:(Ca+Mg), and by fibre content (cellulose, hemicellulose and lignin) which predetermine organic matter digestibility (Hejman *et al.*, 2006; 2010; Pavlů *et al.*, 2006).

The aim of this study was thus to (i) determine the nutritive value of winter collected annual twigs of the main woody species (*Acer platanoides*, *Betula pendula*, *Carpinus betulus*, *Corylus avellana*, *Fagus sylvatica*, *Fraxinus excelsior*, *Picea abies*, *Pinus sylvestris*, *Populus tremula*, *Quercus robur*, *Salix caprea*, *Tilia cordata* and *Ulmus glabra*), leaves of mistletoe (*Viscum album*) and ivy (*Hedera helix*), and to compare them with senescent winter steppe grassland biomass and meadow hay; and (ii) to assess the possible consequences of the nutritive value of twigs for winter feeding of livestock, development of forest vegetation and cattle breeds in Central Europe since the Neolithic.

Materials and methods

Biomass sampling

For the analysis, we selected 15 woody species common in Central Europe at least since the Neolithic (5600 BC). We collected the annual twigs with buds of selected woody species and leaf biomass of ivy and mistletoe from at least three individuals of each species on each of four selected localities during February 2013. Selected localities were broad-leaved forests and their margins in the Bohemia, western part of the Czech Republic: 1) Kozly (50°15'N, 14°32'E, 167 m a.s.l.), 2) Měšice (50°11'N, 14°31'E, 203 m a.s.l.), 3) Kletečná (50°34' N, 13°59'E, 472 m a.s.l.) and 4) Mšec (50°12'N, 13°52'E, 435 m a.s.l.). Mean annual precipitations and temperatures ranged in sampling sites from 614 to 723 mm and from 8 to 9°C, respectively. We collected in total 60 (15 species x four site replicates) annual twigs and winter leaf biomass samples which were then oven-dried at 60 °C for 48 hours and ground to powder.

Annual twigs and winter leaf chemical properties

In twig and winter leaf samples, the concentration of macro-elements (N, P, K, Ca, Mg) and the content of residual ash (ash – (P + K + Ca + Mg)) neutral- (NDF) and acid-detergent fibre (ADF) and acid detergent lignin (ADL) were determined. NDF represents cellulose, hemi-cellulose and lignin together, ADF represents cellulose and lignin. The N concentration in the plant samples was determined using an automated analyser TruSpec (LECO Corporation, USA) by combustion with oxygen in an oven at 950°C. Combustion products were mixed with oxygen and the mixture passed through an infrared detector of CO₂ and by circuit for the aliquot ratio where carbon is measured as CO₂. Gases in the aliquot circuit were transferred into helium as a carrying gas, conducted through hot copper and converted to N.

Biomass samples were burnt in a microwave oven at a temperature of 550°C and weighted in order to determine ash content. Biomass samples were mineralized using *aqua regia* and P, K, Ca and Mg concentrations were then determined in the solution using ICP–OES (Varian VistaPro, Mulgrave, Vic., Australia). Residual ash containing mostly Si was calculated as the ash content minus the sum of P, K, Ca and Mg concentrations. NDF, ADF and ADL contents were determined by standard methods of AOAC (1984).

All analyses were performed in an accredited national laboratory, Ekolab Žamberk (<http://www.ekolab.zamberk.cz>). N:P, Ca:P and K:(Ca+Mg) ratios were calculated from determined concentrations.

Data analyses

Data tested by the Kolmogorov-Smirnov test of normality met assumptions for the use of parametric tests. One-way ANOVA followed by post-hoc comparison using the Tukey's multiple range tests in Statistica 9.0 program (StatSoft, Tulsa, USA) were used to identify significant differences in concentrations of nutrients and NDF, ADF and ADL contents among species.

Unconstrained principal component analysis (PCA) in Canoco for Windows 4.5 program (ter Braak and Šmilauer, 2002) was used to analyze the relationships among annual twig and winter leaf chemical properties and the similarity of the 60 samples. Data were log-transformed before the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram constructed by the CanoDraw program (ter Braak and Šmilauer, 2002).

Results

Calculated by one-way ANOVA, the effect of species was significant on all determined chemical properties of collected winter biomass. Concentration of N ranged from 12.4 g kg⁻¹ in *Fraxinus* to 21.1 g kg⁻¹ in *Viscum*, concentration of P ranged from 1.1 g kg⁻¹ in *Picea* to 2.4 g kg⁻¹ in *Viscum*, concentration of K ranged from 4.8 g kg⁻¹ in *Picea* to 13.8 g kg⁻¹ in *Viscum*, concentration of Ca ranged from 7.4 g kg⁻¹ in *Picea* to 21 g kg⁻¹ in *Populus* and finally concentration of Mg ranged from 0.9 g kg⁻¹ in *Picea* to 2.2 g kg⁻¹ in *Hedera* (Table 1). Values of N:P ratio ranged from 7.8 in *Salix* to 12 in *Carpinus*, values of Ca:P ratio ranged from 3.8 in *Viscum* to 14.7 in *Populus* and finally values of K:(Ca+Mg) ranged from 0.14 in *Tilia* to 0.37 in *Fraxinus* (Table 1). Content of NDF ranged from 431 g kg⁻¹ in *Viscum* to 596 g kg⁻¹ in *Tilia*, content of ADF ranged from

318 g kg⁻¹ in *Hedera* to 533 g kg⁻¹ in *Carpinus* and finally content of ADL ranged from 112 g kg⁻¹ in *Hedera* to 266 g kg⁻¹ in *Betula*. Content of residual ash ranged from 15.6 g kg⁻¹ in *Pinus* to 51.2 g kg⁻¹ in *Corylus* (Table 2).

Results of the PCA analysis are presented in the form of an ordination diagram (Fig. 1). The first ordination axis explained 39%, the first two axes together 61% and the first four axes together 83% variability of biomass chemical data. The first axis of the diagram can be attributed particularly to concentrations of N, P, K, Mg, NDL, ADF and lignin. The second axis can be attributed particularly to concentration of Ca in the biomass. Concentrations of N, P, K and Mg were positively correlated to each other as vectors for all these elements were directed into the same area of the diagram and were negatively related to NDL, ADF and lignin concentrations. The highest concentrations of N, P, K and Mg were recorded in *Viscum* followed by *Hedera* and the lowest in *Carpinus* and *Fagus* in which, on the contrary, the highest concentrations of NDL, ADF and lignin were recorded. The highest concentrations of Ca and Ca:P ratio were recorded in *Populus*, followed by *Tilia*, *Ulmus* and *Salix*. The lowest concentrations of Ca were recorded in *Fraxinus*, followed by *Pinus* and *Picea*.

Discussion

Nutritive value of annual twigs and winter leaves

The main message of our study is that species with winter green leaves such as *Hedera* and *Viscum* belong to the best forage which might have been available in forests during the winter. Their nutritive value, according to the highest N and lowest ADF and lignin concentrations, was higher than the nutritive value of all winter collected annual twigs of woody species. Similar high nutritive value can be recorded in winter leaves of *Rubus fruticosus* (Verheyden-Tixier *et al.*, 2008) which was also among plant species

recorded in Neolithic coprolites of sheep/goat in the Grande Rivoire rock shelter in France (Martin, 2011). The ancient farmers thus probably collected *Hedera* and *Viscum* during the wintertime intentionally and used them for the feeding of animals (Haas, 2004; Nicod *et al.*, 2008), because they are the richest source of N and P in winter. *Viscum* was collected, although the amount of its biomass was relatively small in forests in comparison to the biomass of woody species and its collection was laborious.

Therefore, we suggest that *Viscum* was probably used as a supplement for feeding of privileged animals such as lactating and pregnant cows or goats with the highest N and P requirements. According to our personal experience, *Viscum* is excellently eaten by goats without any detrimental effects on their health (Fig. 2). Macroremains of *Viscum* discovered at archaeological localities (see Akeret and Rentzel, 2001; Deforce *et al.*, 2013; Kühn and Hadorn, 2004; Kühn *et al.*, 2013; Pokorný *et al.*, 2006) could thus represent remains of winter collected *Viscum* used as “an extra forage” for selected categories of livestock. Nowadays the high nutritive value of *Viscum* is also well known to hunters in Austria who still use the biomass of *Viscum* to attract deer to particular places during the winter (G. Glatzer, personal communication). In addition, stems and leaves of *Viscum* are fragile and they frequently fall down from trees after strong winds. Therefore, *Viscum* could be eaten by livestock even without any intentional collection. Similarly to *Viscum*, *Hedera* has higher nutritive value than annual twigs of woody species and this is why it was probably selectively grazed by livestock in winter. In the experiment by Van Uytvanck and Hoffman (2009), for example, *Hedera* completely disappeared from forest managed for several years by year-round cattle grazing. *Hedera* was thus probably scarce or completely missing in prehistoric and medieval forests managed by winter livestock grazing, similarly as other winter green understory species

such as *Vinca minor* or *Rubus* sp. In grazed forests, *Hedera* could survive only as liana on trees, but not as ground covering species. In addition, it is highly probable that old flowering shoots of *Hedera* were intentionally collected and used as green winter fodder for livestock by prehistoric farmers. A decrease in the pollen production of *Hedera* in different periods (see Bottema, 2001; Iversen, 1944; Troels-Smith, 1960) could be thus considered as an indicator of human activities in forests connected with livestock breeding.

