

UNIVERZA V LJUBLJANI
BIOTEHNIŠKA FAKULTETA

Janez JENKO

**GENETSKO VREDNOTENJE DOLGOŽIVOSTI MLEČNIH PASEM
GOVEDI V POPULACIJAH Z MAJHNIMI ČREDAMI**

DOKTORSKA DISERTACIJA

**GENETIC EVALUATION OF LONGEVITY IN DAIRY CATTLE
POPULATIONS WITH SMALL HERDS**

DOCTORAL DISSERTATION

Ljubljana, 2016

Na podlagi Statuta Univerze v Ljubljani ter po sklepu Senata Biotehniške fakultete in sklepa Komisije za doktorski študij Univerze v Ljubljani, z dne 19. 9. 2012 je bilo potrjeno, da kandidat izpolnjuje pogoje za neposreden prehod na doktorski študij Bioloških in biotehniških znanosti ter opravljanja doktorata znanosti na znanstvenem področju genetika. Za mentorico je bila imenovana prof. dr. Milena Kovač.

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Komisija za oceno in zagovor:

Predsednik: prof. dr. Peter DOVČ
Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za zootehniko

Član: doc.dr. Gregor GORJANC
Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za zootehniko

Član: prof. dr. Miroslav KAPŠ
Sveučilište u Zagrebu, Agronomski fakultet

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KLJUČNA DOKUMENTACIJSKA INFORMACIJA

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AI	Napoved plemenskih vrednosti za dolgoživost smo opravili za slovenski populaciji rjave in črno-bele pasme govedi. Za reje govedi na območju Slovenije je značilna majhna velikost čred, kar lahko vpliva na napovedovanje plemenskih vrednosti. Razvili smo modela za oceno prave in funkcionalne dolgoživosti. Korelacija med rangi plemenskih vrednostmi za pravo in funkcionalno dolgoživost je bila 0,94 pri rjavi pasmi in 0,87 pri črno-beli pasmi. Korekcijo za vpliv prostovoljnih izločitev v modelu za oceno funkcionalne dolgoživosti smo opravili glede na mlečnost krav znotraj čred podobnih velikosti. Takšen pristop se je izkazal kot ustrezen za populacije z majhno velikostjo čred. Primerjava na testnem nizu podatkov pri rjavi pasmi je pokazala, da je korelacija med plemenskimi vrednostmi očetov in preživetjem hčera večja pri modelu za oceno funkcionalne dolgoživosti (0,43), kot pri modelu za oceno prave dolgoživosti (0,39). Model živali ni izboljšal napovedne točnosti plemenskih vrednosti. Kot najboljši se je izkazal model očetov in materinih očetov z vključenim naključnim vplivom interakcije med skupnim okoljem v čredi in letom. Pri tem modelu je bila korelacija med plemenskimi vrednostmi očetov in preživetjem hčera testnega niza za različna obdobja po prvi telitvi največja. Za oceno plemenskih vrednosti krav lahko uporabimo aproksimativen model živali in tako zmanjšamo potrebno računalniško zmogljivost in čas. Analiza komponent variance z uporabo večlastnostne linearne analize je pokazala visoko genetsko korelacijsko med dolgoživostjo in življenjsko prirejo mleka (0,98). Genetska korelacija med količino mleka v prvi laktaciji in življenjsko prirejo mleka je bila manjša (0,48). Odbiro živali za večjo življenjsko prirejo mleka lahko opravimo posredno preko odbire živali z visoko plemensko vrednostjo za dolgoživost. Življenjsko prirejo mleka smo napovedali tudi z uporabo večlastnostne naključne regresije na podlagi dnevnih meritev prireje mleka v prvih treh laktacijah. Življenjsko prirejo mleka smo ocenili v 12 scenarijih, ki so se razlikovali glede na vključitev plemenske vrednosti za prirejo mleka in mlečno vztrajnost. Korelacija med plemensko vrednostjo za življenjsko prirejo mleka očetov in korigirano življenjsko prirejo mleka hčera iz testnega niza je bila med 0,07 in 0,09.

KEY WORDS DOCUMENTATION

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LA	sl
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AB	Longevity breeding values were predicted for Slovenian Brown and Slovenian Black and White cattle breeds. Relatively small herd size is feature of the Slovenian dairy cattle production system, which might have an effect on breeding value estimation. A model for the prediction of true and functional longevity was developed. Rank correlation between true and functional longevity breeding values were 0.94 for Brown and 0.87 for Black and White cattle breeds. For the prediction of functional longevity, correction for the effect of voluntary culling was performed with milk yield ranking within herds of a similar size. This approach was appropriate for a cattle population reared in small herds. Correlations between the estimated breeding values of bulls and the survival of their second-crop daughters were higher for functional longevity (0.43) when compared to true longevity (0.39). When animal model was used to predict breeding values, correlations did not improve. A sire-maternal grand sire model with random interaction effect between herd and year was deemed the most appropriate. Here, the correlations between breeding values for bulls and the survival of their second-crop daughters for different periods following the first calving were highest. To obtain estimates of cow breeding values, the approximation method can be used. Using this method, both computation time and required computer memory decreased. The variance component analysis of the multivariate linear model revealed longevity as highly correlated with lifetime milk production (0.98). The genetic correlation between the first lactation milk yield and lifetime milk production was smaller (0.48). Selecting individuals with high breeding values for longevity will also increase breeding values for lifetime milk production. To predict lifetime milk production, a multivariate random regression model with the daily milk records from the first three lactations was used. Lifetime milk production was predicted using 12 different scenarios with different combinations of milk yield and milk persistency. The correlations between the breeding values for lifetime milk production for bulls and corrected lifetime milk production of their daughters from the validation set were between 0.07 and 0.09.

KAZALO VSEBINE

	str.
KLJUČNA DOKUMENTACIJSKA INFORMACIJA	III
KEY WORDS DOCUMENTATION	IV
KAZALO VSEBINE	V
KAZALO ZNANSTVENIH DEL	VI
KAZALO PRILOG	VII
SLOVARČEK	VIII
1 PREDSTAVITEV PROBLEMATIKE IN HIPOTEZE	1
1.1 VELIKOST ČRED KRAV MOLZNIC V SLOVENIJI	1
1.2 DOLGOŽIVOSTI KRAV MOLZNIC	1
1.3 VZROKI IZLOČITVE KRAV MOLZNIC	3
1.4 GENETSKA OCENA DOLGOŽIVOSTI	4
1.4.1 Analiza preživetja	5
1.4.2 Linearni modeli	10
1.4.3 Naključna regresija	11
1.4.4 Primerjava med modelom preživetja in linearnim modelom	12
1.5 ŽIVLJENJSKA PRIREJA MLEKA	13
1.6 GENETSKA OCENA ŽIVLJENJSKE PRIREJE MLEKA	13
1.7 RAZISKOVALNE HIPOTEZE	16
2 ZNANSTVENA DELA	17
2.1 PRIMERJAVA WEIBULLOVIH MODELOV PO DELIH ZA OCENO PRAVE IN FUNKCIONALNE DOLGOŽIVOSTI KRAV MOLZNIC	17
2.2 GENETSKO VREDNOTENJE PRAVE IN FUNKCIONALNE DOLGOŽIVOSTI SLOVENSKE ČRNO-BELE PASME GOVEDI	32
2.3 PRIMERJAVA MED MODELOM OČETOV IN MATERINIH OČETOV Z MODELOM ŽIVALI PRI GENETSKEM VREDNOTENJU DOLGOŽIVOSTI V POPULACIJAH Z MAJHNIMI ČREDAMI PRI GOVEDU MLEČNIH PASEM	41
2.4 GENETSKA POVEZAVA MED ŽIVLJENJSKO PRIREJO MLEKA, PRIREJO MLEKA V PRVI LAKTACIJI IN DOLGOŽIVOSTJO	55
2.5 GENETSKO VREDNOTENJE ŽIVLJENJSKE PRIREJE MLEKA GOVEDA V POPULACIJAH MAJHNIH ČRED Z UPORABO NAKLJUČNE REGRESIJE	66
3 RAZPRAVA IN SKLEPI	93
3.1 RAZPRAVA	93
3.2 SKLEPI	108
4 POVZETEK (SUMMARY)	110
4.1 POVZETEK	110
4.2 SUMMARY	118
5 VIRI	126
ZAHVALA	
PRILOGE	

KAZALO ZNANSTVENIH DEL

str.

Jenko J., Ducrocq V., Kovač M. 2013. Comparison of piecewise Weibull baseline survival models for estimation of true and functional longevity in Brown cattle raised in small herds. <i>Animal: An International Journal of Animal Bioscience</i> , 7, 10: 1583–1591	17
Jenko J., Perpar T. 2015. Genetsko vrednotenje prave in funkcionalne dolgoživosti slovenske črno-bele pasme govedi (neobjavljeno)	32
Jenko J., Gorjanc G., Kovač M., Ducrocq V. 2013. Comparison between sire-maternal grandsire and animal models for genetic evaluation of longevity in a dairy cattle population with small herds. <i>Journal of Dairy Science</i> , 96, 12: 8002–8013	41
Jenko J., Perpar T., Kovač M. 2015. Genetic relationship between the lifetime milk production, longevity and first lactation milk yield in Slovenian Brown cattle breed. <i>Mljekarstvo</i> , 65, 2: 111–120	55
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KAZALO PRILOG

- Priloga A: Dovoljenje založnika za objavo članka: »Comparison of piecewise Weibull baseline survival models for estimation of true and functional longevity in Brown cattle raised in small herds« v tiskani in elektronski verziji disertacije.
- Priloga B: Dovoljenje založnika za objavo članka: »Comparison between sire-maternal grandsire and animal models for genetic evaluation of longevity in a dairy cattle population with small herds« v tiskani in elektronski verziji disertacije.
- Priloga C: Dovoljenje založnika za objavo članka: »Genetic relationship between the lifetime milk production, longevity and first lactation milk yield in Slovenian Brown cattle breed« v tiskani in elektronski verziji disertacije.

SLOVARČEK

Aditivna genetska varianca – je genetska varianca, ki je posledica povprečnih učinkov, ki jih povzročajo zamenjave nekega alela z drugim na določenem lokusu ali na večjem številu lokusov, ki določajo poligeno lastnost.

Doba prieje – je obdobje od prve telitve/jagnjitve/kozlitve, do izločitve živali.

Dolgoživost – je trajanje obdobja od določene začetne točke (rojstvo, odbira, prva telitev/jagnjitev/kozlitev) do izločitve živali. Opisujemo jo lahko z dolžino dobe prieje, preživetjem in dolžino življenja.

Efektivna heritabiliteta – je ocena heritabilitete za dolgoživost podana na logaritemski skali.

Ekvivalentna heritabiliteta – je ocena heritabilitete za dolgoživost v primeru prisotnosti krnjenih meritev.

Funkcionalna dolgoživost – je dolgoživost korigirana za prostovoljne izločitev živali.

Heritabiliteta – izraža delež genetske variance v fenotipski varianci lastnosti v neki populaciji.

Mendelsko vzorčenje – je razlika med plemensko vrednostjo potomca in povprečja plemenske vrednosti staršev.

Neprostovoljna izločitev – je izločitev živali iz reje, do katere vodijo problemi povezani z reprodukcijo (neplodnost, cistični ovariji, poporodna pareza itd.) in zdravjem živali (mastitis, metritis, ketoza, laminitis, pogin itd.).

Pasma – je skupina geografsko regionalno ločenih živali, ki izvirajo od istih prednikov in jih povezujejo lastnosti, ki jih določa pasemske standard ter jih delimo na lokalno prilagojene (avtohtone, tradicionalne) in tujerodne pasme.

Plemenska vrednost – vsota aditivnih učinkov genov za določeno lastnost.

Prava dolgoživost – je dolgoživost brez korekcije za prostovoljno izločitev živali.

Preživetje – je delež živali, ki so ostale žive do poljubnega časovnega mejnika. Časovni mejnik lahko predstavlja naslednja telitev oz. laktacija, določeno obdobje po prvi telitvi (dan, mesec, leto itd.).

Prostovoljna izločitev – je izločitev živali iz reje na podlagi odločitve rejca. Rejec sprejme tako odločitev zaradi nizke prireje mleka, slabih lastnosti zunanjosti (okvir živali, noge, vime ...), mlečnih kvot, spremembe v velikosti črede itd.

1 PREDSTAVITEV PROBLEMATIKE IN HIPOTEZE

1.1 VELIKOST ČRED KRAV MOLZNIC V SLOVENIJI

Za Slovenijo je značilen razgiban relief, ki omejuje možnosti za pridelavo velikih količin krme z majhnim vložkom dela. Posledica tega so majhne črede, katerih velikost se je z leti povečevala. Leta 2003 so na povprečni kmetiji s tržno usmerjeno pritejo mleka redili 14,0 krav. Do leta 2014 je povprečna velikost kmetije zrasla na 15,6 krave. Nekoliko večje so bile črede krav vključene v kontrolo priteje mleka, kjer so v povprečju v letu 2014 redili 20,8 krave (Sadar in sod., 2015). V okviru članic mednarodnega komiteja za kontrolo priteje spada slovenska populacija mlečnih govedi v skupino držav z manjšimi čredami. Primeri populacij velikih čred krav molznic v kontroli priteje mleka so: Madžarska (374,0), ZDA (230,0), Slovaška (206,0), Škotska (183,0), Anglija (176,0), Danska (165,0), Estonija (108,4), Nizozemska (88,3), Švedska (76,1), Italija (72,0), Nemčija (69,3), Irska (69,2) in Francija (52,2). Primeri populacij z velikostjo čred krav molznic v kontroli priteje mleka podobni slovenski so: Poljska (35,4), Finska (35,3), Litva (34), Norveška (24,2), Latvija (23,4), Avstrija (18,6), Švica (18,6), Hrvaška (16,6) in Turčija (11,8) (ICAR, 2015).

1.2 DOLGOŽIVOSTI KRAV MOLZNIC

Dolgoživost krav molznic opisujemo v obliki preživetja, dolžine dobe priteje, števila telitev ali starosti ob izločitvi (Vollema in Groen, 1996; Essl, 1998; Sasaki, 2013). Za slovenske populacije mlečnih pasem govedi je v zadnjih letih opazen trend zmanjševanja preživetja, skrajševanja dobe priteje, zmanjševanja števila laktacij in nižja starost ob izločitvi (Jenko in Perpar, 2013). Glede na dejstvo, da se je genetsko vrednotenje za dolgoživost govedi v Sloveniji pričelo v letu 2011 (Potočnik in sod., 2011), ne gre pričakovati pozitivnih učinkov odbire živali s pozitivno plemensko vrednostjo v tako kratkem obdobju. Vsekakor bi bilo smiselno trenutni model za oceno dolgoživosti nadgraditi ter tako izboljšati napovedno točnost modela.

Učinek dolge dobe priteje molznic je večplasten in je pomemben za rejca, okolje, družbo ter navsezadnje za molznicu samo. Za krave molznice, ki jih redimo zaradi ekonomske

koristi, je zaželena velika prireja mleka, dolga doba prireje in odlično zdravstveno stanje. Dolga doba prireje zmanjša stroške obnove črede in omogoča kravi, da izrazi svojo sposobnost za prirejo mleka (Robertson in Rendel, 1950; Allaire in Gibson, 1992; Stott, 1994). Znano je namreč, da je največja mlečnost v tretji do peti laktaciji, ki jo v slovenskih rejah dočaka le 36 % krav (Jenko in sod., 2007). Robertson in Rendel (1950) poudarjata, da je podaljševanje dobe prireje povezano s povečano živiljenjsko prirejo mleka, večjim številom telitev in nižjimi stroški obnove črede. Podaljševanje dobe prireje omogoča večjo intenzivnost selekcije ženskega dela populacije, kar prinaša dodaten prihodek preko prodaje plemenskih telic, ki niso potrebne za obnovo črede. Selekcija na dolgoživost krav molznic poleg izboljšanja učinkovitosti sistema reje zmanjuje tudi izpuste toplogrednih plinov in s tem prispeva k trajnostni usmeritvi reje domačih živali (Wall in sod., 2009). Izboljšanje dolgoživosti krav molznic je zaželeno tudi z etičnega stališča, saj se v družbi povečuje skrb za dobro počutje živali, kar je močno povezano s trajnostnim kmetijstvom. Z izvajanjem selekcije na dolgoživost lahko posledično pričakujemo izboljšanje dobrega počutja živali, saj bodo krave bolj odporne na dejavnike okoljskega stresa (Vollema, 1998; Vukasinovic in sod., 1999, 2001).

Dolgoživost je posledica več dejavnikov: prireja mleka, plodnost, zdravje živali, delovne sposobnosti idr. (Vollema, 1998; Neerhof in sod., 2000). Izboljšanje rezultatov prireje in povečevanje ekonomske učinkovitosti lahko izvajamo na več načinov, med katerimi selekcija predstavlja eno izmed glavnih orodij. Na polovici prejšnjega stoletja so bili selekcijski cilji pri reji molznic usmerjeni predvsem k povečevanju laktacijske mlečnosti. Sledil je povečan poudarek na odbiri živali z večjo vsebnostjo maščob in beljakovin. V obdobju zadnjih desetih let so se selekcijski cilji razširili na lastnosti plodnosti, zdravja in funkcionalnih lastnosti (Miglior, 2005). Funkcionalne lastnosti so tiste lastnosti živali, katerih izboljšanje povzroči zmanjšanje stroškov pri reji krav molznic. To so na primer: dolgoživost, lastnosti zunanjosti in težavnost telitev. Glavni razlog za spremembe selekcijskih ciljev je bilo poslabšanje zdravja živali, saj so raziskave pokazale, da enostranska selekcija na prirejeno količino mleka v standardni laktaciji poslabša zdravje vimena (Heringstad in sod., 2003) in poveča število reprodukcijskih motenj (Lucy, 2001).

1.3 VZROKI IZLOČITVE KRAV MOLZNIC

Dolgoživost krav molznic je določena z izločitvijo. Vzroke izločitve z vidika rejca delimo na prostovoljne in neprostovoljne. Prostovoljne izločitve so sprejete s strani rejca in so posledica majhne pritege mleka, starosti, neprimernosti živali za rejo, zmanjševanja črede ali prepočasnega pretoka mleka. Neprostovoljne izločitve so posledica zdravstvenih problemov, zaradi katerih je rejec prisiljen izločiti kravo iz črede. Sem sodijo izločitve zaradi bolezni in poškodb parkljev, nog, porodnega kanala, vimena, presnovnih in prebavnih motenj, plodnostnih motenj, poporodne mrzlice, zastrupitve, zakola ali usmrtnitve v sili, pogina, zvrga, vnetja, okužb, pljučnice in drugih bolezni. V slovenski populaciji molznic, ki so imele prvo telitev med 1. 1. 2003 in 31. 12. 2007, ter so bile izločene do 31. 12. 2008, je bilo 28,4 % vseh izločitev posledica plodnostnih motenj (Jenko in Perpar, 2009). Razmerje med prostovoljnimi in neprostovoljnimi izločitvami se razlikuje med pasmami in leti izločitve. Največji delež prostovoljnih izločitev je značilen za krave rjave pasme, medtem ko je delež najmanjši pri kravah črno-bele pasme. V Sloveniji se je delež prostovoljnih izločitev med leti 2009 in 2013 gibal od 7,6 % za krave črno-bele pasme izločene v letu 2010 do 14,9 % za krave rjave pasme izločene v letu 2011 (Jenko in Perpar, 2013).

V primeru, da napovedi plemenskih vrednosti za dolgoživost korigiramo za prostovoljne vzroke izločitev, govorimo o funkcionalni dolgoživosti. O pravi dolgoživosti govorimo takrat, ko te korekcije ne opravimo (Ducrocq in sod., 1988; Boldman in sod., 1992). Ker je končna odločitev o izločitvi krave lahko posledica več sestavljenih vzrokov, izmed katerih se zabeleži le najpomembnejši, so podatki o vzrokih izločitve manj točni. Korekcija za prostovoljne izločitve preko vzrokov izločitve je zato manj primerna. V modelu za oceno plemenskih vrednosti za funkcionalno dolgoživost tako korekcijo za prostovoljne izločitve opravimo posredno preko pritege mleka (Ducrocq, 1987). Pritejeno količino mleka posamezne krave primerjamo s povprečno mlečnostjo črede. Odstopanja laktacijske ali dnevne količine mleka živali od povprečja črede nato vključimo v model za oceno plemenske vrednosti funkcionalne dolgoživosti. Uporaba laktacijske mlečnosti je manj primerna, saj zaradi pomanjkljivih podatkov laktacijske mlečnosti ne moremo korigirati za vpliv bolezni vimena, zdravja živali in plodnostnih motenj. Pri korekciji z uporabo rezultatov dnevne količine mleka vpliv teh dejavnikov zmanjšamo tako, da v model

vključimo le največjo izmerjeno dnevno količino mleka na vrhu laktacije (Samoré in sod., 2003). Odvisno od modela, ki ga uporabimo za napovedovanje plemenskih vrednosti funkcionalne dolgoživosti, lahko dodatno težavo pri vključitvi laktacijske mlečnosti predstavlja čas, ki je potreben za pridobitev podatka o mlečnosti, medtem ko podatek o dnevni količini mleka lahko pridobimo že ob prvi kontroli mlečnosti.

1.4 GENETSKA OCENA DOLGOŽIVOSTI

Napovedovanje plemenskih vrednosti za dolgoživost izvajajo v 21 državah članicah Interbulla (Interbull, 2015). Na nacionalni ravni uporabljajo države članice Interbulla za odbiro živali neposredno ali sestavljeni napoved plemenske vrednosti za dolgoživost. Neposredna ocena dolgoživosti je podana samo na podlagi podatkov o dolžini dobe pireje oziroma preživetja. Sestavljeni oceni dolgoživosti sestavlja neposredna ocena dolgoživosti in napovedane plemenske vrednosti za funkcionalne lastnosti, ki posredno vplivajo na dolgoživost. Za primerjavo plemenskih vrednosti med državami je bolj primerna uporaba neposredne ocene za dolgoživost. Države članice uporabljajo pri sestavljeni oceni različne lastnosti, ki jim pripisujejo različne ekonomske teže, kar otežuje primerjavo med njimi. Raziskava, ki so jo opravili Forabosco in sod. (2009), je pokazala, da izmed 15 vključenih držav le tri (Danska, Finska in Irska) uporabljajo neposredno oceno za dolgoživost.

Razlog večje pogostnosti uporabe sestavljeni napovedi plemenskih vrednosti za dolgoživost gre iskati v času, ki je potreben za pridobitev podatkov, in v pozitivni povezavi med nekaterimi funkcionalnimi lastnostmi z dolgoživostjo. Izmed vseh funkcionalnih lastnosti so z dolgoživostjo krav molznic najtesneje povezane lastnosti vimena in nog (Vukasinovic in sod., 1995; Zavadilová in sod., 2011). Ker bi morali ob uporabi klasičnih linearnih modelov počakati, da so vse živali izločene, za napoved plemenskih vrednosti za dolgoživost uporabimo metode, ki omogočajo tudi vključitev podatkov krav, ki so še vedno v čredi. Prve napovedi plemenskih vrednosti za dolgoživost so bile opravljene na podlagi binarnega podatka, če je žival dosegla določeno starostno mejo oziroma je priredila določeno količino mleka ali ne (Everett in sod., 1976; Van Vleck, 1980). Naslednji korak je predstavljala uporaba analize preživetja, ki je primerna za analizo krnjenih podatkov o

dolžini dobe prireje, življenjski prieji itd. (Cox in Oakes, 1984; Kalbfleisch in Prentice, 2002). Prvi poskus uporabe preživetja za napoved plemenskih vrednosti za dolgoživost je opravil Famula (1981). Delo sta v svojih doktorskih nalogah nadaljevala Smith (Smith, 1983, cit. po Ducrocq in sod., 1994) in Ducrocq (1987). Prvi računalniški program za izračun plemenskih vrednosti za lastnost dolgoživosti z uporabo analize preživetja je predstavil Smith (1987, cit. po Ducrocq V. 1987), a je bila njegova uporaba omejena, saj ni omogočal analize večje količine podatkov. Splošno uporaben programski paket „The Survival Kit“, prilagojen analizi večje količine podatkov, sta nato predstavila Ducrocq in Sölkner (1998).

1.4.1 Analiza preživetja

Analiza preživetja uporablja za modeliranje podatkov o dolgoživosti model sorazmernih ogroženosti, ki omogoča hkratno vključitev podatkov tako izločenih kot živih živali. Podatki o dolgoživosti, pridobljeni na živalih, ki so v času opravljanja analize še vedno žive, niso zaključeni, temveč so krnjeni (Ducrocq in sod., 1988). Vključitev krnjenih podatkov v model za oceno dolgoživosti izboljša točnost napovedanih plemenskih vrednosti, vendar je točnost napovedanih plemenskih vrednosti za mlade bike še vedno nizka (Brotherstone in sod., 1997). Z uporabo analize preživetja je omogočena korekcija modela za vpliv časovno odvisnih spremenljivk in s tem vključitev spremembe določenega vpliva skozi življenjsko obdobje živali. Analiza krnjenih podatkov dolgoživosti je mogoča z uporabo funkcije ogroženosti. Funkcija ogroženosti opisuje dolgoživost v obliki verjetja, da bo žival, ki je dočakala določeno starost, izločena v naslednjem trenutku svojega življenja. Porazdelitveno funkcijo ogroženosti lahko zapišemo v obliki enačbe št. (1) (Ducrocq in sod., 1988):

$$\lambda(t) = \lim_{\delta \rightarrow 0} \frac{\text{prob}[t \leq T < t + \delta | T \geq t]}{\delta} \quad \dots (1)$$

kjer pomeni:

$\lambda(t)$ – funkcija ogroženosti v starosti t , ob preživetju do starosti t

T – vrednost pozitivnega parametra, ki določa starost ob izločitvi

δ – najmanjša izmerjena časovna razlika med dvema opazovanjema, opravljenima na isti

živali

V modelu sorazmernih ogroženosti se spremembra v eni enoti pojasnjevalne spremenljivke izrazi v proporcionalni spremembi tveganja izločitve. Regresijski model ogroženosti za posamezno žival (Ducrocq in sod., 1988), je zapisan v enačbi št. (2):

$$\lambda(t, \mathbf{x}_i) = \lambda_0(t) \kappa_i \exp(\mathbf{x}_i' \boldsymbol{\beta}) \quad \dots (2)$$

kjer pomeni:

$\lambda(t, \mathbf{x}_i)$ – funkcija ogroženosti za žival i v starosti t

$\lambda_0(t)$ – časovno odvisna spremembra ogroženosti za izločitev glede na starost živali

\mathbf{x}_i' – vektor dogodkov za pojasnjevalne spremenljivke

$\boldsymbol{\beta}$ – vektor ocen vplivov za pojasnjevalne spremenljivke

κ_i – parameter krhkosti (ang. »frailty term«); opisuje genetski učinek

Če parameter krhkosti zapišemo kot $s_i = \log(\kappa_i)$ in regresijski model ogroženosti vključuje podatke več živali, potem \mathbf{Z} predstavlja matriko dogodkov za parametre, ki opisujejo krhkosti, in model ogroženosti za več živali zapišemo v obliki enačbe št. (3) (Sasaki, 2013):

$$\lambda(t) = \lambda_0(t) \exp(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{s}) \quad \dots (3)$$

kjer pomeni:

$\lambda(t)$ – funkcija ogroženosti v starosti t

$\lambda_0(t)$ – časovno odvisna spremembra ogroženosti glede na starost živali

\mathbf{X} – matrika dogodkov za pojasnjevalne spremenljivke

$\boldsymbol{\beta}$ – vektor ocen vplivov za pojasnjevalne spremenljivke

\mathbf{Z} – matrika dogodkov za parametre, ki opisujejo krhkosti

\mathbf{s} – vektor ocen vplivov za parametre, ki opisujejo krhkosti

Porazdelitev izhodiščne funkcije ogroženosti lahko opravimo izkustveno na podlagi porazdelitve podatkov, vendar parametre najlažje ocenimo z uporabo parametričnih porazdelitev, kot je na primer Weibullova porazdelitev (Ducrocq in sod., 1988), katere izhodiščna funkcija ogroženosti je zapisana v enačbi (4):

$$\lambda_0(t) = \lambda\rho(\lambda t)^{\rho-1} \quad \dots (4)$$

kjer pomeni:

λ – parameter merila

ρ – parameter oblike

Preživitvena funkcija Weibullovega modela sorazmerne ogroženosti je zapisana v enačbi (5) (Ducrocq in sod., 1988):

$$S_0(t) = \exp[-(\lambda t)^\rho] \quad \dots (5)$$

kjer pomeni:

$S_0(t)$ – preživitvena funkcija Weibullovega modela sorazmerne ogroženosti pri starosti t

Funkcijo lahko preoblikujemo v obliko, zapisano v enačbi (6) (Ducrocq in sod., 1988):

$$\log\{-\log[S_0(t)]\} = \rho \log(t) + \rho \log(\lambda) \quad \dots (6)$$

Če obstaja linearна povezava med $\log\{-\log[S_0(t)]\}$ in $\rho \log(t)$, potem lahko za oceno parametrov v modelu sorazmernih ogroženosti uporabimo Weibullovo porazdelitev. V primeru različnega naklona premice pri linearni povezavi med $\log\{-\log[S_0(t)]\}$ in $\rho \log(t)$ med posameznimi laktacijami in znotraj njih med stadiji laktacije lahko uporabimo različne izhodiščne funkcije ogroženosti glede na laktacijo in stadij laktacije (Sewalem in sod., 2005) zapisane v enačbi (7):

$$\lambda_{0,lp}(t) = \lambda\rho(\lambda t)^{\rho-1} \quad \dots (7)$$

kjer pomeni:

l – zaporedna laktacija

p – stadij laktacije

t – dolžina stadija znotraj laktacije

Uporaba analize preživetja lahko v primeru nepravilne vključitve Weibullove izhodiščne funkcije vodi do precenitve genetskega trenda. Sewalem in sod. (2005) poročajo, da je uporaba enotne izhodiščne funkcije ogroženosti znotraj laktacije precenila genetski trend za dolgoživost. Precenitev genetskega trenda pripisujejo podaljševanju dobe med dvema telitvama, povečanju težav s plodnostjo in večji količini mleka. Z uporabo različnih

izhodiščnih funkcij ogroženosti znotraj leta, laktacije in stadija laktacije, je precenitev genetskega trenda v populaciji goveda z velikim številom živali odpravil Ducrocq (2005). Model tako omogoča večjo prilagodljivost spremembam v tveganju za izločitev molznice znotraj različnih obdobij življenja, ki pa niso povezani s staranjem živali. Zaradi boljšega prileganja modela podatkom se je skrajšal tudi računalniški čas, potreben za napoved plemenskih vrednosti. Uporaba različnih izhodiščnih funkcij v manjših populacijah govedi še ni bila preučena.

Analiza preživetja z uporabo modela sorazmernih ogroženosti v nacionalnih obračunih uporablja model očetov ali model očetov in materinih očetov (Ducrocq, 2002; Roxström in sod., 2003; Forabosco in sod., 2009). Modeliranje aditivne genetske komponente z uporabo modela živali naj bi bilo ustrezejše kot z uporabo modela očetov. Z uporabo modela živali upoštevamo v modelu informacijo obeh staršev in učinek mendelskega vzorčenja. V modelu očetov nimamo učinka mendelskega vzorčenja in informacije po materi. Informacija po materi je vključena v model očetov in materinih očetov preko maternega očeta. Čeprav je model očetov nepopoln, saj v genetski del modela ni vključene tri četrt (11/16 v modelu očetov in materinih očetov) aditivne genetske variance (Ducrocq, 2005), so simulacije pokazale, da ni večjih razlik v korelaciji med napovedanimi in pravimi plemenskimi vrednostmi v primeru, ko se za napoved plemenskih vrednosti uporabi model očetov oziroma model živali (Meuwissen in sod., 2002). V primeru, ko je bila v simulacijah uporabljenha 10-krat večja genetska varianca, kot je značilna za dolgoživost, se je kot precej boljši izkazal model živali (Damgaard in sod., 2003). Uporaba modela živali v modelu sorazmernih ogroženosti ne predstavlja teoretskega problema. Glavna razloga neuporabe modela živali za napoved plemenskih vrednosti za dolgoživost sta (i) računska zahtevnosti in (ii) čas, ki je potreben za pridobitev napovedi plemenskih vrednosti. V primeru, da hočemo napovedati plemenske vrednosti tudi ženskim živalim, lahko uporabimo aproksimativno metodo napovedi plemenskih vrednosti (Ducrocq, 2001). Rezultati simulacije so pokazali, da je korelacija med napovedanimi plemenskimi vrednostmi z modelom živali in z aproksimativno metodo visoka (0,99). Boljši odgovor bi vsekakor ponudila analiza, opravljena na realnih podatkih.