Nutritive value of all winter collected annual twigs of woody species was substantially lower than the nutritive value of meadow hay (Table 1) and also spring collected leaf-fodder of broad-leaved woody species (see Hejmanová *et al.*, 2013, for a comparison with other plant species see also Verheyden-Tixier *et al.*, 2008). Low nutritive value of twigs was given by insufficient concentrations of N and P and also partly by insufficient concentration of Mg for livestock nutrition. On the other hand, twigs were characterised by too high concentrations of Ca, ADF and lignin, and also by too high Ca:P ratio and too low K:(Ca+Mg) (tetanic) ratio. The next characteristic aspect of the chemical composition of twigs was relatively small differences in the concentration of P among individual species in comparison to their leaves in which differences were substantially higher (Hejmanová *et al.*, 2013). Twigs of *Fagus* and *Carpinus* had absolutely the worst nutritive value because of their highest lignin content which is in accordance with their leaves (Hejmanová *et al.*, 2013). Leaf-fodder of *Ulmus* and *Tilia* were the best of all woody species in Central Europe and this is also consistent with the nutritive value of their twigs which was also comparable to *Salix*. Senescent grassland biomass collected in winter on steppe grassland was of better nutritive value than twigs of woody species because of higher concentrations of N and

P, lower concentrations of Ca and lignin, and also a lower Ca:P ratio in senescent grassland biomass than in twigs. This indicates that livestock first of all grazed senescent grassland biomass and then, if no other alternatives were available, started to browse trees. A problem of senescent grassland biomass can be high fungus infection and therefore contamination by mycotoxins, particularly in moderate (“warm”) winters (Skládanka *et al.*, 2011). In some years, senescent grassland biomass was thus probably less consumed by livestock as its consumption could cause health problems. In addition, in summer grazed forests and grasslands, the amount of senescent grass biomass was low in winter and probably insufficient for livestock feeding.

Despite the relatively low nutritive value of annual twigs in comparison to meadow hay and leaf-fodder, twigs are regularly browsed by different deer species, hares and European bison, and serve as winter forage if no other better alternative is available (Ammer, 1996; Kowalczyk *et al.*, 2011). In addition, winter collected annual twigs of woody species are frequently used as a supplementary feed to improve the health status of livestock (Fig. 2).

Winter feeding of livestock and its consequences for cattle breeds

Despite low nutritive value, annual twigs of many woody species probably played a crucial role in the winter feeding of livestock in many regions since the Neolithic and this resulted in the development of wood-pasture habitats in Central Europe (Bergmeier *et al.*, 2010). We suggest that the majority of livestock was probably year-round grazed without any or with only a limited amount of supplementary feeding during the winter and that they were thus subjected to insufficient nutrition conditions. Indirect evidence for very bad livestock feeding during the winter time in the past can be a reduction in

body size during the process of domestication which is, for instance, up to half in cattle in comparison to aurochs, their ancestor (Petrášek, 1972; Zeder, 2006). One of the reasons consists in the fact that cattle in the surroundings of villages had much more limited access to winter forage than free ranging animals. According to our personal experience, heifers with insufficient access to high quality forage over the winter do not reach their full body size. Although evidence for winter feeding of livestock by leaf-fodder has been recorded in archaeological layers, the amount of harvested leaf fodder was probably not sufficient to cover the nutritional requirements of all livestock (Rasmussen, 1990; Thiébault, 2005). This idea is also supported by written records from the 18th century describing insufficient feeding of livestock during the winter and the importance of forests for livestock winter feeding and survival (Klír, 2008; Petrášek, 1972). In the Czech Republic for example, a herd of wild cattle survived in the forests of the Dourov Mts. military area in the 1990s without any supplementary feeding and regularly reproduced each year. Their main winter forage was grassland senescent biomass, annual twigs of woody species and bark. The herd was finally hunted for veterinary reasons (farmers' fear of the spread of diseases) and because of their negative effects on forest regeneration (Z. Macháček, personal communication). In Kraansvlak in the Netherlands, European bison, Highland cattle and Konik horses are bred in deciduous forests without any supplementary winter feeding (Kemp and Cromsigt, 2012). Further recent analogies for the system of no winter feeding can be found in the Altai Mountains where sheep, cattle and horses are still bred with no or only limited supplementary winter feeding. As we recorded, livestock, forced by hunger, freely walked out of the village in the mornings to obtain forage in their surroundings. According to our observations and those of local farmers, sheep and cattle were able to

explore an area up to approximately seven km out of the village and horses approximately two times farther. Simultaneous breeding of sheep, cattle and horses thus enables the best spatial use and partitioning of forage resources in the surroundings of the village. As we recorded, the most explored were the steppe south exposed grasslands where senescent grassland biomass was grazed and alluvial forests where annual twigs of *Salix* sp. and *Populus* sp. were intensively browsed. Woody species formed bonsai-like shrubs and alluvial forests were very open (Fig. 3). In the evenings, livestock slowly returned home (Fig. 3), where they were controlled by farmers and sometimes also partly fed by small amounts of hay or other supplementary fodder. The system of no supplementary winter feeding was very efficient in landscapes with low human density as it required almost no labour and the ancient farmer was able to keep relatively high numbers of livestock. The disadvantages were no or rather negative live weight gain of livestock over the winter, the small size of adult animals, delayed maturity of young animals and the very high pasture area required. A well-known adaptation of adult cattle on this system is the fluctuating of live weight between the summer, when they accumulate fat, and winter, when they metabolize energy from fat reserves gained in summer and fall, similarly as deer in the northern environments (DelGiudice *et al.*, 1992). This adaptation is well known from old (primitive) breeds of cattle such as Highland, Galloway, Czech Reddish or Salers. As we learned in the Altai Mountains, the system of no winter feeding can also be realized with modern European cattle breeds such as Hereford, Simmental or Aberdeen-Angus (Figs. 2 and 3). Doubts of recent authors (see Kreuz, 2008) about the ability of Neolithic cattle to browse twigs of woody species and their ability to survive winter in Central Europe without any

supplementary feeding are therefore unjustified. Winter grazing of livestock in forests could thus play the crucial role in their opening in prehistory.

We suppose that the system of no or limited winter supplementary feeding of livestock was also used in lowland regions of Central Europe from the Neolithic at least up to the Iron ages when the human population density increased, but that to some extent, this system survived up to the 18th century. As the nutritive value of annual twigs of woody species is insufficient for cattle nutrition, browsing of twigs helped livestock to survive the winter but did not enable an increase in live weight or the stimulation of intensive milk production. We suggest therefore that the main selection criteria for prehistoric cattle and other livestock were thus the ability to survive the winter with no or limited supplementary feeding on forage of low nutritional value.

Year-round livestock grazing and its consequences for development of forest vegetation

In Central Europe, the maximum extent of forest occurred during the Atlantic period (ca 8000-4500 cal BC in Central Europe (Chytrý, 2012; Ložek, 2007) and 7350-3900 BC in Northern Germany (Dörfler *et al.*, 2012) with higher temperature and precipitations in comparison to the present. Subsequent vegetation changes were ascribed, in addition to climatic changes, to human activities related especially to deforestation and agricultural activities. Marked vegetation changes consisted, for instance, of *Ulmus* decline (Parker *et al.*, 2002), spread of *Carpinus* and *Fagus* (Chytrý, 2012; Herbig and Sirocko, 2013; Pokorný, 2005), and the emergence of various pasture indicators such as *Trifolium* sp., *Plantago lanceolata* and grasses whose pollen was recorded in different sediments (Brun, 2011; Poschlod and Baumann, 2010). In two basic models of deforestation due to early agriculture Iversen (1941) suggested clearance of forests by fire with the aim of

producing pastures in woodland as the source of food for cattle whereas Troels-Smith (1953) formulated a model which places livestock breeding to an earlier time, based on intensive leaf-foddering of animals in byres, particularly by *Ulmus*. In his model, Troels-Smith assumed the absence of pastures, animal confinement in settlements and limited area for the free ranging of animals according to the lack of pasture indicator plant species in pollen diagrams. At the same time, both authors debated the decline of *Hedera* pollen in sediments at around 5000 BP. Iversen (1944) suggested it as a climate change indicator, whereas Troels-Smith (1960) proposed that *Hedera* declined as a consequence of foddering to livestock.

Livestock keeping could have begun, however, even earlier than indicated by both authors, especially by leaving animals to free range in the forested surroundings of human settlements. Wood-pastures were common in the past (see for instance Jamrichová *et al.*, 2013 and Rösch, 2012), because Central European broad-leaved and mixed forests brim over with forage resources for domestic animals during the vegetation season. Based on our results, we can conclude that even during the winter time, available annual twigs of woody species and especially evergreen *Hedera* and *Viscum* provided sufficient nutrient supply for livestock to survive the winter. This idea is supported also by analyses of prehistoric cattle, goat and sheep dung from wetland settlements in the borderland between Germany and Switzerland in which macro remains of woody species were frequently recorded (Kühn *et al.*, 2013). Based on our experience of winter grazing and the ability of livestock to browse annual twigs of woody species, the most realistic model of livestock breeding in prehistory seems to be year-round livestock grazing. Based on this model, forests exposed to intensive winter grazing and browsing by livestock were open with many bonsai-like shrubs and dead

debarked trees in surrounding of settlements. Our conclusions are partly in agreement with the theory of Vera (2000) that the species composition and succession of vegetation was governed by large herbivores and the Central and Western lowlands were covered by a park-like landscape in areas with adequately high density of megaherbivores. There were probably no strict borders between forests and grasslands in vicinity of settlements, and forests were full of grassland species, although this can hardly be detected by pollen analysis as intensive grazing would have prevented the flowering and pollen production of many grassland species. During Neolithic times the effects of livestock grazing on forest were limited to the vicinity of settlements, therefore settlement density is a very important factor to evaluate the impact of livestock grazing on forests. Additionally, forests grazed by livestock do not necessarily develop a classical meadow park-like landscape. According to our personal experience from the Altai Mts., open areas are mainly found in wet environments around water courses where *Carex* sp., *Salix* sp. and other wetland species are dominating. Livestock grazing had probably important effect on forests, but numbers of livestock in the landscape had been still low during the Neolithic compared to later times and the grazing effect was thus not strong enough to enable development of large scale grasslands. This may explain why large scale grasslands are not visible in hundreds of pollen diagrams from the Neolithic (see Kreuz, 2008). Park-like landscape can develop if the density of livestock in forests is adequately high and well detectable large scale effects of livestock grazing on vegetation is mainly evidenced from the Bronze or Iron Ages onwards (Pokorný, 2005). In the discussion of livestock forest grazing, the time period, the settlement density, the cultural developments and density of browsing animal must be taken into account. Based on our experience we believe that substantial

part of deforestation in the surrounding of prehistoric settlements could be directly ascribed to year-round livestock grazing.