Ker ocnjene vrednosti parametrov v analizi preživetja prihajajo iz Weibullove

porazdelitve, za oceno heritabilitete ne moremo uporabiti klasičnega pristopa, ki velja za parametre, katerih ocene so pridobljene iz normalno porazdeljenih lastnosti. Za oceno heritabilitete na logaritemski skali za Weibullov model očetov tako uporabimo enačbo (8) (Ducrocq, 1987):

$$h_{log}^2 = \frac{4\sigma_s^2}{(\sigma_s^2 + \pi^2/6)} \quad \dots (8)$$

kjer pomeni:

h_{log}^2 – ocenjena heritabiliteta na logaritemski skali

$\pi^2/6$ – varianca porazdelitve ekstremnih vrednosti

σ_s^2 – genetska varianca za vpliv očeta

Ocenjena heritabiliteta na logaritemski skali ni primerna za oceno točnosti plemenskih vrednosti, saj so te napovedane pristransko. Ducrocq (1999) je tako predlagal enačbo za oceno heritabilitete na originalni skali, zapisano v enačbi (9):

$$h_{orig}^2 = \left(\exp\left(\frac{1}{\rho}\nu\right) \right)^{-2} h_{log}^2 \quad \dots (9)$$

kjer pomeni:

h_{orig}^2 – ocenjena heritabiliteta na originalni skali

ν – Eulerjeva konstanta (-0,577)

Enačba (9) se je izkazala kot dobra samo v primeru, ko je bila vrednost parametra ρ blizu 2.0. Alternativo oceni heritabilitete za model očetov na logaritemski skali je predlagal Yazdi (2002) ter jo poimenoval efektivna heritabiliteta, zapisana v enačbi (10):

$$h_{eff}^2 = \frac{4\sigma_s^2}{\sigma_s^2 + 1} \quad \dots (10)$$

kjer pomeni:

h_{eff}^2 – efektivna heritabiliteta

Efektivna heritabiliteta ni odvisna od parametrov Weibullove porazdelitve in jo lahko uporabimo za oceno točnosti plemenskih vrednosti.

V primeru, ko so podatki v določeni časovni točki knjeni, lahko definiramo ekvivalentno heritabiliteto z enačbo (11) (Yazdi in sod., 2002):

$$h_{ekv}^2 = \left(\frac{4\sigma_s^2}{\sigma_s^2 + (1/\bar{p})} \right) \quad \dots (11)$$

kjer pomeni:

h_{ekv}^2 – ekvivalentna heritabiliteta

\bar{p} – delež potomk, ki so bile izločene do določene časovne točke

1.4.2 Linearni modeli

Genetska ocena dolgoživosti z uporabo linearnih modelov je bila predlagana s strani več raziskovalcev. Everett in sod. (1976) so dolgoživost definirali v obliki preživetja do določene starosti. Ugotovili so, da obstaja med genetsko vrednostjo preživetja do 48. meseca starosti in preživetjem do 36., 60., 72. in 84. meseca starosti visoka genetska korelacija ($>0,86$), ter predlagali uporabo preživetja do 48. meseca starosti za genetsko oceno dolgoživosti. Glede na to, da genetska korelacija med preživetjem do posameznih starosti ni popolna oziroma blizu 1, ponovljivostni model ni najprimernejši za genetsko oceno dolgoživosti. Madgwick in Goddard (1989) so tako analizirali uporabo večlastnostnega modela z uporabo podatka o preživetju živali znotraj posameznih laktacij. Jairath in sod. (1998) so v večlastnostni model vključili pet binarnih lastnosti, ki so označevale, ali je žival dosegla določeno starostno mejo ali ne. Prvi dve lastnosti sta merili preživetje krav do 120. in 240. dne po prvi telitvi, medtem ko so preostale tri označevale preživetje do druge, tretje oziroma četrte telitve. Knjenih podatkov ni mogoče vključiti v linearni model, zato so za oceno dolgoživosti Brotherstone in sod. (1997) predlagali model, kjer je za živali, ki so še vedno aktivne, vključena informacija o pričakovanim preživetju do naslednje in poznejših laktacij, ocenjena na podlagi preživetja živali v populaciji. VanRaden in Klaaskade (1993) sta za živali s knjenimi podatki ocenila preživetje v poznejših laktacijah s pomočjo uporabe multiple fenotipske regresije.

1.4.3 Naključna regresija

Veerkamp in sod. (2001) so za genetsko oceno dolgoživosti predlagali uporabo naključne regresije. Naključna regresija namesto točnega časa izločitve uporablja intervale, v katerih binarni zapis označuje, ali je žival dosegla določen starostni interval ali ne. Intervale, v katerih je bila žival živa, so označili z 1, medtem ko je bil zapis v intervalih, ki so sledili intervalu, ko je bila žival izločena, enak 0. V primeru, da je bila žival še vedno živa, so bili njeni podatki krnjeni in meritve v poznejših intervalih manjkajoče. Izločene živali so imele zapise v vseh intervalih, medtem ko so podatki živali s krnjennimi meritvami vsebovali zapise samo v intervalih, ki jih je žival preživila. Zaradi zapisa podatkov o dolgoživosti v obliki intervalov, je možno v model vključiti tudi časovno odvisne vplive. Primer uporabe naključne regresije je podal Mrode (2014). Definiral je 60 intervalov, ki so vsebovali binarni zapis o prisotnosti oz. odsotnosti živali. Živali, ki so bile izločene, so imele zapis v vseh intervalih. V primeru, da so bili podatki živali krnjeni, je bil zapis podan samo za intervale, ki jih je žival preživila. Za analizo podatkov so predlagali naslednji model, zapisan v enačbi (12) (Mrode, 2014):

$$y_{tijk} = \text{sistematski vplivi}_i + \sum_{k=0}^{nf} \beta_k \phi_{jtk} + \sum_{k=0}^{nr} u_{jk} \phi_{jtk} + \sum_{k=0}^{nr} p_{jk} \phi_{jtk} + e_{tijk} \quad \dots (12)$$

kjer pomeni:

y_{ijk} – preživetje pri kravi j , ki ima vrednost 1 (živa) ali 0 (izločena) v času t ob nivoju i za sistematske vplive, ki so od dneva v laktaciji neodvisni vplivi (čreda, leto-sezona telitve)

β_k – vrednost regresijskega koeficiente pri sistematski regresiji

u_{jk} – k -ti regresijski koeficient za aditivni genetski vpliv živali j

p_{jk} – regresijski koeficient k za vpliv permanentnega okolja živali j

ϕ_{jtk} – vektor k -tega Legendrovega polinoma za čas t pri kravi j

nf – stopnja polinoma sistematske regresije

nr – stopnja polinoma pri naključni regresiji za vpliv živali in vpliv permanentnega okolja

e_{tijk} – ostanek

1.4.4 Primerjava med modelom preživetja in linearnim modelom

Glavna prednost napovedovanja plemenskih vrednosti z uporabo modela preživetja je v pravilni vključitvi časovno odvisnih spremenljivk in podatkov živali, ki so še vedno žive v času opravljanja analize. Do nedavnega je bilo to mogoče samo za sistematske vplive, vendar zadnja izdaja programa Survival Kit (Mészáros in sod., 2013) omogoča vključitev časovno odvisnih spremenljivk tudi za naključne vplive. Zaradi možnosti vključitve naključnih časovno odvisnih spremenljivk lahko plemensko vrednost živali napovemo za različna starostna obdobja. S tem je bil odpravljen tudi glavni pomislek, zaradi katerega naj bi bila analiza dolgoživosti z uporabo linearnega modela primernejša. Genetska korelacija med napovedmi plemenskih vrednosti za dolgoživost v prvi in naslednjih laktacijah ni popolna in se s podaljševanjem časovne oddaljenosti med napovedmi zmanjšuje (Jairath in sod., 1998). Korelacije med napovedanimi plemenskimi vrednostmi, pridobljenimi z linearnim modelom in analizo preživetja z uporabo modela sorazmernih ogroženosti, se med raziskavami razlikujejo in so med 0,15 in 0,91 (Boettcher in sod., 1999; Caraviello in sod., 2004; Forabosco in sod., 2006; Potočnik in sod., 2008).

Obširnejši pregled ocen heritabilitet za dolgoživost je opravil Sasaki (2013). Ocene heritabilitet iz 21 raziskav, kjer so uporabili linearni regresijski model, so se gibale med 0,002 in 0,18. Zelo podoben razpon ocen heritabilitet za lastnost dolgoživosti je bil pridobljen tudi z uporabo analize preživetja. Skupno 24 raziskav, v katerih so uporabili model sorazmernih ogroženosti, poroča o ocenah heritabilitet za dolgoživost v razponu med 0,02 in 0,20. Primerjave uporabe linearnega modela in modela sorazmernih ogroženosti so pokazale, da je ocena heritabilitete za lastnost dolgoživosti večja pri uporabi slednjih. Holtsmark in sod. (2009) poročajo, da je bila ocenjena vrednost heritabilitete znotraj črede 0,04 pri uporabi Weibullovega modela sorazmernih ogroženosti in 0,02 pri uporabi linearnih modelov. Do podobne ugotovitve so prišli tudi Raguž in sod. (2014) s to razliko, da so bile ocenjene heritabilitete nekoliko višje in so znašale 0,037 pri uporabi linearnega modela in 0,075 pri uporabi Weibullovega modela sorazmernih ogroženosti. Čeprav razlike v absolutnih vrednostih niso velike, so ocene pridobljene z modelom sorazmernih ogroženosti relativno dvakrat večje glede na ocene pridobljene z linearnim modelom.

1.5 ŽIVLJENJSKA PRIREJA MLEKA

Življenjska prireja mleka je količina mleka, prirejena od prve telitve do zadnje presušitve, ki ji običajno sledi izločitev molznice iz črede. Zaradi izpostavljenosti različnim dejavnikom okolja, vpliva velikega števila genov in časa, ki je potreben za pridobitev podatkov, je genetska ocena življenjske prireje mleka zahtevna. V preteklosti se je selekcija živali z veliko življenjsko prirejo mleka izvajala preko selekcije živali z veliko prirejo mleka v standardni laktaciji. Selekcija na veliko prirejo mleka v standardni laktaciji je v začetku precej pripomogla tudi k povečani količini mleka v življenjski dobi. Poznejše vztrajanje pri selekciji s poudarkom na večjo količino mleka v standardni laktaciji, je vodilo v poslabševanje funkcionalnih lastnosti in s tem k skrajšani dolgoživosti, kar je vplivalo na manjši napredek pri življenjski prireji mleka in s tem nižje prihodke po kravi. Življenjska prireja mleka je odvisna tako od laktacijske mlečnosti kot dolgoživosti. Glavni interes rejca naj bi tako predstavljal povezava med funkcionalnimi lastnostmi in prirejeno količino mleka (Essl, 1998).

Prevelika in premajhna dnevna mlečnost krav zmanjšuje življenjsko prirejo mleka. Nizka dnevna mlečnost ni ekonomsko upravičena in rejci take krave izločijo iz črede. Velika dnevna prireja lahko ob neprimerni oskrbi vodi v presnovne in plodnostne motnje, ki prav tako vodijo do zgodnje izločitve krav iz črede. Haworth in sod. (2008) na 442 kravah črnobele pasme sicer niso potrdili povezave med količino mleka v prvi laktaciji in številom laktacij v življenju, vendar nobena od krav, ki so imele v prvi laktaciji povprečno dnevno mlečnost nad 30 kg, ni dosegla tretje laktacije. Za doseganje velike prireje v življenju priporočajo, naj krave v prvi laktaciji v povprečju dajo med 20 in 30 kg mleka na dan, saj imajo takšne molznice daljšo dobo prireje in večjo življenjsko prirejo mleka.

1.6 GENETSKA OCENA ŽIVLJENJSKE PRIREJE MLEKA

Ocene genetskih parametrov za življenjsko prirejo mleka so se spremenjale z napredkom v metodologiji napovedovanja plemenskih vrednosti. Hargrove in sod. (1969) so genetsko vrednost za življenjsko prirejo mleka napovedali s pomočjo regresijske analize na podlagi 1017 parov podatkov mater in hčera. Ocenili so, da je heritabiliteta za življenjsko prirejo

mleka 0,18. Genetska korelacija med količino mleka v prvi laktaciji in življenjsko pritejo mleka je bila visoka (0,85). Prav tako je bila visoka korelacija med količino mleka v prvi laktaciji in dolžino dobe priteje (0,76), korelacija med življenjsko pritejo mleka in dolžino dobe priteje je bila še višja (0,95). Metodo najmanjših kvadratov sta za oceno genetske in fenotipske korelacije med življenjsko pritejo mleka in dolžino dobe priteje uporabila Hoque in Hodges (1980). Ocenila sta, da je heritabiliteta za življenjsko pritejo mleka 0,11 in genetska korelacija med pritejeno količino mleka v prvi laktaciji in življenjsko pritejo mleka 0,52. Chauhan in sod. (1993), Jairath in sod. (1994; 1995), Zarnecki in Morek-Kopec (2006) so za oceno komponent varianc in kovarianc življenjske priteje uporabili večlastnostni model z uporabo metode največje zanesljivosti. Jairath in sod. (1995) so ocenili heritabiliteto za življenjsko pritejo mleka na 0,13, maščob na 0,11 in beljakovin na 0,12. Genetska korelacija med količino mleka v prvi laktaciji in življenjsko pritejo mleka je bila visoka (0,86). Prav tako visoka je bila genetska korelacija med količino mleka v prvi laktaciji in dolžino dobe priteje (0,84). Zarnecki in Morek-Kopec (2006) sta ocenila, da je heritabiliteta za življenjsko pritejo maščob in beljakovin 0,06. Genetska korelacija med življenjsko pritejo maščob oz. beljakovin in dolžino dobe priteje je bila visoka (0,85 oz. 0,86). Zaradi visoke genetske korelacije med laktacijsko mlečnostjo in življenjsko pritejo mleka, Togashi in sod. (2008) ter Togashi in Lin (2008) za oceno življenjske priteje mleka, predlagajo uporabo večlastnostnega modela z vključitvijo naključne regresije. Kanadski nacionalni genetski obračun življenjske priteje tako vključuje tri laktacije s štirimi lastnostmi (Schaeffer in sod., 2000). Z uporabo modela z naključno regresijo dnevnih meritev napovedujejo plemensko vrednost za količino mleka, maščob in beljakovin ter število somatskih celic za vsako laktacijo. Napovedane plemenske vrednosti za posamezne lastnosti nato vključijo v ekonomski indeks, ki združuje proizvodne in funkcionalne lastnosti.

Ocene genetskih korelacij med dolžino dobe priteje in življenjsko pritejo mleka si niso enotne in se gibljejo med -0,53 in 0,84 (De Lorenzo in Everett, 1982; Jairath in sod., 1995; Dematawewa in Berger, 1998; González-Recio in Alenda, 2007). Essl (1998) v pregledu selekcije na dolgoživost goveda navaja, da je začetna odbira živali na veliko laktacijsko pritejo zaradi negativne genetske korelacije skrajšala dolžino dobe priteje, vendar se je življenjska priteja mleka zaradi pozitivne povezave s količino mleka v prvi laktaciji

povečala. Prevelik poudarek selekcije na veliko laktacijsko mlečnost, poleg krajše življenjske dobe, zmanjša tudi število telitev. Manjše število telitev vodi do manjšega števila telic, ki so na voljo za obnovo črede, in manjše intenzivnosti selekcije. Hare in sod. (2006) ugotavljajo, da je povprečno število laktacij v življenjski dobi s 3,2, pri kravah iz ameriške populacije, ki so imele prvo telitev v letu 1980, padlo na 2,8 laktacije pri kravah, ki so imele prvo telitev v letu 1994. Poleg negativnega trenda za število telitev so ugotovili tudi krašanje dobe prireje do leta 1990, pozneje pa se je ta trend zaustavil.

Izgradnja indeksa življenjske prireje predstavlja možno rešitev problema potencialno negativne genetske korelacije med količino mleka v prvi laktaciji in dolžino dobe prireje. De Jong (2014) je predstavil indeks življenjske prireje, ki je zgrajen iz napovedi genetske vrednosti za prirejo mleka, maščob in beljakovin, stopnje zrelosti (razlika med plemensko vrednostjo v tretji in prvi laktaciji), mlečne vztrajnosti in dobe med telitvama. Ugotavljanje veljavnosti indeksa so opravili na 62 bikih, ki so imeli vsaj 1000 izločenih potomk. Korelacija med napovedmi plemenskih vrednosti in povprečno življenjsko prirejo mleka pri potomkah je znašala 0,79.

1.7 RAZISKOVALNE HIPOTEZE

- (1) Napoved plemenskih vrednosti za lastnost prave in funkcionalne dolgoživosti v populacijah govedi z majhnimi čredami je mogoča z uporabo analize preživetja.
- (2) Model živali z vključenim vplivom skupnega okolja v čredi ali interakcije med skupnim okoljem v čredi in letom ima večjo napovedno točnost za oceno plemenskih vrednosti funkcionalne dolgoživosti kot model očetov in materinih očetov. Uporaba aproksimativne metode za napoved plemenskih vrednosti funkcionalne dolgoživosti za krave predstavlja primerno alternativo modelu živali, katerega uporaba je zaradi računske zahtevnosti omejena.
- (3) Genetsko oceno za življenjsko prirejo mleka lahko ocenimo posredno preko genetske ocene za dolgoživost oziroma količine mleka v prvi laktaciji.
- (4) Napoved plemenskih vrednosti za življenjsko prirejo mleka v populacijah govedi z majhnimi čredami je mogoča z uporabo večlastnostnega modela z vključitvijo naključne regresije.