Conclusion

Based on the higher nutritive value of winter collected *Hedera* and *Viscum* than winter collected annual twigs of woody species, we suppose that both species could have been collected by prehistoric farmers and used for supplementary feeding of privileged animals. In addition, *Hedera* was probably preferentially grazed by livestock during the winter up to its total disappearance in forests. Prehistoric farmers could also feed livestock directly in forests by driving herds to intentionally cut trees or their branches with *Hedera* or *Viscum*. The presence of *Hedera* pollen in sediments could thus indicate forests which were not used for winter feeding of livestock, but validation of this conclusion requires further research. Winter collected annual twigs of all woody species were characterized by very low nutritive value, much lower than the quality of meadow hay, leaf-fodder or senescent steppe grassland biomass. After grazing of senescent grassland biomass, annual twigs of woody species were probably browsed by livestock. Insufficient winter nutrition could thus explain the low body size of cattle recorded since the Neolithic up to the 18th century. Year-round livestock grazing practised by ancient farmers seems to be the key driver for the formation of open forest with many bonsai-like shrubs.

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Table 1. Concentration (means \pm standard error of mean) of N, P, K, Ca, Mg and N:P, Ca:P and K:(Mg+Ca) ratios in leaf-fodder of studied species. Calculated by one-way ANOVA, differences among species for all chemical properties were significant ($P<0.01$). Using the Tukey post-hoc comparison test, species with the same letter were not significantly different. Chemical properties of good quality meadow hay follow Hejcman *et al.* (2010, 2012), Hrevušová *et al.* (2009) and Tallowin and Jefferson (1999), and optimum range for cattle follows Kudrna (1998) and Whitehead (1995).

Species	N (g kg ⁻¹)	P (g kg ⁻¹)	K(g kg ⁻¹)	Ca (g kg ⁻¹)	Mg (g kg ⁻¹)	N:P ratio	Ca:P ratio	K:(Mg+Ca)
<i>Acer platanoides</i>	15.6 \pm 1.4 ^{ab}	1.8 \pm 0.2 ^{ab}	8.0 \pm 1.1 ^{bc}	14.7 \pm 1.3 ^{ab}	1.5 \pm 0.2 ^{ab}	8.7 \pm 0.6 ^{ab}	8.5 \pm 1.5 ^{abc}	0.25 \pm 0.05 ^a
<i>Betula pendula</i>	13.9 \pm 0.4 ^a	1.6 \pm 0.1 ^{ab}	5.1 \pm 0.6 ^{ab}	12.3 \pm 1.8 ^{ab}	1.3 \pm 0.3 ^{ab}	8.8 \pm 0.5 ^{ab}	7.7 \pm 1.0 ^{ab}	0.19 \pm 0.02 ^a
<i>Carpinus betulus</i>	14.7 \pm 0.8 ^a	1.3 \pm 0.1 ^a	3.9 \pm 0.4 ^a	11.1 \pm 1.3 ^a	1.2 \pm 0.1 ^a	12.0 \pm 1.2 ^b	8.9 \pm 1.0 ^{abc}	0.16 \pm 0.01 ^a
<i>Corylus avellana</i>	17.9 \pm 2.1 ^{ab}	1.8 \pm 0.2 ^{ab}	8.5 \pm 0.5 ^{bc}	10.9 \pm 1.3 ^a	1.8 \pm 0.2 ^{ab}	10.0 \pm 0.9 ^{ab}	6.3 \pm 1.0 ^{ab}	0.32 \pm 0.02 ^a
<i>Fagus sylvatica</i>	14.4 \pm 1.1 ^a	1.3 \pm 0.1 ^a	4.6 \pm 0.7 ^{ab}	12.2 \pm 2.1 ^{ab}	1.0 \pm 0.1 ^a	11.7 \pm 1.2 ^{ab}	9.6 \pm 1.1 ^{abc}	0.17 \pm 0.01 ^a
<i>Fraxinus excelsior</i>	12.4 \pm 0.7 ^a	1.5 \pm 0.1 ^{ab}	8.5 \pm 0.7 ^{bc}	9.9 \pm 0.6 ^a	1.2 \pm 0.1 ^a	8.5 \pm 0.6 ^{ab}	6.8 \pm 0.7 ^{ab}	0.37 \pm 0.04 ^a
<i>Hedera helix</i>	16.9 \pm 1.0 ^{ab}	1.4 \pm 0.05 ^a	9.5 \pm 1.1 ^c	14.7 \pm 2.7 ^{ab}	2.2 \pm 0.3 ^b	11.9 \pm 1.0 ^b	10.3 \pm 0.9 ^{bc}	0.27 \pm 0.03 ^a
<i>Picea abies</i>	13.5 \pm 1.1 ^a	1.1 \pm 0.1 ^a	4.8 \pm 0.3 ^{ab}	7.4 \pm 0.7 ^a	0.9 \pm 0.1 ^a	12.0 \pm 0.6 ^b	6.5 \pm 0.3 ^{ab}	0.28 \pm 0.04 ^a
<i>Pinus sylvestris</i>	15.7 \pm 1.4 ^{ab}	1.5 \pm 0.1 ^{ab}	5.2 \pm 0.6 ^{ab}	7.8 \pm 1.0 ^a	1.1 \pm 0.04 ^a	10.3 \pm 0.6 ^{ab}	5.3 \pm 1.0 ^{ab}	0.29 \pm 0.06 ^a
<i>Populus tremula</i>	12.5 \pm 0.7 ^a	1.5 \pm 0.2 ^{ab}	6.6 \pm 0.8 ^{abc}	21.0 \pm 2.5 ^b	1.5 \pm 0.2 ^{ab}	8.7 \pm 0.8 ^{ab}	14.7 \pm 2.1 ^d	0.15 \pm 0.02 ^a
<i>Quercus robur</i>	14.0 \pm 0.3 ^a	1.2 \pm 0.1 ^a	5.1 \pm 0.7 ^{ab}	9.7 \pm 0.8 ^a	1.3 \pm 0.2 ^{ab}	11.8 \pm 0.7 ^{ab}	8.1 \pm 0.3 ^{abc}	0.22 \pm 0.02 ^a
<i>Salix capraea</i>	15.9 \pm 0.6 ^{ab}	2.1 \pm 0.2 ^{ab}	5.5 \pm 0.5 ^{abc}	16.2 \pm 1.7 ^{ab}	1.4 \pm 0.2 ^{ab}	7.8 \pm 0.5 ^a	8.2 \pm 1.7 ^{abc}	0.16 \pm 0.02 ^a
<i>Tilia cordata</i>	15.2 \pm 1.2 ^{ab}	1.9 \pm 0.2 ^{ab}	6.1 \pm 0.8 ^{abc}	20.7 \pm 3.0 ^b	1.5 \pm 0.3 ^{ab}	8.3 \pm 0.7 ^{ab}	11.4 \pm 1.8 ^{bc}	0.14 \pm 0.03 ^a
<i>Ulmus glabra</i>	14.6 \pm 0.6 ^a	1.5 \pm 0.05 ^{ab}	5.9 \pm 0.3 ^{abc}	14.7 \pm 0.3 ^{ab}	1.4 \pm 0.1 ^{ab}	9.7 \pm 0.1 ^{ab}	9.8 \pm 0.6 ^{abc}	0.18 \pm 0.01 ^a
<i>Viscum album</i>	21.1 \pm 2.3 ^b	2.4 \pm 0.4 ^b	13.8 \pm 1.2 ^d	8.5 \pm 1.2 ^a	1.7 \pm 0.2 ^{ab}	8.2 \pm 1.0 ^{ab}	3.8 \pm 0.4 ^a	0.68 \pm 0.11 ^b
meadow hay	20.0 - 28.7	2.7 - 3.7	24.1 - 34.0	6.0 - 8.4	1.5-4	5 - 10	1.7 - 2.5	-
Steppe grass winter biomass	17.9	2	3.7	6.6	1.2	9	3.3	0.22
optimum range	19.2 - 25.6	2.3 - 3.7	5-10	2.9 - 5.8	1.5-3.5	5-10	1-2	1-2.2

Table 2. Concentration (means \pm standard error of mean) of neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL) and residual ash in leaf-fodder of studied species. Calculated by one-way ANOVA, differences among species for all chemical properties were significant ($P<0.01$). Using the Tukey post-hoc comparison test, species with the same letter were not significantly different. Chemical properties of good quality meadow hay follow Worrel *et al.* (1986) and Isselstein *et al.* (2007) and optimum range for cattle follows Kudrna (1998) and Whitehead (1995).

Species	NDF (g kg ⁻¹)	ADF (g kg ⁻¹)	ADL (g kg ⁻¹)	Res. ash(g kg ⁻¹)
<i>Acer platanoides</i>	577 \pm 14 ^{cd}	514 \pm 9 ^{cd}	225 \pm 14 ^{def}	25.6 \pm 2.6 ^a
<i>Betula pendula</i>	600 \pm 24 ^{cd}	525 \pm 9 ^d	266 \pm 24 ^f	23.3 \pm 2.9 ^a
<i>Carpinus betulus</i>	642 \pm 27 ^d	533 \pm 12 ^d	206 \pm 10 ^{bcd}	25.3 \pm 2.9 ^{ab}
<i>Corylus avellana</i>	551 \pm 58 ^{bcd}	510 \pm 45 ^{bcd}	255 \pm 20 ^f	51.2 \pm 14.8 ^b
<i>Fagus sylvatica</i>	632 \pm 31 ^d	547 \pm 20 ^d	261 \pm 17 ^f	34.5 \pm 5.1 ^{ab}
<i>Fraxinus excelsior</i>	587 \pm 31 ^{cd}	455 \pm 28 ^{bcd}	144 \pm 15 ^{ab}	29.0 \pm 7.6 ^{ab}
<i>Hedera helix</i>	392 \pm 9 ^a	318 \pm 10 ^a	112 \pm 5 ^a	35.6 \pm 2.8 ^{ab}
<i>Picea abies</i>	498 \pm 35 ^{abcd}	413 \pm 19 ^{abc}	166 \pm 5 ^{abcde}	20.2 \pm 1.6 ^a
<i>Pinus sylvestris</i>	512 \pm 12 ^{abcd}	416 \pm 11 ^{ab}	163 \pm 7 ^{abcd}	15.6 \pm 1.3 ^a
<i>Populus tremula</i>	577 \pm 38 ^{cd}	491 \pm 27 ^{bcd}	226 \pm 20 ^{def}	38.4 \pm 5.7 ^{ab}
<i>Quercus robur</i>	582 \pm 29 ^{cd}	495 \pm 17 ^{bcd}	238 \pm 8 ^{ef}	20.8 \pm 0.1 ^a
<i>Salix capraea</i>	488 \pm 10 ^{abc}	455 \pm 14 ^{bcd}	207 \pm 18 ^{bcd}	29.6 \pm 2.8 ^{ab}
<i>Tilia cordata</i>	596 \pm 23 ^{cd}	495 \pm 25 ^{bcd}	215 \pm 9 ^{cdef}	33.8 \pm 5.4 ^{ab}
<i>Ulmus glabra</i>	456 \pm 6 ^{abc}	408 \pm 6 ^{ab}	213 \pm 6 ^{bcd}	37.3 \pm 0.3 ^{ab}
<i>Viscum album</i>	431 \pm 13 ^{ab}	327 \pm 12 ^a	150 \pm 7 ^{abc}	27.0 \pm 2.8 ^{ab}
meadow hay	500-680	340	40	
Steppe grass winter biomass	724	433	89	76
optimum range	330-450	190-300	max. 80	

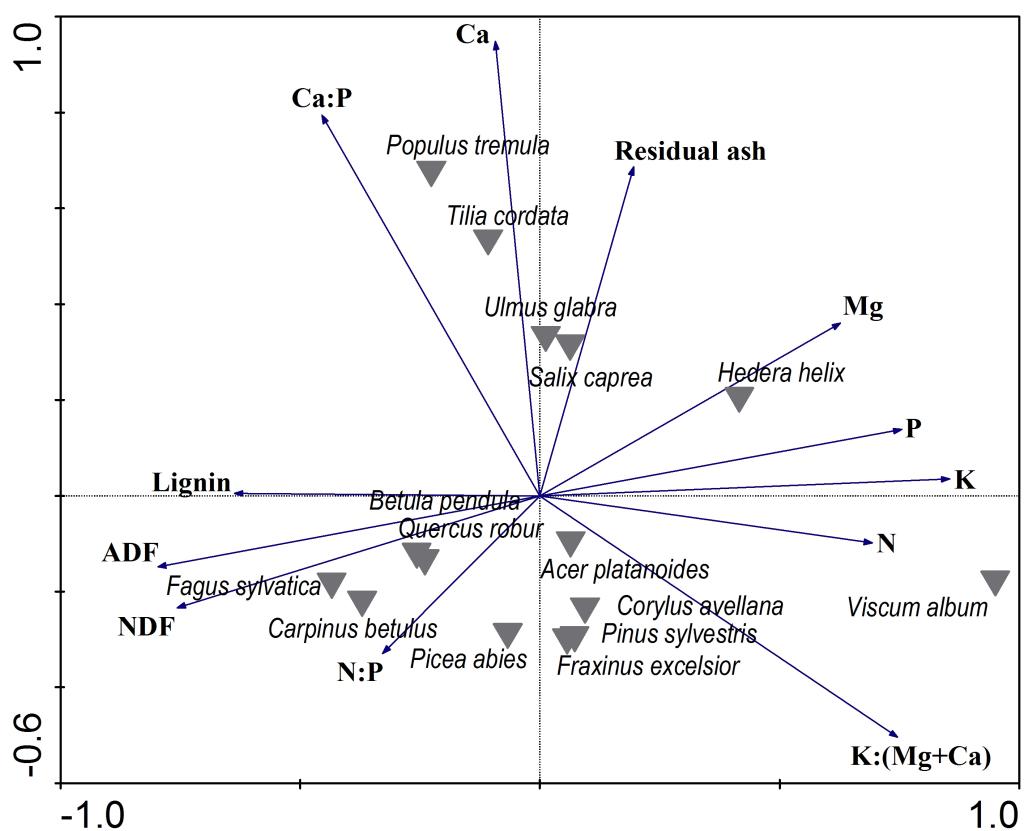


Fig.1. Ordination diagram showing results of PCA analysis of relationships among chemical properties of winter biomass of studied species, N, P, K, Ca and Mg concentrations; N:P, Ca:P and K:(Ca+Mg) ratios, NDF (neutral detergent fibre), ADF (acid detergent fibre) and lignin (ADL).

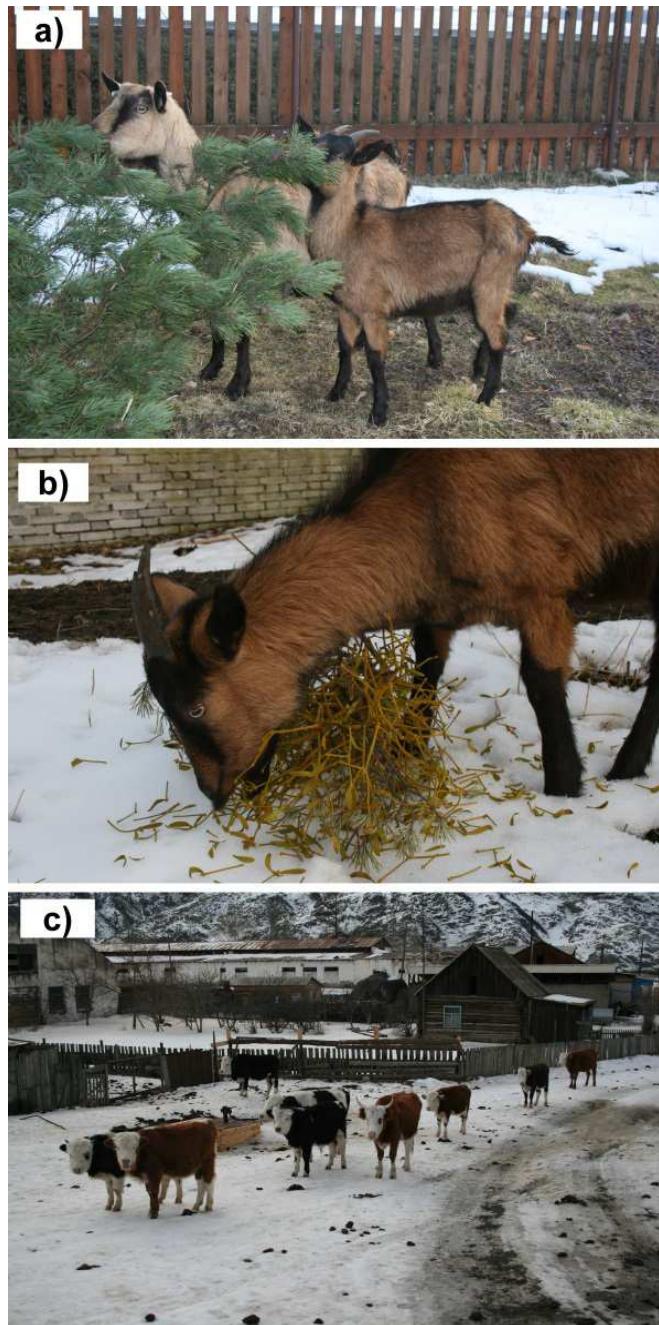


Fig. 2. (a) *Pinus sylvestris* is sometimes used by Czech farmers as supplementary winter fodder to improve health status of goats. (b) According to our feeding experiments, *Viscum album* is very well eaten by goats during the winter. (c) Ruminating young cattle in the evening on their way home from winter pastures in the Altai Mts. All photographs taken by Pavla and Michal Hejcmán in early March 2013.