2 ZNANSTVENA DELA

2.1 PRIMERJAVA WEIBULLOVIH MODELOV PO DELIH ZA OCENO PRAVE IN FUNKCIONALNE DOLGOŽIVOSTI KRAV MOLZNIC

Comparison of piecewise Weibull baseline survival models for estimation of true and functional longevity in Brown cattle raised in small herds

Janez Jenko, Vincent Ducrocq, Milena Kovač

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Izvleček:

Za oceno učinka genetskih in okoljskih dejavnikov na lastnosti funkcionalne in prave dolgoživosti pri slovenski rjavi pasmi goveda je bil uporabljen Weibullov model sorazmernih ogroženosti. V analizo je bilo vključenih 37908 krav rjave pasme iz 2401 slovenske črede. Povprečna velikost čred, ki so redile molznice rjave pasme, je bila majhna in je znašala med 6,7 v letu 1999 in 8,7 v letu 2008. Zaradi majhne povprečne velikosti čred je bilo razvrščanje krav glede na njihovo pritejo mleka namesto znotraj črede opravljeno na ravni različnih velikostnih razredov čred. Tveganje za izločitev molznice je bilo najmanjše za krave v začetku vsake laktacije in je naraščalo s potekom laktacije. Krave iz čred, ki so povečevale stalež molznic, so imele večjo pritejo mleka in so prihajale z območja s težjimi pogoji za vzrejo, izpostavljene so bile manjšemu tveganju izločitve iz reje. Manjše tveganje za izločitev krav z območja s slabšimi razmerami za rejo krav molznic je presenetljivo in ga lahko pripisemo večji skrbi za živali, čeprav njihova priteja morda ne dosega primerne ravni. Uvedba mlečnih kvot in suša sta izkazali pomemben vpliv na izločitev krav v obdobju med zadnjo sezono leta 2001 in zadnjo sezono leta 2003. Vpliv sezone ni bil povezan s kvotnim letom za mleko, temveč s pomanjkanjem krme v zimskem obdobju. Vpliv starosti ob prvi telitvi in interakcija med letom in količino pritejenega mleka sta se izkazala kot neznačilna. Ocenjeni heritabiliteti za pravo in funkcionalno dolgoživost sta bili podobni in sta znašali okoli 10 %. Zaradi vključitve vpliva pritejene količine mleka v model za oceno funkcionalne dolgoživosti se je povečala varianca naključnega vpliva interakcije leta in skupnega okolja v čredi za 53 %, medtem ko se je varianca za vpliv očeta povečala samo za 14 %. Korelacija med rangi plemenskih

vrednosti za lastnost prave in funkcionalne dolgoživosti je bila visoka (0,94). Ocjenjeni genetski trendi se niso izkazali kot statistično značilno različni od 0. Za namen ocene napovedne točnosti smo napovedane plemenske vrednosti iz obeh modelov primerjali s preživetjem testnega vzorca 4212 potomk starejših bikov. Povprečna vrednost koeficiente korelacije med napovedanimi plemenskimi vrednostmi in preživetjem potomk starejših bikov v različnih obdobjih življenja je bila 0,39 za pravo in 0,43 za funkcionalno dolgoživost. Rezultati analize so pokazali, da razvrščanje krav glede na njihovo prirejo mleka na ravni različnih velikostnih razredov čred primerno korigira učinek prostovoljnih izločitev v majhnih čredah.

Comparison of piecewise Weibull baseline survival models for estimation of true and functional longevity in Brown cattle raised in small herds

J. Jenko^{1†}, V. Ducrocq² and M. Kovač³

¹Agricultural Institute of Slovenia, Hacquetova ulica 17, 1000 Ljubljana, Slovenia; ²INRA, UMR 1313 Génétique Animale et Biologie Intégrative, F-78350 Jouy-en-Josas, France; ³Department of Animal Science, Biotechnical Faculty, University of Ljubljana, Groblje 3, 1230 Domžale, Slovenia

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Piecewise Weibull proportional hazard models were used to investigate the effect of genetic and nongenetic factors on functional and true longevity traits of the Slovenian Brown cattle breed. Records of 37 908 Brown cows from 2401 Slovenian herds were used. As these herds were characterised by a relatively small average herd size starting from 6.7 in 1999 and increasing to 8.7 Brown cows per herd in 2008, milk yield classification was made within different herd size groups. The hazard rate was the lowest in the first part of each lactation and was increasing for later stages. Culling risk was lower for cows from herds increasing in size, for cows with higher milk production and for cows from a region with smaller herd sizes and tougher conditions for cattle breeding. The latter result is surprising and may be related to better attention to maintain the animals, despite their lower milk production. The introduction of the milk quota system and drought was found to have an important effect on culling policy between the last seasons of the years 2001 and 2003. Seasonal effects were not related to the milk quota year (from April to March), but to the effect of shortage in fodder during the winter time. The effect of age at first calving and the interaction between year and milk yield class were not found to be significant. Heritability for functional and for true longevity were similar at around 10% each. Inclusion of a correction for class of milk yield to approximate functional longevity increased the herd-year random effect variance by 53%, whereas the sire variance increased by only 14%. The correlation coefficient between ranks of breeding values for functional and true longevity was high (0.94), whereas genetic trends were not found to be significant. To assess their predictive ability, models were compared looking at the survival rate of 4212 second-crop daughters not included in the initial models. The average correlation between estimated breeding values and survival at different stages was 0.39 for true longevity and 0.43 for functional longevity. Results showed that ranking milk yield at population level is appropriate to correct for voluntary culling on low production in small herds.

Keywords: dairy cattle, longevity, survival, genetic analysis, small farms

Implications

In countries with less-favourable socio-economic conditions and small dairy herds, genetic evaluation for longevity traits is important to keep milk production profitable. Longevity traits for dairy cows in small herds require careful modelling because of their specific culling policy, which affects breeding value prediction. Functional and true longevity are commonly used for genetic evaluations. The correlation between these two traits underlines the impact of voluntary culling on breeding value evaluation.

Introduction

Sustainability of milk production systems relies on economical, societal and environmental benefits. Increasing survival and longevity is the first solution for reduction in replacement costs (Boichard and Brochard, 2012). Routine genetic evaluation for longevity (or length of productive life) of dairy cows is carried out in most developed countries now. In August 2011, 19 countries with different numbers of breeds were involved in the multiple across-country evaluation (MACE) on longevity (Interbull, 2011). Out of these 19 countries, 10 were using survival analysis assuming a sire or sire-maternal grand sire model to predict the breeding values for functional or true longevity (Forabosco *et al.*, 2009). Survival analysis usually

[†] E-mail: janez.jenko@kis.si

Jenko, Ducrocq and Kovač

models a longevity measure through a hazard function, which describes the limiting probability for a cow to die or to be culled at a specific time, given she was alive in the same herd just before it. All survival analysis models currently used for genetic evaluations are proportional hazard models (Kalbfleisch and Prentice, 1980). One of the reasons for not applying survival analysis to the remaining nine countries might be the more complex and demanding computations required compared with linear mixed models. Countries where it is considered that an animal model must be applied, mixed models may be preferred because computation time and memory requirements are lower, although some approximate animal model evaluations have been proposed (Ducrocq, 2001).

For genetic evaluation, different definitions of longevity have been used: stayability (e.g. Van Doormaal *et al.*, 1985), survival to the next lactation (e.g. Jairath *et al.*, 1998), number of lactations (e.g. Yazdi *et al.*, 1999) and so on; however, length of production life (e.g. Chirinos *et al.*, 2007) is the most popular way of defining longevity. Moreover, it is also possible to distinguish between genetic effects resulting in a voluntary or involuntary culling. Voluntary culling occurs when cows are not profitable and can be replaced by more profitable cows, whereas involuntary culling occurs when cows have health or reproductive problems and must be disposed of, regardless of their production. For this reason, Ducrocq (1987) proposed defining two different traits: true and functional stayability. True stayability is the ability to delay any culling, whereas functional stayability is defined as the ability to delay involuntary culling only. As there is no direct measure of functional stayability, an approximation can be obtained by correcting length of production life for the main criteria on which breeders take the decision to voluntarily cull the cow.

Inclusion of time-dependent covariates and stratification are approaches to accommodate situations for which the proportional hazard assumption is not valid for all effects or throughout the whole time interval studied. Piecewise Weibull baselines accommodate the cyclic pattern of the hazard function over lactations in the cow's life (Ducrocq, 2005; Terawaki *et al.*, 2006). Therefore, application of a piecewise Weibull baseline proportional hazard model is a natural step forward to evaluate longevity breeding values for populations such as Slovenian Brown cattle. In addition, for accurate evaluation of breeding values, all known factors (e.g. effect of age at first calving, of change in herd size) need to be accounted for if they have a significant effect on the hazard function.

Longevity genetic evaluation for the Brown dairy cattle population in Slovenia was first implemented by Potočnik *et al.* (2011). Breeding values were estimated using a unique baseline hazard for the whole period considered. A sire–maternal grand sire model was applied because of its computing feasibility. Slovenia is currently not included in the MACE for longevity carried out by Interbull (2011).

The objectives of this study were to develop a piecewise proportional hazard model to estimate the breeding values for longevity of Slovenian Brown cattle breed and to compare

breeding values obtained from models with or without correction for milk production. As the commonly used approach for the definition of within herd milk production classes is not applicable in small herds, an alternative, on the basis of milk production classes within group of herds with similar number of cows, was tested. Model validations in populations characterised by small herd size are scarce in the literature and are of interest for practical application.

Material and methods

Data

All the data necessary for the creation of productive life records were obtained from the central cattle database GOVEDO, maintained by the Agricultural Institute of Slovenia. Records from milk recorded Brown cows with at least one of their first five calvings occurring between 1 January 1998 and 31 December 2008 were considered in the creation of the data set. The cows were included in the data set as soon as at least one milk recording existed. Where only second and/or later lactations were observed in the period analysed, truncation was performed on the day of first calving after 1 January 1998, that is, the period before the truncation point was ignored in the analysis. Cows younger than 20 (142 cows) or older than 48 months (352 cows) at first calving, and cows with missing date of first calving (2696 cows), were excluded. In total, lifetime records of 42 120 cows from 2401 herds were included in the data set. Out of them, 10% (4212) of the second-crop daughters of bulls with >50 progeny were randomly selected from bigger herds (>10 cows) to create a validation data set. The rest (90%, i.e., 37 908) formed a training set to estimate sire breeding values. Actual survival curves of the cows in the validation set were compared with these estimated breeding values.

With the model constraint that the genetic effect is time independent – that is, the sire effect does not change during the lifetime – and our focus on the ability to avoid early culling, only the first five lactations were taken into account: records of cows with more than five lactations were censored on the day of their sixth calving, whereas those that were still alive at the end of the study and had less than six calvings were censored on 31 December 2008. For lactations longer than 800 days, the cow lifetime was considered as censored on the 800th day after calving of that lactation: these long lactations might have been related to abortions or poor recording of culling date. In case a cow was sold to another herd, her record was considered as censored on the day of last milk recording in the initial herd because she may have been treated differently in her new herd. Whenever a reliably recorded culling date existed, it was used as a terminal date. For the cases when it was missing and the cow was recorded as dead, the last known day of milk recording or dry day was considered as her culling date. Because the number of animals with a calving in 1998 was small, only one calving year class was created for those with calvings in 1998 and 1999.

Altogether, 20.4% of the cows had their first calving before 1 January 1998 and their records were truncated in

True and functional longevity in small herds

our analysis. This means that only calvings occurring after 1 January were included and the date of first calving was kept only as starting point of length of productive life. Out of the 20 963 cows with censored records, 38.2% were censored because they reached their 6th calving, 48.2% because they were still alive at the end of the study period and the rest (13.6%) for other reasons such as lactations longer than 800 days, herd change or the herd was no longer in milk recording system. Out of the 21 157 disposed cows, 72% had their culling date recorded. Small herd size is an important feature of the data set, although a slight increase in herd size was apparent over the years, going from 6.7 in 1999 to 8.7 Brown cows per herd in 2008.

Cows with records were progeny of 590 sires and 612 maternal grand sires. Some bulls were present as both sire and maternal grand sire of recorded cows. The pedigree was traced back for bulls only. At most, five generations of male ancestors were built and those that did not contribute to the relationships between cows with records were discarded. Finally, the complete pedigree file consisted of 886 bulls. For the validation data set, progeny of 63 bulls were included.

Models

As in some previous studies (Ducrocq, 2005; Terawaki *et al.*, 2006), the hazard function ($\lambda(t)$) at time t was modelled with a piecewise Weibull baseline hazard function of general form $\lambda_{0,sp}(t) = \lambda\rho(\lambda\tau)^{\rho-1}$ with scale parameter λ and shape parameter ρ . Different baselines (i.e. different scale and shape parameters) were defined for each combination of lactation c (1 to 5), stage of lactation p (1 to 5), leading to 25 different baseline hazard functions. Changes of hazard function were assumed to occur at $\tau = 0, 60, 270, 380$ and dry day of each consecutive lactation, where τ denotes the days since the last calving. The τ time scale is needed here because the values of t at the second and later calvings differ between cows. Times of change in the lactation stage were chosen according to the variation of the raw estimate of the hazard derived from the Kaplan–Meier estimate of the survivor function (Kaplan and Meier, 1958) within lactations as in a study by Ducrocq (2005) and Terawaki *et al.* (2006).

Genetic and nongenetic effects on length of productive life were estimated with two proportional hazard models. Model 1 estimated breeding values for true longevity, whereas in model 2 the effect of milk yield was included to correct for low milk production (i.e. the main source for voluntary culling), hence revealing functional longevity. Differences in culling policies for increasing and decreasing herds were explained with a fixed effect of change in herd size ($d_i(t')$) with i (1 to 6) classes and changes occurring at $t' = 1$ January of each year. Classes of change in herd size were defined according to the change in maximum number of recorded cows during the first three milk recordings of each year. Class $i=1$ defined a decrease in herd size by $>30\%$, $i=2$ a decrease from 10% to 30%, $i=3$ stable herd size (change from -10% to 10%), $i=4$ an increase from 10% to 30%, $i=5$ an increase by $>30\%$ and $i=6$ 'unclassified' herds with fewer than five cows in a year.

The fixed effect of region within year of production ($y_{jk}(t')$) with j (1, 2, 3) for three different regions defined for Brown cattle breed by productive year k (1999 to 2008) and changes occurring at $t' = 1$ January of each year, accounted for systematic differences in culling policies due to various environmental conditions for dairy cow breeding. Region 1 (Supplementary Figure S1) represented the subpannonial Slovenia with some Prealpine Hills; region 2 represented the Prealpine Hills with Dinaric Karst of inner Slovenia; and region 3 represented the sub-Mediterranean Slovenia with also a small portion of other previously mentioned landscape types. The environment conditions for production of high quality fodder are the least favourable in region 3. As a consequence, production of replacement heifers is more costly and animals with good morphological aptitudes (better legs, udder) are looked for. The fixed effect of year of production by season interaction ($y_{skl}(t')$) with k (1999 to 2008) years and l (1, 2, 3, 4) seasons accounted for the differences in culling policies within different year-seasons. Changes for the four seasons occurred at $t' = 1$ January, 1 April, 1 July and 1 October of each year.

The fixed effect of milk yield ($m_n(g)$) within lactation number (1, 2+) and stage of lactation (1 to 5), on which farmers base their voluntary culling decision for low productivity, was similar to the definition of Beaudeau *et al.* (1995). Peak lactation yield was estimated from the first two milk recordings within 120 days after calving. Normal distribution was assumed for peak yield. Mean, standard deviation and deciles of milk yield were calculated within a year of calving, different herd size groups, and for the first and later lactations separately. As the number of records within herds was small, the deviation from the mean milk yield was done within different herd size groups rather than at the herd level, which is the general practice in other studies. The problem of small herds is the low number of cows available to form a comparison. For that reason, the within-herd rank for production, which is usually used in large herds to assess whether a cow is at higher risk of being culled, is no longer valid. Consider, for example, a herd with five cows with respective peak yields of 30, 29, 28, 20 and 20 kg. The within-herd rank will consider the third and fourth cows as 'relatively close', whereas the use of deviation within different herd size groups will better identify the third cow as a good cow (unlikely to be culled for low production) and the last two as bad. Therefore, a population partition according to the herd group size on production seems more appropriate to model the effect of milk yield on risk of culling in small herds than the standard within-herd classification. Herd size groups were formed differently for cows in first and later lactations. The four classes for primiparous cows were: 1 to 3, 4 to 6, 7 to 9 and >9 cows in first lactation in the herd, whereas the four classes for multiparous cows were: 1 to 5, 6 to 10, 11 to 15 and >15 cows in later lactations in the herd. According to peak yield, cows were grouped in different deciles ($n = 1$ – best milk producers to 10 – worst milk producers) with changes occurring on the milk test recording day (ζ) of the maximum milk yield, after each calving.

Jenko, Ducrocq and Kovač

All primiparous cows were considered as unclassified ($n = 0$) until the date of first lactation peak yield. Altogether, 11 classes were created. The random effect part included a log-gamma (with shape and scale parameters both equal to γ in order to force its mean to be 1) distributed herd-year effect ($hy_o(t')$) with o classes ($o = 1$ to 18 684) and changes occurring at $t' = 1$ January of each year, and a multinormally distributed additive genetic effect $s_u + 0.5 mgs_v$ with *sire u* ($u = 1$ to 590) and maternal grand *sire v* ($v = 1$ to 612). Note that the maternal grand sire effect equals half the sire effect.

In summary, the two models used can be written as

$$\lambda(t) = \lambda_{0,cp}(T) \exp \left\{ d_i(t') + ry_{jk}(t') + ys_{kl}(t'') + hy_o(t') + s_u + 0.5 mgs_v \right\} \quad (1)$$

$$\lambda(t) = \lambda_{0,cp}(T) \exp \left\{ d_i(t') + ry_{jk}(t') + ys_{kl}(t'') + m_n(\zeta) + hy_o(t') + s_u + 0.5 mgs_v \right\} \quad (2)$$

Heritability (h^2) was calculated from the sire variance (σ_s^2), and the variance of the log-gamma herd-year effect, which is equal to the trigamma function $\psi^{(1)}(\gamma)$ of the γ parameter. The trigamma function is the second derivative of the log-gamma function (Abramowitz and Stegun, 1964):

$$h^2 = \frac{4 \times \sigma_s^2}{(5/4 \times \sigma_s^2 + \psi^{(1)}(\gamma) + 1)} \quad (3)$$

This formula was derived from the sire–maternal grand sire equivalent heritability equation by Mészáros *et al.* (2010) and is known as the effective heritability, as the amount of censoring in the data is not taken into account (see Yazdi *et al.*, 2002, for details).

The estimated breeding values (\hat{a}) were averaged by year of birth to estimate genetic trend. They were standardised (EBV), dividing them by the estimated sire genetic standard deviation (σ_s). Higher genetic values of \hat{a}_t are associated with a higher risk of culling. In addition, they were multiplied by -1 to be easier to interpret: a positive EBV is related to a better longevity:

$$EBV = -\hat{a}/\sigma_s \quad (4)$$

For the estimation of reliability (R), the following equation for a sire model on the basis of the number of uncensored daughters of a sire (n) and the effective heritability (h^2) was applied (Yazdi *et al.*, 1999):

$$R = n/(n + (4 - h^2)/h^2) \quad (5)$$

The analyses were performed with the survival kit package, version 6 (Mészáros *et al.*, 2013). The survival kit enables inclusion of time-dependent and random effects

with strata in Weibull proportional hazard models. The gamma parameter of the herd-year effect distribution was estimated jointly with the other effects, after exact algebraic integration of the log-gamma herd-year random effect (Ducrocq and Casella, 1996). The sire variance was estimated as the mode of its approximate marginal posterior density obtained after Laplacian integration of the other parameters (Ducrocq and Casella, 1996).

Results

Median length of productive life for cows in the training data set was 1192 days (Supplementary Table S1). Half of the uncensored cows were in production for <1035 days, whereas half of the censored cows were in the herd for <1501 days. Median length of productive life for cows in the validation data set was 1131 days (1020 and 1346 days for uncensored and censored records, respectively). The empirical hazard function derived from the Kaplan–Meier estimate (Figure 1) shows that after a slight rise in the first 60 days, the hazard function was relatively stable until about 270 days for the first lactation, whereas it clearly increased during this period in the next four lactations. Later, a more rapid increase of hazard rate for all lactations was observed up to 380 days of lactation. Because the number of animals with lactations longer than 380 days was small, estimates oscillated with larger amplitude, whereas the increasing trend of hazard rate was still evident. In general, the hazard was lower in the first two lactations. However, it was similar in the first few days for all lactations considered.

Graphical test of proportional hazard assumptions for the first three lactations (Supplementary Figure S2) showed that the lines in graph of $(\ln(-\ln S_{0,s}(t))$ against $\ln(t)$ were nearly parallel throughout the lactation period and a unique Weibull baseline could be used. When comparing the curve slopes between lactation stages, a relatively different slope was recognised, especially in the first three lactation stages and also some crossings between curves were evident. Thus, it was decided not to use a common baseline across lactations and lactation stages.

Fixed effects of the model

The initial effects included in the proportional hazard model were the effects of class of change in herd size, region by year of production, year of production by season, class of peak yield, age at first calving and the interaction between year of production and peak yield class. This last interaction corrects for the phenotypic trends in milk production over the years. When the effects were tested using sequential likelihood ratio tests, the latter two effects were found to be non-significant (Supplementary Table S2). All the other effects (change in herd size, region by year of production, year of production by season, milk yield class) were highly significant and were kept in the final proportional hazard model 2, whereas in model 1 peak yield class effect was excluded to estimate true longevity breeding values.

True and functional longevity in small herds

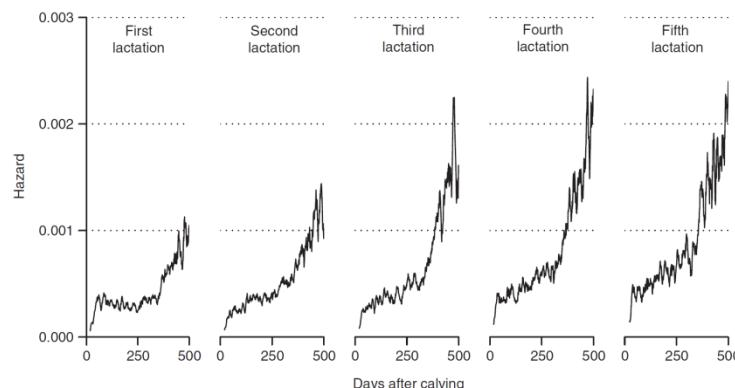


Figure 1 Empirical hazard function derived from the Kaplan–Meier estimator of survival function for the first five lactations.

The Weibull shape parameter ρ describes the decreasing ($\rho < 1$) or increasing ($\rho > 1$) shape of the baseline hazard function. Estimates of Weibull shape parameters during the first stage of all five lactations, was between 1.68 and 1.93 and in the second stage it was between 1.26 and 1.67. In the third and fourth lactation stage it was similar, ranging from 2.72 to 3.51. Cows were at a much higher risk of being culled at the end of lactation than at the beginning. Only lactations resulting in a later calving are allowed to enter the fifth (the last) stage of lactation (from day when dried to the day of next calving). As a consequence, no culling could occur and the risk of being culled was equal to 0 during this period.

Changes in herd size between consecutive years modified the relative risk of cow culling. Cows in herds decreasing in size by $>30\%$ or between 10% and 30% had a 1.4 and 1.1 higher relative risk of being culled, compared with cows in stable herds. Cows in herds where an increase in size occurred had a relative risk of being culled between 0.8 and 0.9 compared with stable herd size. Relative risk of cows being culled in small herds (unspecified class) was similar to herds increasing in size. For the estimation of the region by year of production effect, three regions of origin were defined. The differences in relative risk of culling presented in Figure 2 show that, except for year 2002, differences were important between regions, and that this effect needed to be accounted for in the model.

Within different years of production, the highest risk of culling occurred in the fourth season (Figure 3). Compared with the first season of 1999, the relative risk of culling ranged from 1.32 to 2.04 for this last season. This cyclic pattern was changed between the last seasons of 2001 and 2003.

The effect of peak yield on the relative risk of culling is presented in Figure 4. Average milk production represented with class 5 was used as a reference for all stages within lactations. Results for stage 5 (dry period) in which cows cannot be culled (no risk) are not presented. If the cow production in the first stage of lactation was estimated to be

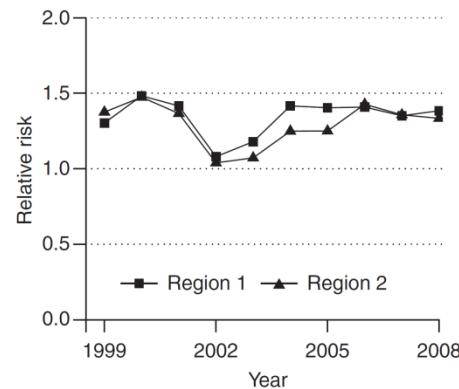


Figure 2 Relative risk of culling for regions 1 and 2 by year (1999 to 2008) compared with region 3 as a reference (relative risk = 1).

among the best 10% (class 1), then her relative risk of being culled was 0.2 for the first lactation and 0.8 for later lactations. This means that chances of being culled for a cow in class 1 were 0.2 (0.8) times the chances of being culled of a cow with an average milk production (class 5). On the other hand, if the cow production in the first stage of lactation was estimated to be among the worst 10% (class 10), then the relative risk (i.e. compared with an average cow) of a cow being culled was 3.2 in the first and 2.1 in later lactations. Relative risk of a cow being culled in the second stage was 0.7 for class 1, regardless of the lactation number, and 4.0 for primiparous and 2.1 for multiparous cows in class 10. For the third and fourth lactation stages, differences in culling risk between peak yield classes were smaller. Relative culling risk for primiparous Brown dairy cows in the third stage was 0.6 for class 1 and 1.7 for class 10, whereas for multiparous it was 0.9 for class 1 and 1.3 for class 10. For the fourth lactation stage, it was 1.0 for class 1 and 1.6 for class 10 for primiparous and 0.9 for class 1 and 1.1 for class 10 for multiparous cows.

Jenko, Ducrocq and Kovač

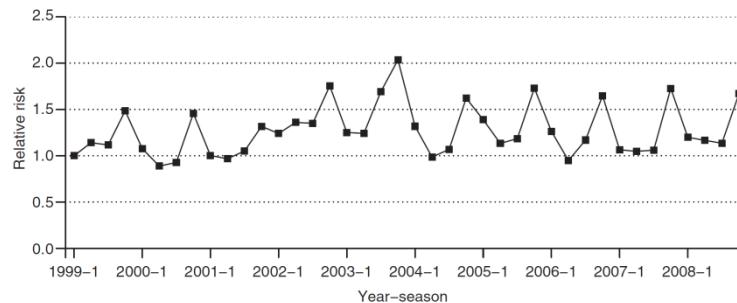


Figure 3 Relative risk of culling for different year-seasons compared with season 1 in year 1999 as a reference (relative risk = 1).

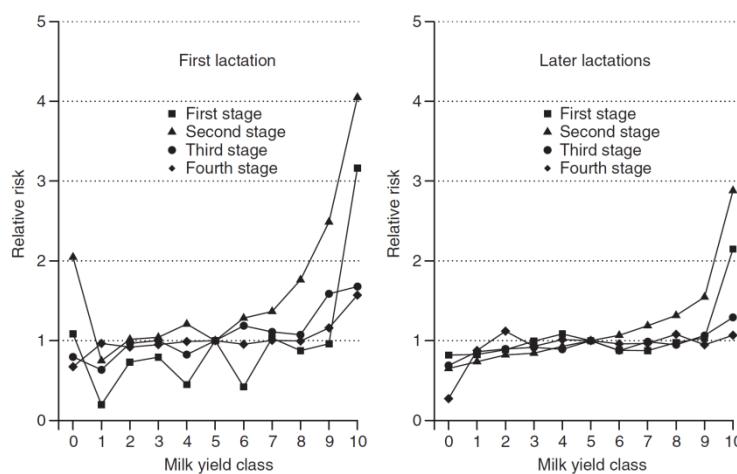


Figure 4 Estimates of relative risk of culling for 11 milk yield classes (0 – unclassified, 1 – best, 10 – worst) in the first (left) and later (right) lactations on the first four lactation stages with the average milk production class (class 5) as reference.

Estimation of genetic parameters and variance of random effects

Estimates of genetic parameters are presented in Table 1. The variance of the log-gamma herd-year random effect as well as the sire genetic variance and the heritability were higher in model 2, that is, the model for functional longevity: in particular, the variance of herd-year random effect was 42% higher. This shows that the correction for milk production reduces the within-herd year variance. The difference between sire genetic variances was much smaller (11%) reflecting the fact that part of the differences in milk production had a genetic origin. More evidence of smaller differences in sire genetic variance is shown in Figure 5 where the approximate posterior densities of the sire genetic variance are presented for both models. The shape of the posterior density is similar between the models, and as the difference in mean value of sire genetic variance is small the overlap is relatively large.

Rank correlations between sire breeding values obtained from models were high for all restrictions in reliability. They were 0.94, 0.96, 0.97, 0.96 and 0.93 for no restriction to reliability or a restriction to reliability of $\geq 20\%$, $\geq 40\%$, $\geq 60\%$ or $\geq 80\%$, respectively. The genetic trends on a

Table 1 Estimates of genetic and nongenetic random effect parameters for the estimation of true (model 1) and functional (model 2) longevity

Variables	Model 1	Model 2
γ	7.589	5.347
$\psi^{(1)}(\gamma)$	0.141	0.206
σ_s^2	0.028 ± 0.004	0.031 ± 0.005
H^2	0.094	0.099

γ = shape and scale parameters (assumed to be equal) and $\psi^{(1)}(\gamma)$ = variance of the log-gamma herd-year random effect; σ_s^2 = sire genetic variance; H^2 = heritability.

standardised scale (expressed as genetic standard deviations) are presented in Figure 6. They were almost flat for model 1 (0.003) and slightly negative for model 2 (-0.011). However, they were not found significantly different from 0. In general, differences in mean breeding values between models were increasing over the years.

The predictive ability of the two models was assessed on the validation data set after 183, 365, 547, 730, 1095 and 1460 days after first calving (Table 2). On average, the

True and functional longevity in small herds

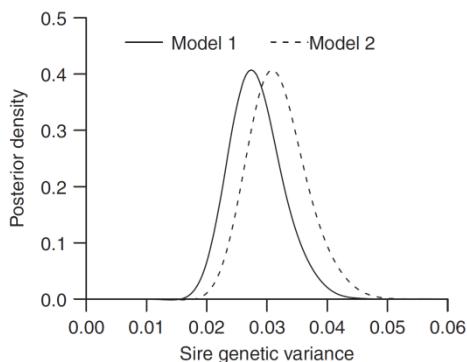


Figure 5 Approximate posterior densities of the sire genetic variance for the estimation of true (model 1) and functional (model 2) longevity.

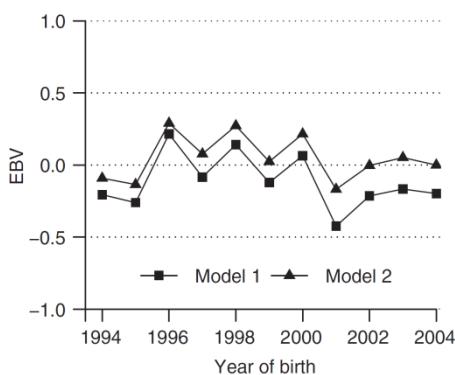


Figure 6 Estimates of genetic trends using true (model 1) and functional (model 2) longevity for sires born between years 1994 and 2004.

Table 2 Correlation coefficient between the sire estimated breeding values and the survival rate of new second crop daughters after different number of days since the first calving for true (model 1) and functional (model 2) longevity

Days after first calving	Model 1	Model 2
183	0.47	0.50
365	0.41	0.46
547	0.38	0.43
730	0.34	0.39
1095	0.37	0.41
1460	0.36	0.38
Average	0.39	0.43

correlation between the predicted breeding values obtained from the training data set and the survival of the cows from the validation data set was 0.39 for model 1 and 0.43 for model 2. The highest correlations 0.47 for model 1 and 0.50 for model 2 were obtained for the early survival (183 days after the first calving). Later on, they dropped and ranged between 0.34 and 0.41 for model 1 and between 0.38 and

0.46 for model 2. The raw survivor curve for second-crop daughters from the validation data set (Supplementary Figure S3) showed the range between the extreme groups is 0.15 in terms of survival, five years after first calving. Clearly, the differences were the smallest between the top two quartiles for both true and functional longevity.