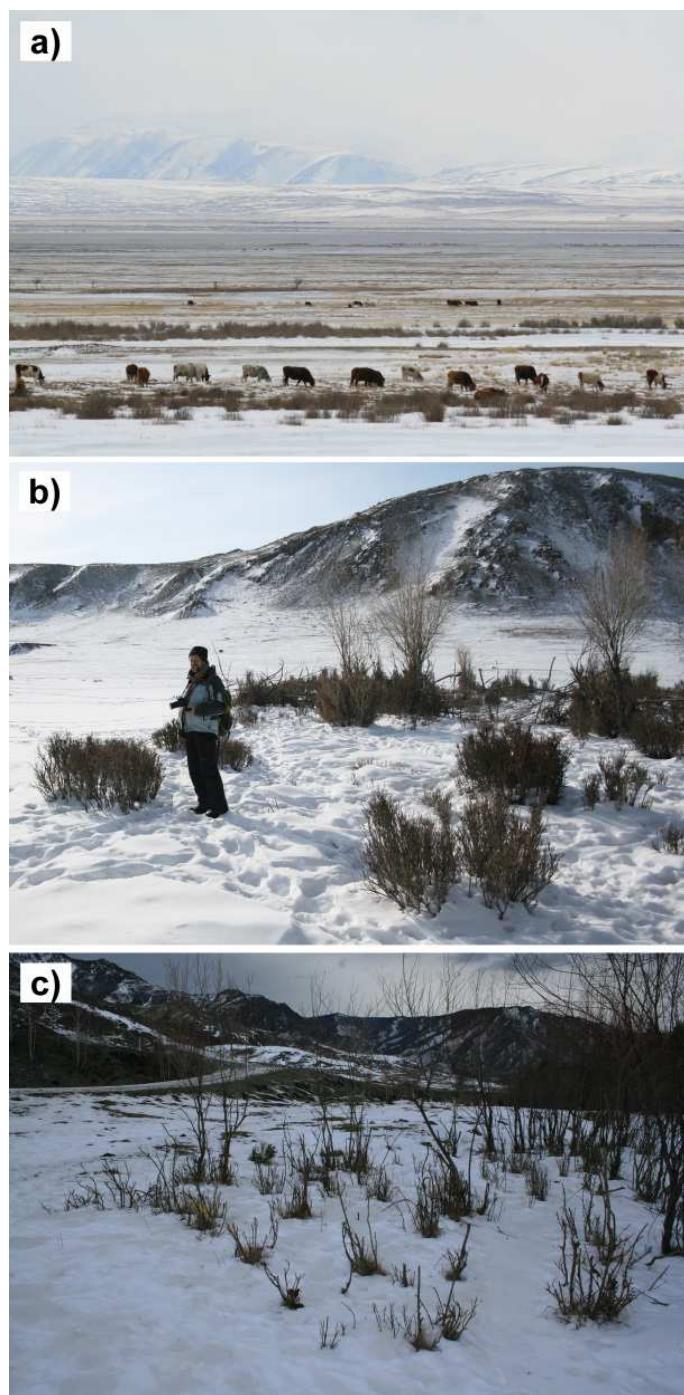


Fig. 3. Winter livestock grazing is still practiced in the Altai Mountains (South Siberia, Russia). (a) Cattle grazed senescent biomass on alluvial grasslands or browsed annual twigs of *Salix* sp. shrubs in the foreground. (b) Prof. Vilém Pavlů in bonsai-like alluvial shrub land (*Salix* sp. and *Populus* sp.) maintained by winter browsing of annual twigs by cattle and horses. (c) Alluvial *Salix* sp. forest heavily affected by the winter browsing of cattle and horses. All photographs taken by Michal Hejcman in early March 2013.

6. Komentář k výsledkům dizertační práce

Předkládaná dizertační práce měla za úkol zkoumat vliv pastvy a určit parametry, které mají vliv na chování skotu, respektive jalovic, při různých systémech či intenzitě pastvy, vliv různé intenzity pastvy na selektivitu neboli vyhledávání a příjem potravy dle složení a výšky porostu a též zkoumala nutriční hodnoty větviček dřevin či rostlin neboli letníny a jejich vliv na využívání tohoto krmení jako zimního krmení pro skot v období pravěku, což navazuje na selektivitu neboli výběr krmiva dle kvality porostu, v tomto případě letorostů dřevin či rostlin.

Pochopení chování zvířat ve vztahu k měnícím se podmínkám životního prostředí a dynamiky píce je rozhodující při navrhování strategií řízení pro živočišnou výrobu (Demment et al., 1986) a z tohoto důvodu je nezbytné se těmto tématům věnovat.

Výsledky první studie (článek I) týkající se chování skotu na různém typu pastvy, rotační a kontinuální, přinesly některé zajímavé výsledky. V této práci bylo porovnáváno pastevní chování jalovic při rotačním (RSS) a kontinuálním (CSS) systému pastvy. Výzkum probíhal na experimentální pastvině Amerika nedaleko Oldřichova v Hájích v Jizerských Horách na druhově bohaté horské pastvině, kde se páslo čtyři až šest jalovic na 1 ha plochy v každém systému během hlavní pastvení sezóny. Měřili jsme 24-hodinové chování zvířat, metodou etologického snímkování, tzv. „scan sampling“, každých 15 minut během dne a každou 1 hodinu během noci, a to přímým pozorováním stanovených typů chování, a dále živé hmotnosti jednotlivých jalovic od července do září. Dále jsme zkoumali strukturu a vlastnosti porostu a kvalitu píce. Dalším cílem pokusu bylo porovnat příjem potravy jalovic (pasení, žvýkání a přežvykování za minutu) z rozdílných systémů pastvy.

Dle našich výsledků, systém pastvy neměl žádný vliv na charakteristiky porostu, kromě jeho výšky. Průměrná výška porostu byla 5,9 cm u CSS a 12,8 cm a 7,2 cm u RSS před ($p < 0,001$) a po ($P > 0,05$) pastvě. Nebyl nalezen žádný důkaz vývoje porostu struktury během postupující sezóny, a to ani na CSS ani na RSS. Mnoho jiných parametrů porostu, jako například hustota trav a bylin a délka výhonů jetele plazivého,

bylo stejných během celého pětiletého výzkumu a nelišilo se ani různým systémem pastvy. Píce na CSS měla vyšší obsah dusíkatých látek ($p < 0,001$), rostoucí v sezóně, než RSS. Porost na CSS byl kontinuálně pasen jalovicemi po celou dobu pastvení sezóny, a proto byl zachován stejný růst rostlin, kterým nebylo umožněno vykvést. Porost na RSS byl jednou ročně sekán a pasen jalovicemi, jeho obsah dusíkatých látek byl však rozdílný. Výška porostu korelovala s obsahem vlákniny a představovala tak přímou souvislost s kvalitou píce. Nicméně, studie porovnávající chemické složení píce mezi kontinuálním a rotačním systémem pastvy přinesly rozporné výsledky. Například, Pulido a Leaver (2003) zjistili, že není žádný rozdíl v obsahu dusíkatých látek a v obsahu vlákniny (NDF – natural detergent fiber) mezi oběma systémy pastvy. Naše výsledky jsou v rozporu s těmi, co popsal například Walton et al. (1981), Heitschmidt et al. (1982), Jung et al. (1985) a Lehmkuhler et al. (1999), kteří všichni zaznamenali vyšší obsah dusíkatých látek a nižší koncentrace hrubé vlákniny u rotačního systému pastvy. Lze předpokládat, že tyto výsledky se liší v důsledku nižšího obsahu sušiny v porostu a byly ovlivněny zvýšenou přítomností luštěnin na RSS. Navíc, ve všech těchto studiích, můžeme vidět vyšší tlak pastvy na RSS a častější rotace v období pastvy. To znamená, že základním prvkem stanovení struktury a kvality porostu není systém pastvy, ale intenzita pastvy (jak uvádí např. Pavlu et al. 2006). Ačkoli je struktura porostu a kvalita píce udávaná jako klíčová vlastnost pro stanovení chování zvířat na pastvě, jak uvádí Hejcmanová a Mládek (2012) a druhově bohaté porosty s vysokou diverzitou a heterogenitou porostu ovlivňují rozhodování zvířat na pastvě (Wang et al. 2012), dle našich výsledků vliv pastvy a sezóny se na žádném z typů chování neprojevil průkazně ($p > 0,05$). Celková denní pastva ukázala slabou reakci na strukturu porostu a kvalitu píce. Jalovice měly vyšší intenzitu pastvy na krátkých porostech, což koresponduje i s výsledky Erlingera et al. (1990), Barretta et al. (2001) a s výsledky článku II. Dalšími charakteristikami porostu je nižší hustota trav a bylin. Příjem potravy za minutu měl pozitivní vztah k obsahu hrubé vlákniny ($r = 0,48$) a dusíkatých látek ($r = 0,34$) a obsahu popelovin ($r = 0,16$, $p < 0,05$).



Obr. 1. Přímé pozorování jalovic. Jizerské hory. Foto: Hejmanová

Mezi parametry kvality porostu jsme zjistili, že nejlepším prediktorem pastevního chování byl obsah hrubé vlákniny. Našli jsme pozitivní vztah mezi hrubou vlákninou a příjemem potravy, který by se mohl zdát rozporuplný, protože vláknina je obvykle limitujícím faktorem příjmu píce, kvůli nasycení bachoru (Mertens a Ely 1979, McLeod a Smith 1989). Pravděpodobně je toto způsoben nižším obsahem hrubé vlákniny v porostu, který se pohyboval mezi 14-21% CF v biomase. Tento nízký obsah CF je faktorem, který aktivuje žvýkání a akce v bachoru. Oba, kontinuální a rotační systém pastvy, proto můžou zajistit kvalitní porost stimulující příjem píce po celé pastevní období. I když se vliv pastvy na žádném z typů chování neprojevil průkazně, příjem potravy a žvýkání za minutu byly vyšší u CSS a zvyšovaly se s postupující sezónou ($P < 0,05$). Vzhledem k tomu, že příjem píce je funkcí celkového času pastvy, rychlosť pasení a velikosti sousta (jak popsalo například Hodgson 1985, Forbes 1988, WallisDeVries et al. 1998 či Griffiths et al. 2003), naše výsledky naznačují, že jalovice, které by měly mít vyšší příjem píce na CSS, by se následně měly lišit i v denních přírůstcích (LWG). To ovšem potvrzeno nebylo, jak ostatně též odpovídá výsledkům, které popsalo Kitessa a Nicol (2001) a Pulido a Leaver (2003). Důvodem může být i to, že je potřeba investovat více energie na vyhledávání potravy v rámci většího prostoru na CCS, než na RSS (Hepworth et al. 1991, Hart et al. 1993) a tudíž denní přírůstek u jalovic klesá. Individuální denní přírůstek živé hmotnosti v našem případě byl 683 g na

CSS a 652 g na RSS, s nejnižšími sezónními výkyvy v polovině sezony. Individuální užitkovost negativně korelovala s celkovou denní pastvou, hustotou trav, vlákninou a popelovinami, a pozitivně souvisela s obsahem dusíkatých látek.