Discussion

A piecewise Weibull hazard model was applied with time-dependent covariates (class of change in herd size, region by year of production, year of production by season and milk yield class) to cope with changes in hazard rate within and between lactations, and to correct breeding values for systematic environmental factors. It was shown as, in the study by Roxström *et al.* (2003), that different slopes exist within lactation segments and that the stratification on stages of lactation should be included. Cut-off points for setting up the baseline within lactation were chosen on the basis of the nonparametric estimates of the within lactation hazards, as in other studies (Ducrocq, 2005; Terawaki *et al.*, 2006). The first two cut-off points (0 and 60 days after calving) were defined on the same day as the earliest in the model with the best fit described by Terawaki *et al.* (2006), whereas the last three (270 and 380 days after calving and drying-off day) matched with those specified by Ducrocq (2005). Finally, different baselines were defined for each combination of parity and lactation stage.

Comparing culling risks between lactations, the lowest hazard was found in the first lactation, as in French Holstein (Ducrocq, 2005) and Japanese Holstein cattle (Terawaki *et al.*, 2006; Terawaki and Ducrocq, 2009) using a similar approach. The differences between shape parameters were small for the third and fourth stages, and the two stages could have been merged; however, as the number of records was large enough, five different lactation stages were retained. The lowest Weibull parameters ρ were found in the first and the second stage of lactation, which is consistent with some other studies (Ducrocq, 2005; Terawaki *et al.*, 2006).

Similar to some studies on dual purpose cattle breed (e.g. Ducrocq, 1994), our analysis also revealed that age at first calving did not have a significant effect on culling. Many other studies, mainly in the Holstein breed (e.g. Dürr *et al.*, 1999) and some other breeds, for example, Pintzgau (Mészáros *et al.*, 2008), Braunvieh and Simmental (Vukasinovic *et al.*, 2001), found that the age at first calving had an impact on productive life. One explanation for these differences might be given by Bielfeldt *et al.* (2006), who found out that the target age at first calving significantly differed between herd management systems. Wathes *et al.* (2008) concluded from a review that the main factor when heifers conceive is the pre-pubertal growth rate, which is under both environmental and genetic effect.

Hazards of extreme changes in herd size are not in complete agreement with previous studies. Some authors (Ducrocq, 1994 and 2005; Mészáros *et al.*, 2008) reported an increase in culling rate for decreasing herd size between

Jenko, Ducrocq and Kovač

1.4 and 2, and on the other hand a decrease between 0.5 and 0.8 for expanding herds. These findings are in accordance with our results. In contrast, some others (Dürr *et al.*, 1999; Sewalem *et al.*, 2005) obtained higher culling risk for decreasing as well as increasing herd sizes, with a relatively low effect on changes in culling risk. The considerably lower risk of cows being culled in the 'unspecified class' for changes in herd size might be a result of a 'preferential treatment' of less-productive cows in small herds.

Seasonal changes of relative hazard revealed that the highest risk of culling was observed in the last quarter of each year and not at the end of a milk quota year (30 April). The reason for a change in hazard within a year could be justified with the feed shortage during the winter time. Change in culling policy between the last seasons of 2001 and 2003 can be explained with the planned introduction of the milk quota system (Vlada Republike Slovenije, 2004) and the lack of fodder because of drought in 2003, when there was only between 40% and 70% of the expected average yearly rainfall (Ceglar and Kajfež-Bogataj, 2008). The region by year of production effect revealed that the cows from region 3, where conditions for cattle breeding are tough, had a lower culling risk. However, the differences were small in years 2002 and 2003, showing that the expectations of the milk quota system implementation and the lack of fodder had different effects between regions. Breeders tried to increase their milk quotas by reducing culling, which as seen from the graph, was not an alternative in region 3 characterised by an already low culling rate, small herds and lower average milk production in standard lactation (Sadar *et al.*, 2010). If only increases in herd size occurred, this would already be accounted with the effect of change in herd size; however, a change in culling reasons also happened.

To limit possible confusion with estimation of milk yield from records in progress, the correction for voluntary culling on production was included, considering the peak yield from the first two milk recordings as an indicator of milk yield potential (Beaudeau *et al.*, 1995; Roxström and Strandberg, 2002). The other common approach would be the extrapolation from incomplete lactation records to a standard lactation milk yield (Dürr *et al.*, 1999; Ducrocq, 2005). When the dry date occurs before the 305th day of lactation or only a few milk yield records are known within lactation, inclusion of peak milk yield is believed to account better for voluntary culling. Because of small herd sizes, production levels were not compared within the herd, as is usual practice in most longevity studies. The number of milk yield classes was in the range of those defined by Beaudeau *et al.* (1995), Ducrocq (2005) and Chirinos *et al.* (2007) with 19, 10 and 8 categories, respectively. Smaller differences in risk of being culled in later stages of first and later lactations could be the result of disposal of very low-producing cows early in the first and second lactation stages and disposal of high-producing cows because of fertility problems and sterility in the last stages. As in all other studies, including a milk yield effect, the relative risk of being culled was higher for low- than for high-producing cows (e.g. Chirinos *et al.*, 2007).

Cows with an extremely low milk yield were mainly culled in the first lactation, which is in agreement with the studies by Vukasinovic *et al.* (2001), Roxström and Strandberg (2002) and Ducrocq (2005). These similarities with other studies show that creating milk yield classes as a function of herd size group and at a population level is not detrimental and can be applied in practice for the estimation of functional longevity in small herds.

Heritability values for length of productive life were slightly lower with model 1. This is in disagreement with the studies by Vollema and Groen (1996) and van der Linde *et al.* (2007), where a slight increase in heritability was noticed when the correction for milk yield was excluded. Rank correlation (0.94) between breeding values for the herd life obtained with the two models are considerably higher than the one reported by van der Linde *et al.* (2007) for the Dutch Holstein population (0.80), and even higher than the one reported by Vollema and Groen (1996) where it was about 0.90. Rank correlation for all bulls in the evaluation was lower because some sire breeding values had low reliability, whereas with the restriction to reliability >80%, the correlation was lower because too few bulls were considered. The variability of the nongenetic random herd-year effect was considerably different between the two models. With model 2, the variability of nongenetic random effect was higher (+42%) than with model 1. These results were unexpected and in disagreement with the study by Buenger *et al.* (2001), where a decrease of 53% was observed, and the study by van der Linde *et al.* (2007), where a slight reduction in herd-year variance was found (from 0.229 to 0.224). Correction for milk production reduced the variability between herd-year quite importantly, whereas the change in total variability was not as large.

The genetic trend for model 2 was slightly unfavourable. This is not surprising, given the negative genetic correlation between functional longevity and milk production traits for which selection has been intensively practised in the past years. However, when breeding values were not corrected for milk yield, the genetic trend was almost flat. The correlation between the estimated breeding values and the realised survival of the second-crop daughters were lower than the one obtained from the study by Holtmark *et al.* (2009). What most farmers are interested in is functional longevity, as a measure of the ability of the cow to delay involuntary culling: this information is approximated by making longevity independent from milk yield, which is the main underlying reason for voluntary culling. Hence, model 2 should be favoured when estimation of (functional) longevity breeding value is desired. Most countries, but not all, are taking advantage of survival analysis to analyse functional longevity.

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True and functional longevity in small herds

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Supplementary materials

For supplementary material referred to in this article, please visit <http://dx.doi.org/10.1017/S1751731113001055>

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Supplementary material

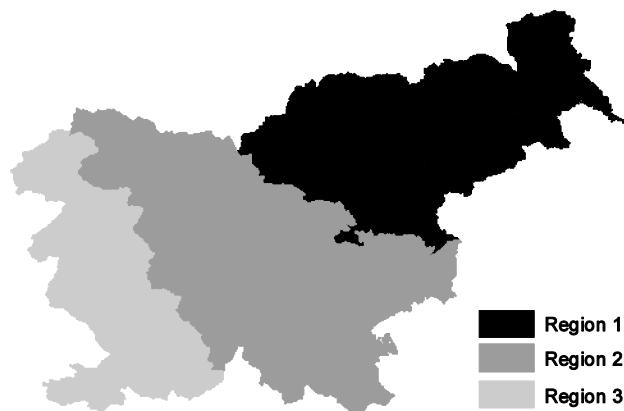


Figure S1 Regions of Slovenia as used for the breeding values prediction.

Table S1 Descriptive statistics for censored and uncensored cows of training¹ and validation data sets²

	Median		Mean		s.d.	
	Training	Validation	Training	Validation	Training	Validation
Length of productive life	1192	1131	1197	1161	682	670
Uncensored	1035	1020	1058	1046	613	612
Censored	1501	1346	1335	1289	718	708
Number of lactations	3	3	2.7	2.9	1.4	1.5
Uncensored	2	2	2.4	2.6	1.3	1.3
Censored	3	3	2.9	3.2	1.5	1.5
Maximum milk yield in first lactation ³	19.7	20.4	20.0	20.7	4.3	4.2
Uncensored	19.6	20.2	19.8	20.5	4.3	4.2
Censored	19.9	20.7	20.2	20.9	4.3	4.2
Maximum milk yield in 2 nd to 5 th lactation ³	24.2	25.5	24.6	25.9	5.8	5.8
Uncensored	23.8	25.3	24.1	25.5	5.7	5.8
Censored	24.4	25.6	24.8	26.0	5.8	5.8

¹Total number of records in the training data set: 37 908; number of uncensored records: 18 936; number of censored records: 18 972.

²Total number of records in the validation data set: 4212; number of uncensored records: 2221; number of censored records: 1991.

³Maximum of the first two recordings.

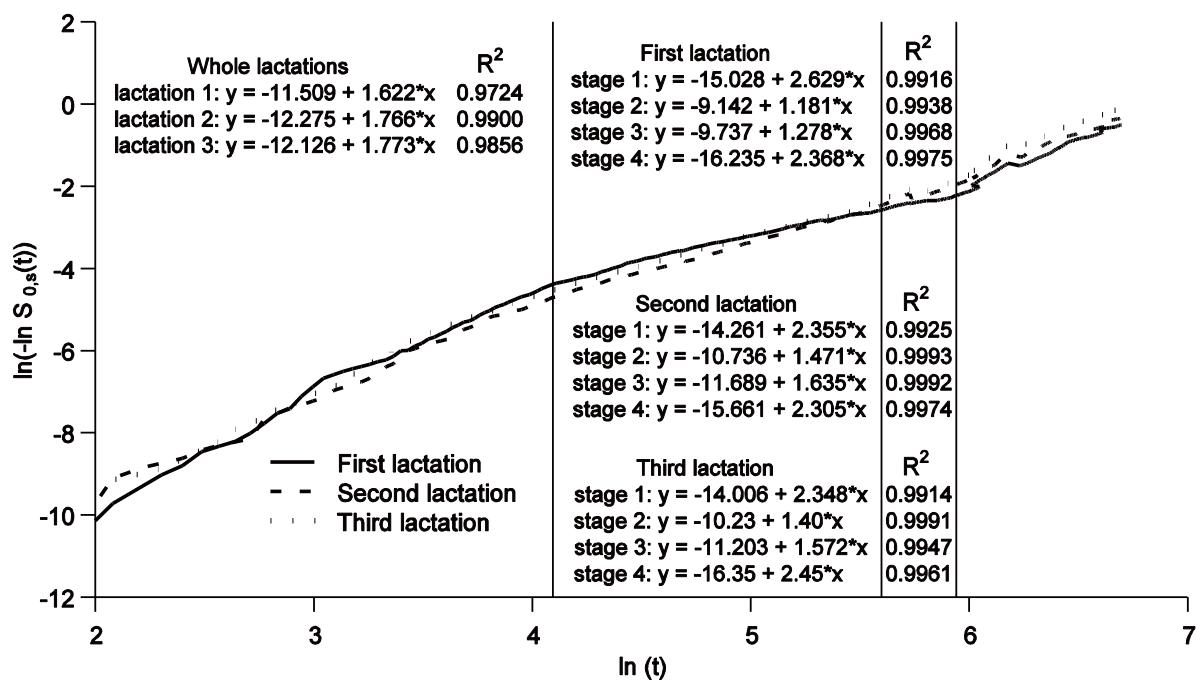


Figure S2 Survivor function ($\ln(-\ln S_{0,s}(t))$) versus logarithm of days ($\ln(t)$) from previous calving from cox analysis for first three lactations with vertical lines showing the boundaries for the stage of lactation.

Table S2 Test statistics for the likelihood ratio test ($-2\Delta LL$) for initial fixed environmental effects added sequentially in the model, degrees of freedom (d.f.) and statistically significance (P)

Covariate	d.f.	$-2\Delta LL$	P
D	5	226.23	<0.001
ry	20	173.2	<0.001
ys	39	709.0	<0.001
M	80	1401.5	<0.001
Afc	6	5.3	0.510
Ym	90	103.6	0.156

d = change in herd size; ry = region by year of production; ys = year of production by season; m = milk yield within lactation; afc = age at first calving; ym = within year and lactation milk yield.

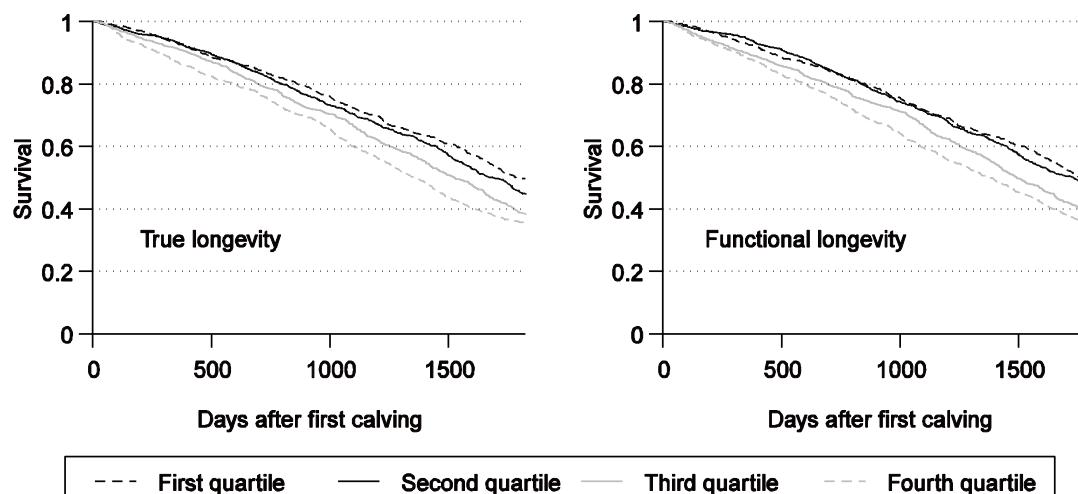


Figure S3 Raw survivor curves of the second crop daughters from the validation data set, grouped by estimated breeding values for length of productive life of their sire grouped into quartiles (highest breeding values – first quartile, lowest breeding values – fourth quartile).

2.2 GENETSKO VREDNOTENJE PRAVE IN FUNKCIONALNE DOLGOŽIVOSTI SLOVENSKE ČRNO-BELE PASME GOVEDI

Janez Jenko¹, Tomaž Perpar¹

¹Kmetijski inštitut Slovenije, Hacquetova 17, 1000 Ljubljana, Slovenija

Neobjavljeno delo

IZVLEČEK

Za oceno prave in funkcionalne dolgoživosti smo na populaciji 89808 krav molznic slovenske črno-bele pasme govedi, ki so imele eno izmed prvih petih telitev v času od 1. 1. 1998 do 31. 12. 2008, opravili obračun genetskih parametrov. Tveganje izločitve krav se je manjšalo z večjo prirejo mleka in povečevalo s padanjem količine mleka. Ocenitveni heritabilitet za pravo in funkcionalno dolgoživost sta znašali 0,084 oziroma 0,085. Korelacija med napovedanimi plemenskimi vrednostmi za obe lastnosti je bila 0,87. Ker je iz obračuna funkcionalne dolgoživosti izločen vpliv mlečnosti, je le-ta v primerjavi s pravo dolgoživostjo bolj primerna za uporabo v praksi, saj so napovedi plemenskih vrednosti za mlečnost v slovenskem rejskem programu obračunane posebej.

UVOD

Podaljševanje dobe prireje krav molznic ima pomemben vpliv na ekonomiko reje. Stroški prirejenega kilograma mleka krav, ki so bile izločene v prvi laktaciji, so za 34 % višji, glede na mleko krav, ki so bile izločene v drugi laktaciji. Razlike se z vsako naslednjo laktacijo manjšajo in so nižje od 2 % za krave v šesti in naslednjih laktacijah (Jenko in sod., 2007). Selekcija na dolgoživost krav molznic poleg izboljšanja učinkovitosti sistema reje zmanjšuje tudi izpuste toplogrednih plinov in s tem prispeva k trajnostni usmeritvi reje domačih živali (Wall in sod., 2009).

Za namen genetskega vrednotenja dolgoživosti se uporablja različni pristopi merjenja in metode analize dolgoživosti. Preživetje do določene starosti, število telitev, dolžina življenja, dolžina dobe prireje in življenska prireja mleka so različni pristopi merjenja

dolgoživosti krav molznic (Vollema in Groen, 1996). Napovedovanje plemenskih vrednosti za dolgoživost krav molznic z metodo analize preživetja je v uporabi v večini držav vključenih v mednarodno izmenjavo podatkov za namen primerjave med plemenskimi biki. Metoda linearnih modelov je uporabljena v manjšem številu držav v obliki enolastnostnega ali večlastnostnega modela ali v obliki ponovljivostnega modela ali naključne regresije (Forabosco in sod., 2009). Prednost analize preživetja je v optimalni uporabi krnjениh podatkov krav, ki so še vedno žive v času opravljanja analize. Prav tako je omogočena vključitev časovno odvisnih spremenljivk, s katerimi v modelu za napoved plemenskih vrednosti odpravimo spremembe v vzrokih za izločitev živali (Yazdi in sod., 2002).

Kadar govorimo o pravi dolgoživosti, model za napoved plemenskih vrednosti ne vključuje vpliva količine mleka, medtem ko je ta vključen v modelu za oceno funkcionalne dolgoživosti (Ducrocq, 1987). Z vključitvijo vpliva količine mleka korigiramo genetski model za napoved plemenskih vrednosti glede na prostovoljne in neprostovoljne izločitve živali. Izločitev zaradi manjše prireje je posledica prostovoljne odločitve rejca in ne bolezni ali poškodb, zaradi katerih živali ne bi bilo mogoče obdržati v rej.

Prvi so napoved plemenskih vrednosti za pravo dolgoživost pri črno-beli pasmi v Sloveniji podali Potočnik in sod. (2011). Prehod s prave na funkcionalno dolgoživost zahteva predhodno oceno genetskih komponent modela za napoved plemenskih vrednosti. V raziskavi smo na populaciji slovenske črno-bele pasme govedi razvili model za napoved plemenskih vrednosti za funkcionalno dolgoživost in napovedane plemenske vrednosti primerjali z napovedanimi vrednostmi za pravo dolgoživost.

MATERIAL IN METODE DELA

Podatki

Podatke o dolgoživosti smo pridobili iz centralne podatkovne zbirke Govedo, ki se hrani in vzdržuje na Kmetijskem inštitutu Slovenije. V analizo smo zajeli krave črno-bele pasme, ki so imele eno izmed prvih petih telitev v času od 1. 1. 1998 do 31. 12. 2008; zanje je obstajal tudi zapis o prvi telitvi in so bile takrat stare med 20 in 44 meseci. Ob predpostavki, da se genetski vpliv bika skozi življenje ne spreminja in ker največje prihranke dosežemo s preprečevanjem izločitev v prvih laktacijah, smo podatke krav po zaključeni peti laktaciji krmili. Prav tako smo krmili podatke krav, ki so imele laktacije daljše od 800 dni ali so bile preseljene v drugo čredo. Skupno smo v analizo vključili 89808 molznic, pri katerih smo meritve pri 39509 molznicah krmili. Za namen genetskega vrednotenja smo oblikovali poreklo, kamor smo vključili očete in materine očete. Poreklo smo dopolnili z moškimi predniki očetov in materinih očetov za predhodne tri generacije. Skupno je bilo v poreklo vključenih 1682 bikov.

Statistična analiza

Dolgoživost smo definirali kot število dni od prve telitve do izločitve oziroma krenjenja. Znotraj metodologije analize preživetja smo uporabili Weibullova model sorazmernih ogroženosti po delih s splošno obliko:

$$\lambda_{0,lp}(t_i) = \lambda\rho(\lambda\tau)^{\rho-1}$$

kjer pomeni:

$\lambda_{0,lp}(t)$ – izhodiščna Weibullova funkcija sorazmernih ogroženosti po delih za laktacije ($l = 1-5$) in stadije laktacij ($p = 1-5$)

ρ – parameter oblike Weibullove porazdelitve

λ – parameter lokacije

t – čas od prve telitve

τ – čas od zadnje telitve

Za napoved plemenskih vrednosti prave dolgoživosti smo uporabili naslednji model:

$$\lambda(t) = \lambda_{0,lp}(\tau) \exp \left\{ d_i(t') + ry_{jk}(t') + ys_{kl}(t'') + hy_o(t') + s_u + 0,5 mgs_v \right\}$$

kjer pomeni:

$\lambda(t)$ – funkcija ogroženosti

$\lambda_{0,lp}(\tau)$ – osnovna Weibullova funkcija sorazmernih ogroženosti po delih za laktacije ($c = 1-5$) in stadije laktacij ($p = 1-5$)

t' – prvi januar vsakega leta

t'' – prvi januar, april, julij in oktober vsakega leta

d_i – časovno odvisen sistematski vpliv spremembe velikosti črede ($i = 1-6$)

ry_{jk} – časovno odvisen sistematski vpliv interakcija med območjem ($j = 1-5$) in letom ($k = 1998-2008$)

ys_{kl} – časovno odvisen sistematski vpliv interakcije med letom in sezono ($l = 1-4$)

hy_o – časovno odvisen naključni vpliv interakcije med skupnim okoljem v čredi in letom ($o = 1-17873$), ki je porazdeljen po logaritemski gama porazdelitvi s parametrom (γ in γ)

s_u – naključni genetski vpliv očeta ($u = 1-1031$)

$0,5 mgs_v$ – naključni genetski vpliv materinega očeta ($v = 1-1220$), ki je enak polovici učinka očeta

Model za napoved plemenskih vrednosti prave dolgoživosti poleg zgoraj omenjenih vplivov vsebuje še časovno odvisen sistematski vpliv količine mleka: m_n ($n = 1-11$). Krave so uvrščene v enega od 11 razredov glede na maksimalno količino mleka v prvih dveh kontrolah posamezne laktacije. Razvrstitev se opravi znotraj vsake laktacije v času ς - število dni od telitve do kontrole z najvišjo mlečnostjo izmed prvih dveh kontrol prireje mleka vsake laktacije:

$$\lambda(t) = \lambda_{0,lp}(\tau) \exp \left\{ d_i(t') + ry_{jk}(t') + ys_{kl}(t'') + m_n(\varsigma) + hy_o(t') + s_u + 0,5 mgs_v \right\}$$

Heritabiliteto (h^2) smo ocenili na podlagi variance naključnega vpliva očeta (σ_s^2) in variance naključnega vpliva interakcije skupnega okolja v čredi in leta, ki je enaka trigama funkciji ($\Psi^{(1)}(\gamma)$) parametra (Mészáros in sod., 2010):

$$h^2 = \frac{4\sigma_s^2}{\left(\frac{5}{4}\sigma_s^2 + \psi^{(1)}(\gamma) + 1\right)}$$

Točnost napovedi plemenskih vrednosti (R) je določena s številom izločenih živali posameznega bika, katerih podatki so nekrnjeni (n) in heritabiliteto (h^2) (Yazdi in sod., 2002):

$$R = \frac{n}{\left(n + \frac{4 - h^2}{h^2}\right)}$$

Genetsko vrednotenje dolžine dobe prireje smo opravili v statističnem paketu Survival Kit V6 (Mészáros in sod., 2010).

REZULTATI IN RAZPRAVA

Osnovna statistika

Polovica krav je proizvajala mleko več kot 987 dni (Preglednica 1). Čas, ko je bilo število krav prepolovljeno, je bil sicer daljši pri kravah s končnimi podatki, vendar je bila povprečna dolžina dobe prireje daljša pri kravah s krnjениmi podatki. To kaže na vpliv krvitve meritev pri kravah, ki so imele več kot 5 telitev. V analiziranem obdobju so imele krave v povprečju 2,6 telitve. Povprečna maksimalna prireja mleka v prvih dveh kontrolah prve laktacije je bila za 6,4 kg manjša od povprečne prireje mleka krav v prvih dveh kontrolah poznejših laktacij.

Preglednica 1: Opisna statistika dolgoživosti in priteje mleka krav glede to, ali so bili podatki krnjeni ali ne

	Mediana	Povprečje	SD*
Dolžina dobe priteje (dni)	987	1045	643
Nekrnjeni	1006	1028	588
Krnjeni	949	1068	706
Število laktacij	2	2,6	1,4
Nekrnjeni	2	2,5	1,3
Krnjeni	2	2,6	1,5
Največja priteja mleka v prvih dveh kontrolah 1. laktacije (kg)	25,4	25,5	5,4
Nekrnjeni	25,3	25,3	5,5
Krnjeni	25,5	25,7	5,3
Največja priteja mleka v prvih dveh kontrolah med 2. in 5. laktacijo (kg)	31,8	31,9	7,6
Nekrnjeni	31,3	31,4	7,5
Krnjeni	32,2	32,3	7,6

*SD - standardni odklon

Vpliv pritejene količine mleka na tveganje za izločitev

Pri kravah z majhno pritejo mleka je verjetnost izločitve večja kot pri kravah s povprečno pritejo mleka (Preglednica 2). Krave z majhno pritejo mleka imajo največje tveganje izločitve v prvem in drugem stadiju laktacije. Tveganje za izločitev je tako pri takih kravah v prvi laktaciji večje za 12,47-krat glede na krave s povprečno pritejo mleka v prvi laktaciji. Vendar manjša priteja mleka v tem obdobju ni nujno posledica slabšega genetskega potenciala za pritejo mleka, ampak je lahko tudi rezultat presnovnih motenj. V poznejših stadijih prve laktacije tveganje pada in je v zadnjem stadiju 1,39-krat večje od tveganja izločitve krav s povprečno pritejo mleka. V drugi in naslednjih laktacijah je

tveganje izločitve glede na prvo laktacijo nižje. Pri kravah z veliko priejo mleka je tveganje za izločitev manjše, kot pri kravah s povprečno priejo mleka. Razen pri prvem stadiju druge in naslednjih laktacij, ko je tveganje izločitve manjše za 0,95-krat glede na krave s povprečno priejo mleka, se tveganje izločitve z vsakim nadaljnjam stadijem povečuje. Razlog za to gre iskati v povečevanju težav s plodnostjo, kar lahko vodi do izločitve krav z veliko priejo mleka.

Preglednica 2: Ocena relativnega tveganja za izločitev krav glede na priejeno količino mleka za krave z največjo (1) in najmanjšo (10) priejo mleka, glede na krave s povprečno priejo mleka, kjer je tveganje za izločitev enako 1

Stadij laktacije (dni laktacije)*	Razred prieje mleka**	Laktacija	
		1	2-5
		Tveganje za izločitev	
1 (1 – 60)	1	0,50	0,95
	10	12,47	2,62
2 (61 – 270)	1	0,66	0,67
	10	4,93	3,90
3 (271 – 380)	1	0,84	0,73
	10	2,18	1,57
4 (380 – dan presušitve)	1	0,83	0,74
	10	1,39	1,26

*Predpostavljeno je, da so presušene samo krave, ki imajo tudi naslednjo telitev in te vstopijo v zadnji stadij laktacije, kjer ocena relativnega tveganja ne obstaja.

**V razrede od 1 do 10 so krave razvrščene glede na količino priejenega mleka, medtem ko so v dodatnem razredu krave, ki nimajo podatka o mlečnosti.

Ocena komponent variance in heritabilitete

Varianca naključnega vpliva interakcije med skupnim okoljem v čredi in letom je v modelu napovedi plemenskih vrednosti za funkcionalno dolgoživost večja za 74 % v primerjavi z modelom prave dolgoživosti (Preglednica 3). Ta porast ni pričakovani, saj so raziskovalci v podobni primerjavi ugotovili majhne spremembe v variabilnosti naključnega vpliva okolja (Van der Linde in sod., 2007). Pri modelu za napoved funkcionalne

dolgoživosti je nekoliko večja tudi genetska varianca očetov, vendar pa je tu razlika precej manjša (12 %). Nasprotno sta si oceni heritabilitet med modeloma podobni in se nahajata znotraj območja ocenjenih heritabilitet za dolgoživost (0,05–0,189) v državah vključenih v mednarodno primerjavo (Forabosco in sod., 2009).

Preglednica 3: Ocena komponent variance in heritabilitete za pravo in funkcionalno dolgoživost

	$\Psi^{(1)}(\gamma)^*$	σ_s^2**	h^2***
Prava dolgoživost	0,139	0,024	0,084
Funkcionalna dolgoživost	0,242	0,027	0,085

* $\Psi^{(1)}(\gamma)$ = varianca naključnega vpliva interakcije med skupnim okoljem v čredi in letom

** σ_s^2 = genetska varianca očetov

*** h^2 = heritabiliteta

Povprečna točnost napovedi plemenskih vrednosti je znašala 0,10. Za dosego točnosti nad 0,50 mora imeti bik vsaj 47 izločenih potomk, medtem ko je za točnost napovedi nad 0,75 potrebnih več kot 140 izločenih potomk s končnimi podatki. Koeficient korelacije med rangi napovedanih plemenskih vrednosti za pravo in funkcionalno dolgoživost je 0,87. Van der Linde in sodelavci (2007), ki so opravili podobno primerjavo na populaciji črno-belega goveda na Nizozemskem, poročajo o nekoliko nižjem koeficientu korelacije (0,80) med funkcionalno in pravo dolgoživostjo. Ko smo izločili bike, katerih točnost napovedane plemenske vrednosti je bila manjša od 0,50, se je vrednost korelacijskega koeficiente povečala na 0,97.

ZAKLJUČKI

Tveganje izločitve se povečuje z manjšo prirejo mleka in se manjša z večanjem količine mleka. Heritabiliteta za funkcionalno dolgoživost znaša 0,085, kar nakazuje, da je selekcija možna, vendar visoka varianca vpliva skupnega okolja v čredi znotraj let kaže, da so največji napredki možni z izboljšanjem okolja. Kljub visokemu koeficientu korelacije med pravo in funkcionalno dolgoživostjo je slednja primernejša za napoved plemenskih vrednosti za lastnost dolgoživosti, saj je napoved plemenskih vrednosti za količino mleka obračunana že kot samostojna lastnost.

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2.3 PRIMERJAVA MED MODELOM OČETOV IN MATERINIH OČETOV Z MODELOM ŽIVALI PRI GENETSKEM VREDNOTENJU DOLGOŽIVOSTI V POPULACIJAH Z MAJHNIMI ČREDAMI PRI GOVEDU MLEČNIH PASEM

Comparison between sire-maternal grandsire and animal models for genetic evaluation of longevity in a dairy cattle population with small herds

Janez Jenko, Gregor Gorjanc, Milena Kovač, Vincent Ducrocq

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Izvleček:

Genetsko oceno dolgoživosti populacije slovenske rjave pasme govedi, za katero je značilna reja v majhnih čredah, smo opravili z uporabo analize preživetja. Znotraj analize preživetja smo uporabili model očetov in materinih očetov ter model živali. Primerjali smo napovedi plemenskih vrednosti na podlagi treh različnih genetskih modelov: (i) model očetov in materinih očetov za bike in aproksimativni model živali z uporabo ocen iz modela očetov in materinih očetov za krave, (ii) model živali in (iii) model živali z uporabo ocen komponent variance iz modela očetov in materinih očetov. Naključni vpliv okolja je bil v model vključen v obliki vpliva skupnega okolja v čredi ali v obliki interakcije med vplivom skupnega okolja v čredi in leta. Z uporabo različnih spodnjih mej, za velikost razreda črede in leta (med vsaj 1 in vsaj 10 krav v posameznem razredu), smo pripravili različne nize podatkov, na katerih smo analizirali spremembe v ocenah komponent variance in napovedih plemenskih vrednosti v modelu očetov in materinih očetov ter modelu živali. Varianca interakcije skupnega okolja v čredi in leta je bila manjša kot varianca vpliva skupnega okolja v čredi. Sprememba spodnjih mej za velikost vpliva interakcije skupnega okolja v čredi in leta, ni imela bistvenega vpliva na ocene aditivne genetske komponente variance v modelu očetov in materinih očetov. V modelu živali se je aditivna genetska varianca povečala v primeru, ko je bil vpliv okolja vključen v obliki interakcije skupnega okolja v čredi in leta, kar nakazuje na potencialno mešanje vpliva napovedane plemenske vrednosti živali in vpliva interakcije skupnega okolja v čredi in leta. Ocene heritabilitet pridobljene na podlagi modela očetov in materinih očetov so se gibale med 0,091 in 0,119. Razlike med ocenami so izhajale pretežno iz uporabe različnih omejitev za črede in leta. Heritabilitete ocenjene z modelom živali so bile višje in so se

gibale med 0,125 in 0,160 v modelu, z naključnim vplivom skupnega okolja v čredi in med 0,171 in 0,210 v modelu z uporabo naključne interakcije skupnega okolja v čredi in leta. Korelacje med rangi plemenskih vrednosti, napovedanimi z modelom živali in aproksimativnim modelom živali z uporabo napovedi iz modela očetov in materinih očetov so bile visoke in so znašale 0,94 za krave in 0,93 za bike, ko je bil v model vključen vpliv skupnega okolja v čredi oziroma 0,90 za krave in 0,93 za bike, ko je bil v model vključen vpliv interakcije skupnega okolja v čredi in leta. Testiranje točnosti modelov, opravljeno na neodvisnem nizu podatkov, je pokazalo, da je korelacija med napovedanimi plemenskimi vrednostmi očetov in preživetjem hčera nekoliko višja pri uporabi modela očetov in materinih očetov z aproksimativnim modelom živali, kot pri modelu živali. Vrednost korelacijskega koeficienta med očetovo napovedjo plemenske vrednosti in preživetjem hčera je bila večja, ko je model vključeval interakcijo skupnega okolja v čredi in leta, kot v primeru, ko je bil v model vključen vpliv skupnega okolja v čredi. Z namenom izognitve učinku mešanja in zmanjšanja potrebne računalniške moči je za napoved plemenskih vrednosti dolgoživosti pri govedu priporočljiva uporaba aproksimativnega modela živali z uporabo napovedi iz modela očetov in materinih očetov za krave in vpliva interakcije skupnega okolja v čredi in leta.