Další studie (článek II a III) poskytly výsledky týkající se pastevního chování jalovic při různé intenzitě kontinuální pastvy a hodnocení vlivu sezóny na chování jalovic (článek II) a vliv porostu na selektivitu pastvy, založené na příjmu a vyhledávání vegetačních plošek na základě jejich druhového složení a výšky heterogenního porostu a na základě tzv. funkční vlastnosti rostlin („plant functional traits“), které jsou udané pro dané složení porostu z databáze (článek III).



Obr. 2. Měření výšky porostu na extenzivní pastvině a stanovení rostlinných druhů ve vegetaci. Jizerské hory, Foto: Stejskalová

Ve druhé studii bylo porovnáváno pastevní chování jalovic při různé intenzitě pastvy, při pastvě intenzivní (IG) a pastvě extenzivní (EG), kdy intenzita pastvy byla definována výškou porostu, a to 5 cm při IG a 10 cm při EG. Data byla sbírána metodou etologického snímkování podobným způsobem jako u studie číslo 1. Výzkum probíhal během pěti pastevních sezón na experimentální pastvině Betlém v Oldřichově v Hájích nedaleko Liberce. V průběhu výzkumu byl dále zkoumán a porovnáván příjem potravy jalovic, a to pasení, žvýkání a přežvykování za jednotku času. Porovnáván byl i vliv počasí a teplota vzduchu.

Vliv intenzity pastvy se na žádném z typů chování neprojevil průkazně, jak zjistili ve svých experimentech též Huber et al. (1995) a Dumont et al. (2007). Ačkoli však vliv pastvy nebyl jednoznačně průkazný, je zde patrný trend, kdy se jalovice na pastvě intenzivní pásly více a nepřerušovaně nežli jalovice na pastvě extenzivní. Ty

přerušovaly pasení častěji přežvykováním, což uvádí například i Arnold a Dudzinski (1978).

Průkazně se lišil příjem potravy za minutu mezi IG a EG. Pro zachování denních energetických požadavků, jalovice na intenzivní pastvě, pasoucí se na krátkém porostu, kompenzovali méně dostupné píce tím, že zvyšovali intenzitu pasení (Jamieson a Hodgson 1979, Allison 1985, Penning et al. 1991, Ginnane et al. 2003). V obou případech v průběhu sezóny zvířata vykazovala sestupnou tendenci pasení. Tuto tendenci potvrdily i analýzy závislosti pasení na výšce porostu. Žvýkání ani přežvykování za minutu se však typem pastvy nikterak nelišilo, vliv sezóny se jevil průkazný u obou typů chování. Průkazný se jevil u pastvy a odpočinku vliv sezóny a teploty. V průběhu sezóny jalovice strávily více času pastvou, což bylo v návaznosti na snižující se nabídku píce na pastvě. Ke stejným závěrům došly též studie například Stricklina et al. (1976), Funstona et al. (1991), Hubera et al. (1995) nebo Realiniho et al. (1999). Odpočívání vykazovalo opačný trend, zatímco přežvykování se lišilo ve vztahu k různé intenzitě pastvy a sezóně, další aktivity nevykazovaly žádné významné trendy. Zároveň, příjem píce jasně ukazuje klesající trend, i přes měnící se parametry kvality píce, a to dusíkatých látek a obsahu hrubé vlákniny (Pavlů et al. 2006). To je v rozporu s výsledky výzkumu Realini et al. (1999) nebo Ginane a Petit (2005), kde zaznamenali nárůst příjmu píce v průběhu sledovaného období. Zvyšování času pastvy společně se zvýšením žvýkáním je obvykle příznakem snižující se dostupnosti píce (např. Chacon a Stobbs 1976, Penning et al. 1991, Linnane et al. 2004). V našem experimentu, při zachování stejně výšky porostu během celé pastvení sezóny, a tudíž zajištění dostatečné dostupnosti píce na obou intenzitách, mělo za efekt, že jalovice mohly vyrovnat jejich denní příjem prostřednictvím snížení míry pastvy, podobně jak je popsáno ve Funston et al. (1991). Pouze v červenci 2006 můžeme vidět rozdíly v klesající době pastvy a přežvykování, oproti zvyšujícímu se odpočinku. Tato skutečnost však byla způsobena velmi vysokými teplotními rozdíly. Vliv teploty na chování skotu na pastvě uvádí ve svých experimentech též Seath a Miller (1946), Arnold a Dudzinski (1978) či Beverlin et al. (1989). Stejně tak i Ginane a Petit (2005) uvádí, že zejména velmi teplé počasí může mít za následek snížení příjmu potravy a zvýšení celkové odpočinku skotu během dne.



Obr. 3. Jalovice pasoucí se na intenzivní pastvě, Jizerské hory. Foto: Stejskalová

Závěrem tedy můžeme dovolit říci, že vyšší intenzita pastvy by mohla mít za následek zvýšení doby pasení, vyšší příjem píce a naopak snížení doby odpočinku a přežvykování nežli u jalovic při pastvě extenzivní. Drobné rozdíly ve výsledcích by mohly být způsobeny stálou dostupností kvalitní píce po celou dobu pastevní sezóny, a to na obou oplůtcích s různými intenzitami.

Předpokládali jsme, že selektivita jalovic na kontinuálním systému pastvy na druhově bohatém heterogenním porostu se bude lišit v závislosti na různém typu porostu, jak je předmětem výzkumu v článku III, stejně tak se bude lišit i různou intenzitou pastvy. Jako ukazatele této selektivity jsme vybrali a využili tzv. fukční vlastnosti rostlin. V rámci 2letého experimentu (2008, 2009) jsme pozorovali hlavní typy chování jalovic dvou různých intenzit (IG a EG) po dobu 14 hodin každých 5 minut, a to přímým pozorováním stanovených typů chování, stejně, jak tomu bylo u experimentu č.II. Před vlastním pozorováním bylo nezbytné stanovit typy porostu podle aktuálního stavu vegetace pastviny. Byla měřena výška porostu (dle Correl et al. 2003) ve vytýčených transektech a porost byl stanoven dle velikosti jako nízký (0-5 cm), střední (5.5-10 cm) a vysoký (10.5 a více). Složení rostlin v daném porostu bylo stanoveno a měřeno na 40 odběrných místech (nomenklatura druhů rostlin vyplývá z publikace Kubát et al. 2002). U všech zaznamenaných druhů rostlin jsme přiřadili

ukazatele, tzv. rostlinné funkční znaky z databází BIOFLOR a LEDA (nutriční hodnota, pastvení tolerance, tolerance proti sešlapu, specifická plocha listu (SLA), obsah sušiny v listu (LDMC) (Briemle et al. 1996, Cornelissen et al. 2003). Selektivita byla určena pomocí Jacobova indexu selektivity, což je modifikace Ivlevova indexu selektivity (Jacobs 1974).

Dle našich výsledků, se jalovice pásky selektivně pro daný specifický porost (ploška). Vliv intenzity pastvy se projevil na selektivitu průkazně. Jalovice se pásky nejvíce na nízkých porostech, což je způsobeno vyšší nutriční hodnotou na nižších porostech nežli na porostech vyšších (Dummont et al. 2007a, Wallis De Vries and Daleboudt 1994, Cingolani et al. 2005), avšak selektivita byla vyšší na pastvě extenzivní. Selektivita pro střední porost se též intenzitou pastvy lišila. Na intenzivní pastvě se jalovice zcela vyhýbaly ploškám se středním porostem. Toto bylo pravděpodobně způsobeno tím, že na IG se převážně vyskytovaly plošky s nízkým porostem, neboť porost byl po celou dobu pastvy intenzivně pasen a převládala tedy místa s nižším porostem. Místa se středními ploškami vznikají pouze na místech pokálených, tzv. nedopasky či mastná místa, jak uvádí Frame (1992) či Pavlů et al. (2006a). Tato pokálená místa jsou jalovicemi záměrně opomíjeny z důvodu jejich velkého zápachu. Jalovice na extenzivní pastvě místa se středními ploškami využívala v souladu s nabídkou. Místa s nízkým porostem jsou na pastvě extenzivní méně zastoupeny, tudíž je nutné doplnit denní příjem pro doplnění energie z těchto porostů, kde se nutriční hodnota píce nemusí tolík lišit od porostu nízkého. Též Dumont et al. (1997) uvádí, že ovce, kterým byla nabízena potrava s nižší kvalitou, která byla volně dostupná a kvalitní seno, avšak v omezeném množství, ovšem vzdálenější, si vybraly spíše seno nekvalitní (kompromis mezi odměnou a vzdáleností). Dle našich výsledků, nebyl prokázán žádný vliv intenzity pastvy na selektivitu vysokého porostu. Tento porost byl opomíjen jalovicemi obou intenzit, pravděpodobně z důvodu nízké nutriční hodnoty a vysokého obsahu vlákniny (Wallis De Vries and Dalebout 1994).

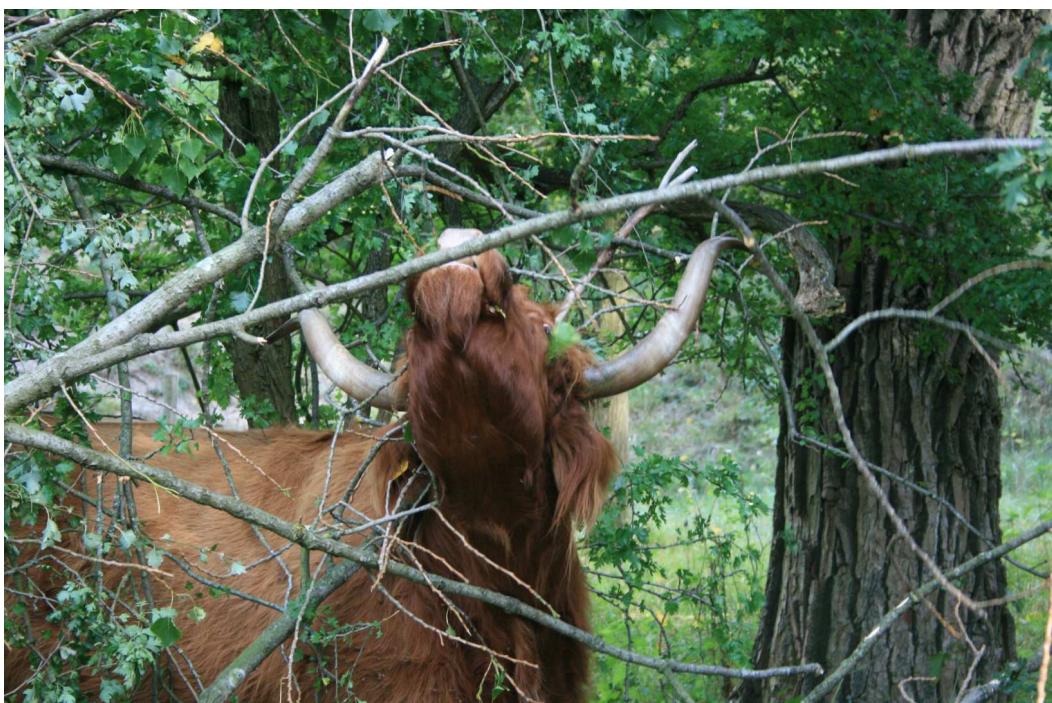


Obr. 4. Nedopasek na pastvině Betlém, Jizerské hory. Foto: Stejskalová

Za ukazatele selektivity můžeme v našem případě považovat tzv. funkční znaky rostlin, otázkou ovšem bylo, která z těchto vlastností rostlin je hnací silou selektivity jalovic. Proč právě daný flek si jalovice vybírají a co je tomu vede. Dle našich výsledků, kde selektivita jalovic byla pozitivně korelovaná s nutriční hodnotou a LDMC a negativně korelovaná s výškou porostu, můžeme usuzovat, že největší prioritou je měnící se nutriční hodnota daného fleku. Četné studie prokázaly stejné výsledky, a to že kvalita krmiva a jeho množství může ovlivnit selektivitu a distribuci býložravců (Bailey a Provenza 2008). Jak uvádí například i Dumont et al. (1995), ovce si i při snižování kvality pastvy stále vybíraly místa s vyšší nutriční hodnotou a místa s nižšími hodnotami opomíjela.

Nejzajímavější výsledky však přinesly studie zabývající se nutričními hodnotami listí dřevin, tzv. letniny či zimní biomasy dřevin (článek IV a V). Tyto studie tematicky navázaly na selektivitu skotu na nutriční složení potravy. Letnina, neboli též zimní krmení (sušené větvičky různých druhů dřevin či rostlin), byla využívána pravděpodobně již během Neolitu až do Mladší doby železné (500-0 př. Kr.) téměř v celé Evropě (Rasmussen 1990, Austad 1988, Halstead 1998, Slotte 2001). Využívalo se zejména listí a větvičky dubu, lípy, jilmu, javoru, jasanu a lísky. V některých oblastech

je však možné tuto tradici vidět i dnes. Například v oblasti Alp: v údolí jižního Tyrolska (Itálie), na jihu Francouzských Alp nebo v údolí Lötschen ve Švýcarsku (Haas 1998), nebo ve Švédsku (Slotte 2001), Norsku (Austad 1988), v Řecku (Halstead 1998) či v Dánsku (Rasmussen 1990). Cílem výzkumu bylo stanovit a porovnat obsah chemických látek z hlediska nutriční hodnoty pro výživu zvířat vybraných druhů listnatých dřevin využívaných jako zimní krmivo a dřevin nevyužívaných (*Tilia cordata* Mill., *Ulmus glabra* Huds., *Acer platanoides* L., *Fraxinus excelsior* L. *Corylus avellana* L., *Quercus robur* L., *Fagus sylvatica* L., *Populus tremula* L. a *Carpinus betulus* L.) sbíraných na jaře ihned po rozpuku. Hlavním poznatkem tohoto výzkumu bylo, že existují veliké rozdíly v kvalitě píce mezi jednotlivými posuzovanými dřevinami. Dle kvality nutričních látek můžeme hovořit o dřevinách s nízkou kvalitou porostu, to jsou *Carpinus*, *Fagus* a *Quercus*, se střední kvalitou porostu, jako je *Coryllus* a *Populus* a dřeviny s vysokou kvalitou, což jsou především *Ulmus*, dále pak *Fraxinus*, *Tilia* a *Acer*. Koncentrace dusíku (N) v listech všech druhů dřevin byla optimální pro výživu zvířat a porovnatelná s obsahem N v lučním seně. Nároky skotu na N byly tudíž splněny.



Obr. 5. Skotský náhorní skot okusující listy topolu (*Populus* ssp.), Nizozemí.
Foto: Hejcmánková

Rozdíl nastal v obsahu fosforu (P), především obsah P habru (*Carpinus*) a buku (*Fagus*), v kontrastu s ostatními dřevinami, byl pod optimálním rozmezím na nároky pro skot. Nedostatek P však představuje velký problém z hlediska výživy zvířat, především pro laktující krávy a telata, kteří potřebují opravdu velkou koncentraci P v potravě, více než 3 g P na kg váhy (Liebisch et al. 2013). Takto velké požadavky na P může splnit pouze jasan (*Fraxinus*) a lípa (*Tilia*), ovšem sklízená pouze v jarních obdobích, ihned po pučení. Jak uvádí Kobe et al. (2005), koncentrace N a P jsou nejvyšší v prvních jarních listech, v průběhu sezóny se koncentrace obou prvků snižuje. S výjimkou buku (*Fagus*), koncentrace draslíku (K) v listech ostatních dřevin byla více než vysoká. Vysoká koncentrace K se však objevuje i v běžném krmivu a zvířata jsou velice dobře přizpůsobena se nadbytku K zbavit, převážně močí (Kayser a Isselstein 2005). I obsah vápníku (Ca) byl více než vysoký u všech druhů testovaných dřevin, což ovšem může způsobovat různé zdravotní problémy především v kombinaci s nedostatkem P v potravě. Ačkoli jsou oba prvky pro zvířata velmi potřebné ve větším množství, především na stavbu kostí, jejich příjem musí být v poměru. Nadbytek Ca totiž může snižovat příjem P z potravy a tím pak způsobit nedostatek P v těle. Důležitý je tedy poměr Ca:P, který byl 2x až 3x větší u všech druhů studovaných dřevin. Proto je tedy možné říci, že větvičky těchto druhů dřevin, mají nižší kvalitu nežli seno s ideálním poměrem Ca:P. Obsah hořčíku (Mg) byl u všech druhů dřevin podobný a splňoval nároky na nutriční hodnotu pro skot. Obsah K byl optimální a poměr K/(Ca+Mg), který indukuje syndrom pastevní tetanie (Swerczek 2007), se nacházel pod kritickou hodnotou 2.2 (Butler 1963). Obsah vlákniny (NDF) byl v rozmezí nebo svými hodnotami odpovídal hodnotám lučního sena z polopřirozených travních porostů, v některých případech dokonce nižší. Vhodný obsah NDF stimuluje aktivitu báchoru. Důležitým zjištěním je, že listy dřevin měly velmi vysoký obsah ligninu, který představuje antinutriční, nestravitelnou složku v krmivu. Velké množství zimního krmiva může omezit příjem píce a brzdit trávicí enzymy a následně vyvolat nepříznivé účinky na užitkovost zvířat. Z tohoto důvodu se domýváme, že letnina pravděpodobně hrála pouze roli umožňující dobytku přežít kritické období během zimy, kdy nebyl dostatek potravy.

Letnina byla pravděpodobně využívána především pro ovce a kozy, které jsou i přirozeně krmeny větvičkami či listy dřevin a jsou lépe fyziologicky přizpůsobeny

(Papachristou et al. 2005). Zejména kozy mají mechanismy, které tlumí nežádoucí účinky ligninu a sekundárních metabolitů (Howe et al. 1988) a jejich přirozená potrava může obsahovat více než 50% listů z různých dřevin (Papachristou a Nastis 1993). Na druhou stranu, použití zimního krmení bylo široce zaznamenáno na archeologických lokalitách u ovcí a koz, protože jejich exkrementy jsou kompaktní a snadno rozpoznatelné (Akeret et al. 1999) ve srovnání s exkrementy skotu, které tvoří hrudky typického tvaru a obvykle se smísí se zbytkem sedimentu (Akeret a Rentzel 2001, Shahack-Gross 2011).

Jak již bylo zmíněno, letnina je využívána na některých místech i dodnes. V mnoha evropských regionech, farmáři využívají převážně dřeviny jako je *Acer*, *Fraxinus*, *Ulmus* či *Tilia* (Dreslerová 2012). Dle našich výsledků se můžeme domnívat, že tyto dřeviny jsou využívány především pro jejich vysoké nutricí hodnoty. Obdobné výsledky byly popsány i ve Středomoří (Papachristou 1997). Dnes je však kvalita píce zjišťována různými moderními metodami, které jsou schopné rozpozнат rozdíly ve složení jednotlivých dřevin. Víme však, že farmáři byli schopni rozpozнат tyto rozdíly v nutričním složení i pomocí mléčné produkce či váhového přírůstku na zvířatech. Například, využití jilmu jako krmiva pro hospodářská zvířata se doporučuje již Marcusem Cato (234-149 B.C.) v jeho knize zvané *De Agricultura* (Hooper a Ash 1935). Stejně tak na Islandu byl jilm využíván jako krmivo pro krávy již v 6-8 století A.D. (Kelly 2000). Tak jako farmáři dokáží vybrat nutričně zajímavější dřeviny pro zvířata, také ona sama dokáží velmi dobře uspokojovat své nutriční požadavky, výběrem jednotlivých dřevin. Například laktující skot či mladá telata, která mají vyšší požadavky na obsah P, více pasou po biomase bohaté na fosfor. Listy habru a buku, velmi chudé na obsah fosforu proto byly skotem během lesní pastvy opomíjeny, za předpokladu, že se v blízkém okolí nacházely dřeviny s vyšším obsahem P a nižším obsahem ligninu. Šíření těchto dvou druhů především v době bronzové v České republice (Pokorný a Kumeš 2005) bylo pravděpodobně spojeno s opomíjením těchto druhů dřevin jako zimního krmiva. Selektivní spásání a sklízení dřevin jako je *Acer*, *Fraxinus*, *Tilia* a *Ulmus* mělo pravděpodobně za následek pokles těchto dřevin v době bronzové a žezezné a podpořilo tak expanzi druhů, jak je *Carpinus* a *Fagus*.

Cílem dalšího výzkumu (článek V.) bylo hlavně prohloubení výzkumu předešlého (článek IV.), a to stanovit obsah nutričních hodnot z větviček u 9 vybraných druhů listnatých dřevin (*Tilia cordata* Mill., *Fraxinus excelsior* L. *Corylus avellana* L., *Quercus robur* L., *Fagus sylvatica* L., *Populus tremula* L., *Carpinus betulus* L., *Betula pendula* L., *Salix caprea*), 2 druhů jehličnatých dřevin (*Pinus sylvestris* L., *Picea abies*), břečťanu a jmelí (*Hedera helix*, *Viscum album*, L.), sbíraných v zimním období, které byly využívány jako zimní krmivo pro hospodářská zvířata.

Výsledky tohoto výzkumu byly velmi překvapivé, neboť druhy s listy zelenými i v zimě, jako je například břečťan či jmelí vykazovali velmi vysoké nutriční hodnoty (vysoký obsah N a nízký obsah ADF a ligninu) a patřily tak k nejlepším druhům využívaným k zimnímu krmení. Obdobné vysoké hodnoty byly stanoveny též pro v zimě sbírané listy rostliny *Rubus fruticosus* (Verheyden-Tixier et al. 2008), které byly též využívané ve Francii jako zimní krmivo pro ovce a kozy (Martin 2011). Staří zemědělci tedy pravděpodobně sbírali břečťan a jmelí během zimního období záměrně a používali je ke krmení zvířat (Haas 2004, Nicod et al. 2008), pravděpodobně z důvodu jejich vysokého obsahu N a P. Jmelí bylo též sbíráno, ačkoli množství jeho biomasy bylo relativně malé a jeho sběr byl velmi pracný. Z tohoto důvodu se domníváme, že jmelí bylo sbíráno pouze pro zvířata s vyššími nároky na nutriční složení (vyšší obsah N a P), jako jsou březí či laktující krávy či kozy. Pozůstatky jmelí na archeologických lokalitách (viz Akeret a Rentzel 2001, Kühn a Hadorn 2004, Kühn et al. 2013, Pokorný et al. 2006), představovaly pravděpodobně zbytky využívané jako speciální zimní krmivo pro zvířata s vyššími nároky.

Také břečťan má vyšší nutriční hodnotu než druhy dřevin využívané v zimě jako krmivo a právě proto byl velmi vyhledáván skotem v rámci zimní pastvy. V experimentu Van Uytvancka a Hoffmana (2009), například, *Hedera* zcela zmizel z lesa, který byl obhospodařován několik let celoroční pastvou dobytka. V lesích, které byly využívány na pastvu, *Hedera* mohl přežít jen jako liána na stromech, ne však jako pozemní krytí některých druhů. Kromě toho, je též vysoce pravděpodobné, že i staré kvetoucí výhonky *Hedera* byly úmyslně sbírány a využívány jako zelené zimní krmivo pro hospodářská zvířata již pravěkými zemědělci. Pokles produkce pylu z *Hedera* v různých obdobích (viz Bottema 2001, Iversen 1944, Troels-Smith 1960), by mohly být

takto považována za ukazatel lidské činnosti v lesích spojených s chovem hospodářských zvířat.



Obr. 6. Koza okusující větvičky jmelí. Foto: Hejcmánková

Nutriční hodnota různých druhů dřevin sbíraných v zimním období byla nižší než nutriční hodnota lučního sena a dokonce též nižší než nutriční hodnoty obdobných dřevin, sbíraných na jaře ihned po rozpuku (viz článek IV). Nízká nutriční hodnota větviček byla dána nedostatečnou koncentrací N a P a také částečně nedostatečným obsahem Mg. Větvičky byly charakteristické příliš vysokou koncentrací Ca, ADF a ligninu, vysokým poměrem Ca:P a příliš nízkým tetanickým poměrem K:(Ca+Mg). Dalším charakteristickým rysem chemického složení větviček byly relativně malé rozdíly v koncentraci P mezi jednotlivými druhy v porovnání s jejich listy na jaře, kde rozdíly byly výrazně vyšší (článek IV.). *Fagus* a *Carpinus* měli absolutně nejhorší nutriční hodnotu, naopak *Ulmus* a *Tilia* měli nutriční hodnotu velmi příznivou, stejně jako tomu bylo u jarních vzorků (v porovnání s článkem IV). I přes relativně nízkou nutriční hodnotou větviček ve srovnání s lučním senem či letninou, jsou větvičky pravidelně okusovány různými druhy vysoké zvěře, zající či zubrem evropským a slouží jako zimní krmení v případech, že žádná jiná lepší alternativa není k dispozici (Ammer 1996, Kowalczyk et al. 2011).

Jak již bylo zmíněno, větvíčky dřevin využívané jako zimní krmivo, hrály velmi důležitou roli převážně v Neolitu a měly pravděpodobně za následek rozvoj lesní pastvy ve Střední Evropě (Bergmeier et al. 2010). Předpokládáme, že téměř všechny zvířata se pásala v lesích celoročně, bez jakéhokoli či sporadického příkrmování v zimním období. To hrálo roli pravděpodobně i při formování postavy, a to snížení velikosti těla během procesu domestikace, až na polovinu velikosti těla pratura (Petrášek 1972). Jeden z důvodů také může být ten, že zvířata, pasoucí se v okolí vesnic, neměli tak velký přístup k lesní píci jako volně žijící zvířata. Ačkoli byly v archeologických vrstvách nalezeny důkazy pro zimní krmení hospodářských zvířat letninou, množství sklizeného letního by pravděpodobně nestačilo k pokrytí nutričních požadavků všech zvířat (Rasmussen 1990, Thiébault 2005). Tato myšlenka je podpořena i písemnými záznamy z 18. století, které popisují nedostatečné krmení hospodářských zvířat během zimy a význam lesů pro zimní krmení hospodářských zvířat a jejich přežití (Klír 2008, Petrášek 1972). Pochybnosti některých autorů (viz Kreuz 2008), o schopnosti skotu v Neolitu k okusování letorostů dřevin a jejich schopnost přežít zimu ve střední Evropě bez příkrmování, jsou tedy neopodstatněné. Zimní pastva dobytka v lesích by tak mohla hrát klíčovou roli v jejich otevřání v pravěku.

Závěr

Pokud shrneme naše výsledky týkající se pastevního chování jalovic na různých systémech pastvy (článek I), můžeme tedy říci, že rotační či kontinuální systém pastvy neměl žádný vliv na chování nebo užitkovost zvířat. Klíčovými parametry pro chování jalovic a užitkovost se však jevila výška porostu, hustota trav a bylin a obsah vlákniny a bílkovin v píci.

Ačkoli výsledky článku II. ukazují, že vliv pastvy se na žádném z typů chování neprojevil průkazně, můžeme si dovolit říci, že vyšší intenzita pastvy by mohla mít za následek zvýšení doby pasení, vyšší příjem píce naopak snížení doby odpočinku a přežvykování nežli u jalovic na pastvě extenzivní. Drobné rozdíly ve výsledcích by mohly být způsobeny stálou dostupností píce vysoké kvality po celou dobu pastevní sezóny, a to na obou oplūtcích s různými intenzitami.

Selektivitu pastvy jalovic (článek III) při extenzivním a intenzivním pastevním režimu v průběhu sezóny lze shrnout následovně. Jalovice pod oběma intenzitami

pastvy si vybíraly hlavně nízké porosty a vyhýbaly se vysoké vegetaci. Za ukazatele selektivity můžeme v našem případě považovat tzv. funkční znaky rostlin, především nutriční hodnotu neboli měnící se složení v rámci jednotlivých fleků.

Z výsledků, týkajících se nutričních hodnot dřevin využívaných jako zimní krmivo pro hospodářská zvířata (článek IV), jejichž nutriční hodnota je vyšší než u dřevin, které využívány nebyly, je patrné, že praxe našich předků byla založena na znalosti nutriční hodnoty druhů těchto dřevin a nebyla tudíž pouhou otázkou dostupnosti. Výsledky nutričního složení dřevin, sbraných v zimních měsících (článek V) ukazují, že nutriční hodnota letorostů dřevin je nedostatečná pro výživu hospodářských zvířat, okusování větví pomohlo zvířatům pouze přežít zimu, ale neumožnilo jim růst hmotnosti nebo zvýšení produkce mléka. Předpokládáme, že hlavním kritériem pro výběr těchto dřevin pravěkého skotu a jiných hospodářských zvířat byla tedy schopnost přežít zimu bez nebo s omezeným přikrmováním s nízkou nutriční hodnotou. Hospodářská zvířata se pásala celoročně, tj. i v zimě. Celoroční pastva však měla za následek i ovlivňování lesních porostů. Jak již bylo řečeno, některé druhy následkem výběru zcela vymizely, jiné naopak expandovaly. Jednalo o ústup jilmu (*Ulmus* sp.) a expanzi buku (*Fagus sylvatica*) a habru (*Carpinus betulus*) v době bronzové a železné (Troels-Smith 1960), dále pak ústup břečťanu (*Hedera helix*) okolo roku 5000. Dřeviny hrály nezastupitelnou roli v krmení zvířat. Nedostatečné podmínky krmení však měly důsledky i na šlechtění a na snižující se velikost skotu v průběhu domestikace.

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