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Comparison between sire-maternal grandsire and animal models for genetic evaluation of longevity in a dairy cattle population with small herds

J. Jenko,^{*†} G. Gorjanc,[†] M. Kovač,[†] and V. Ducrocq[‡]

^{*}Agricultural Institute of Slovenia, Hacquetova ulica 17, 1000 Ljubljana, Slovenia

[†]Department of Animal Science, Biotechnical Faculty, University of Ljubljana, Groblje 3, 1230 Domžale, Slovenia

[‡]INRA, UMR 1313 Génétique Animale et Biologie Intégrative, 78350 Jouy-en-Josas, France

ABSTRACT

Survival analysis techniques for sire-maternal grandsire (MGS) and animal models were used to test the genetic evaluation of longevity in a Slovenian Brown cattle population characterized by small herds. Three genetic models were compared: a sire-MGS model for bulls and an approximate animal model based on estimated breeding values (EBV) from the sire-MGS model for cows, an animal model, and an animal model based on the estimated variance components from the sire-MGS model. In addition, modeling the contemporary group effect was defined as either a herd or a herd-year (HY) effect. With various restrictions on the minimum HY group size (from 1 to 10 cows per HY), changes in estimates of variance components, and consequently also in EBV, were observed for the sire-MGS and animal models. Variance of contemporary group effects decreased when an HY effect was fitted instead of a herd effect. In the case of a sire-MGS model, estimates of additive genetic variance were mostly robust to changes in minimum HY group size or fitting herd or HY effect, whereas they increased in the animal model when HY instead of herd effects was fitted, possibly revealing some confounding between cow EBV and contemporary group effect. Estimated heritabilities from sire-MGS models were between 0.091 and 0.119 and were mainly influenced by the restriction on the HY group size. Estimated heritabilities from animal models were higher: between 0.125 and 0.160 when herd effect was fitted and between 0.171 and 0.210 when HY effect was fitted. Rank correlations between the animal model and the approximate animal model based on EBV from the sire-MGS model were high: 0.94 for cows and 0.93 for sires when a herd effect was fitted and 0.90 for cows and 0.93 for sires when an HY effect was fitted. Validation performed on the independent validation data set revealed that the correlation between sire EBV and daughter survival were slightly higher with

the approximate animal model based on EBV from the sire-MGS model compared with the animal model. The correlations between the sire EBV and daughter survival were higher when the model included an HY effect instead of a herd effect. To avoid confounding and reduce computational requirements, it is suggested that the approximate animal model based on EBV from the sire-MGS model and HY as a contemporary group effect is an interesting compromise for practical applications of genetic evaluation of longevity in cattle populations.

Key words: longevity, survival analysis, genetic evaluation, dairy cattle

INTRODUCTION

Longevity in dairy cattle is most commonly defined as the length of productive life (Ducrocq, 2005; Terawaki et al., 2006; Chirinos et al., 2007). Common approaches for the analysis of such data are survival analysis (Forabosco et al., 2009), due to a finer time scale (in days rather than in months, years, or lactations), the ability to treat living cows as censored, and the effective handling of time-dependent explanatory variables (Smith and Quaas, 1984; Ducrocq, 1987). Genetic evaluation of longevity based on survival analysis is commonly performed with sire or sire-maternal grandsire (MGS) models (Forabosco et al., 2009) as implemented in the Survival Kit software (Mészáros et al., 2013). This software implements a Bayesian approach to estimate parameters of frailty (i.e., mixed survival) models, assuming a conjugate log-gamma or nonconjugate normal prior distribution for the frailty (random) terms. Inferences on random hyperparameters are drawn from their marginal posterior density using Laplacian approximation (Ducrocq and Casella, 1996; Mészáros et al., 2013).

The main reason for using sire and sire-MGS versus animal models is computational. The joint maximization of a complex nonlinear function with many parameters such as the one used in survival mixed models is very demanding. Efficient optimization of such functions requires repeated computation and storage

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^{*}Corresponding author: janez.jenko@kis.si

of a Hessian matrix, which is usually denser than in standard linear mixed models. The use of AI in dairy cattle leads to a much smaller number of sires than the number of recorded animals, which makes sire and sire-MGS models the only computationally tractable ones in very large populations, in contrast to animal models.

To obtain EBV also for cows in the case of large populations, a 2-step approximate procedure was developed using results obtained from sire-MGS models (Ducrocq, 2001). This approximate animal model procedure is incorporated in the Survival Kit software (Mészáros et al., 2013). In the first step, a sire-MGS survival model is applied to obtain sire EBV. Then, in the second step, cows are evaluated assuming that other effects are known (Ducrocq, 2001).

Even if computationally possible, the application of an animal model for genetic evaluation of longevity in populations with small contemporary groups is questionable because of the lack of information for decisive separation of genetic and environmental effects. Namely, the amount of information per individual cow is limited in the presence of a single (potentially censored) record per cow for a lowly heritable trait. Therefore, modeling the contemporary group effect and its interplay with genetic effects is of considerable importance. Some authors distinguished variation in culling policy only between herds (Potočnik et al., 2011). However, within-herd culling policy also varies between years and between seasons within year, leading to the standard use of time-dependent herd-year (**HY**; e.g., Dürr et al., 1999; Terawaki et al., 2006) or herd-year-season (e.g., Ducrocq, 2005; Sewalem et al., 2005; Chirinos et al., 2007) interaction effects in survival analysis models. Modeling contemporary groups in a time-dependent manner within herd can better account for the conditions around the time of culling, but no clear guidelines exist to determine which approach is favorable in the case of limited amount of information per contemporary group.

In Slovenia, cattle populations are small with rather small herds, representing an example where sire-MGS and animal models can be tested and the interaction with contemporary group definition can be explored. The objective of this research was therefore to compare the application of different genetic models and different definitions of contemporary groups for genetic evaluation of longevity of Slovenian Brown cattle.

MATERIALS AND METHODS

Data

Data on longevity defined as time from the first calving until culling or the sixth calving of Brown cows

between January 1998 and December 2008 in Slovenia were used. In the data preparation procedure, records from cows <20 mo and >48 mo at the time of first calving or with the missing date of the first calving were discarded. Lengths of productive life beyond lactation 5 were censored to concentrate the study on the risk of being culled early in life, because culling of older cows may involve reasons different from those in younger cows and early cullings are the most expensive. Censoring was also applied to cows changing herds during their lifespan, with censoring occurring at the date of last milk recording in their first herd. The final data set included 42,120 cows with phenotype data. A relatively small herd size (from 6.7 on average in 1999 to 8.7 Brown cows per herd in 2008) is an intrinsic feature of herds of the Brown cattle breed in Slovenia. Therefore, a series of 5 data sets were prepared for the comparison of estimated variance components under different restrictions on minimum number of cows per HY group (1, 2, 3, 5, or 10). A pedigree file with 5 generations was created for each data set separately. To test the predictive ability of the models, the data were divided into a training set for the estimation of variance components and the prediction of breeding values and a validation data set for testing the predictive ability of survival in cows. The training data set comprised 90% of all the cows with records (37,908 cows), whereas the remaining 10% (4,212 cows) were used for validation. Cows in the validation data set came from larger herds (≥ 10 cows per HY class) and were second-crop progeny of 63 sires.

Base Model

The analysis was based on a proportional hazards model with Weibull distributions:

$$t_i \sim \text{Weibull}(\lambda_i, \rho_i), \quad [1]$$

where t_i is the longevity record of the i th cow, and λ_i and ρ_i are scale and shape parameters, respectively, of the Weibull distributions that were modeled. Proportional hazards provide a flexible framework to describe hazard functions $h(t_i)$ separately for the general aging process—the so-called baseline hazard function, $h(t_i)_0$ —and the multiplicative effect of a function of genetic and nongenetic factors $f(t_i)$:

$$h(t_i) = h(t_i)_0 \times f(t_i). \quad [2]$$

The baseline hazard function was modeled in a piecewise fashion, assuming a different Weibull hazard function for each combination of lactation number and stage of lactation, as in Terawaki et al. (2006). The

cutpoints defining stages of lactation were chosen according to the observed changes in the estimated hazard distribution derived from the Kaplan-Meier estimate of the raw survivor function (Kaplan and Meier, 1958). Cutpoints were set at d 0, 60, 270, and 380 d of lactation, and the day of drying off. Each piecewise baseline hazard function $h(t_i)_{0,p}$ was of the Weibull form [1]:

$$h(t_i)_{0,p} = \lambda_p \rho_p (\lambda_p t_i'')^{\rho_p - 1}, \quad [3]$$

with specific values of λ_p and ρ_p for each of the 25 (5 lactations \times 5 stages) periods generated by the cutpoints. In [3], t_i'' is the number of days since the previous calving (e.g., since the second calving, for any period covering the second lactation).

To focus on functional rather than true longevity, the effect of (relative) milk production was included to correct for culling due to low production, which is the major source of voluntary culling (e.g., Vukasinovic et al., 1995; Dürr et al., 1999). This effect was modeled through the definition of time-dependent groups $m_j(t_i)$ with j (1 to 10) classes on peak milk yield m (defined as the highest value out of the first 2 milk recordings within the first 120 d of lactation). Peak milk yields were compared within calving year on a whole-population basis. To test the influence of herd size on risk of culling due to low production, the comparison was done for 5 groups of herd size separately for the first and later lactations. Group sizes for primiparous cows were: 1 to 3, 4 to 6, 7 to 9, and >9 , and for multiparous they were: 1 to 5, 6 to 10, 11 to 15, and >15 cows in a herd. According to the mean and standard deviation of peak milk yield, limits of 10 deciles (groups) were calculated. The change in milk yield group during the cow's herdlife was assumed to occur on the day of peak yield. Primiparous cows were included in a special "dummy" group until the peak yield of the first lactation was obtained.

Six groups k (1 to 6) of change in herd size $s_k(t_i')$, were defined according to the difference in maximum number of recorded cows during the first 3 recording days of each year. Cows from herds decreasing in size by more than 30% were in group 1, cows from herds decreasing from 10 to 30% were in group 2, cows in stable herd size group (changes from -10 to 10%) were in group 3, cows from herds increasing from 10 to 30% were in group 4, cows from herds increasing by more than 30% were in group 5, and finally, a "dummy" group 6 was created for small herds with fewer than 5 cows. The change between groups of herd size variation occurred on January 1 of each year.

For the effect of region, 3 territories were defined that were distinguished mainly on the basis of the agricultural and climatic conditions. The change in region r by year-season group yp , $ryp_l(t_i')$, with l (1 to 132) classes occurred on January 1, April 1, July 1, and October 1 of each year.

The time-dependent contemporary group effect $c_m(t_i')$ or time-independent contemporary group effect c_m and additive genetic effect a_n were modeled according to different models as described in the next section. In all cases, these effects were modeled assuming a log-gamma distribution (for computational convenience, e.g., Ducrocq and Casella, 1996) for the contemporary group effect:

$$c_m \sim \text{Log-Gamma}(\gamma, \gamma), \quad [4]$$

and a normal distribution for additive genetic effect:

$$\mathbf{a} \sim N(0, k\mathbf{A}\sigma_a^2), \quad [5]$$

where the 2 hyperparameters of the log-gamma distribution are equal to γ (i.e., the mean is equal to 1 and the variance is equal to $\sigma_c^2 = \psi^{(1)}(\gamma)$, where $\psi^{(1)}$ is the trigamma function), \mathbf{A} is the numerator relationship matrix between additive genetic values \mathbf{a} , and k is the proportion of additive genetic variance σ_a^2 , with different proportions according to the models described in the next section. The final model equation was

$$f(t_i'') = \exp \left\{ m_j(t_i) + s_k(t_i') + ryp_l(t_i') + c_m(t_i') + a_n \right\}. \quad [6]$$

One complex aspect of the model is that 3 time scales are simultaneously considered: the number of days since the first calving (t_i), calendar time (t_i') "controlling" the definition of year or season, and the number of days since the previous calving (t_i'') to model a baseline hazard that follows the cyclic pattern across lactations.

Alternative Models

Alternative definitions of contemporary group and additive genetic effect were tested. Two alternatives were tested for the contemporary group effect defined as either the time-independent effect of herd or the time-dependent effect of HY, with changes occurring on January 1 of each year. In both cases, restrictions on minimum number of records were applied on the HY group. If the HY group size was below a given

threshold (1, 2, 3, 5, or 10 cows) in a certain year, all length of productive life records of cows in that herd were considered censored from that year onward.

Two models were tested to estimate the additive genetic effect of bulls and cows. The first model was a sire-MGS model, with the additive genetic effect of bulls represented as

$$a_n = a_o + \frac{1}{2} a_p, \quad [7]$$

where a_o is the additive genetic effect of the o th sire and a_p is additive genetic effect of the p th MGS of the n th cow. The relationship matrix was built for all sires based on the available male pedigree. The heritability for this model can be calculated as

$$h^2 = \frac{4\sigma_s^2}{\frac{5}{4}\sigma_s^2 + \sigma_c^2 + 1}, \quad [8]$$

where σ_s^2 is the additive sire genetic variance; the additional $1/4$ added to the denominator of [8] corresponds to the maternal grandsire genetic variance; σ_c^2 is the variance of contemporary group effects, and 1 is the standard environmental variance. Expression [8] is the theoretical heritability that would be obtained in the absence of any censoring. It is higher than when censoring is accounted for, when the standard environmental variance is $1/p$, with p the proportion n of uncensored records (Yazdi et al., 2002; Mészáros et al., 2010).

With the sire-MGS model, cow EBV can be approximated by her (male) pedigree index derived from the sire-MGS model. An alternative is to derive the cow EBV using an approximation of an animal model as proposed in Ducrocq (2001).

The second model was an animal model with the inclusion of the additive genetic effect of the n th cow (a_n) directly. With the relationship matrix built for all animals in the study, recorded cows and ancestors in pedigree, the heritability for this model corresponded to

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_c^2 + 1}, \quad [9]$$

where σ_a^2 is the additive genetic variance, σ_c^2 is the variance of contemporary group effects, and 1 is the standard environmental variance. Two variants of the animal model were tested, using for σ_a^2 and σ_c^2 the value estimated from either the animal model or the sire-MGS model. The different estimates of cow breeding value were compared, considering only cows that had both their sire and MGS known.

Computation

The Survival Kit v6 package (Mészáros et al., 2013) was used to estimate parameters in all models following the theoretical development by Ducrocq and Casella (1996). Approximate animal model solutions for cows were obtained as a combination of EBV from the sire-MGS model for sires and an approximation of remaining part of additive genetic effect for cows, assuming that all other effects are known and equal to their sire-MGS model estimates (Ducrocq, 2001). Estimates of variance components and correlations between evaluated breeding values were compared for all models and data sets. Predictive accuracies of the models were tested for sire-MGS and animal models separately and for bulls only. Two approaches were used to show the predictive ability of the models. First, survival of the second-crop daughters was correlated with the EBV of sires and, second, sires were grouped into 4 equal-sized groups based on their EBV in the training data set. The first group consisted of the 25% sires that had the highest EBV and so on, to the last group where the 25% sires with the lowest EBV were included. Finally, the differences in survival were visualized and compared between groups with the Kaplan-Meier survival curve.

RESULTS

Data Structure

The number of animals in each data file and the associated pedigree file are presented in Table 1, where the percentages of left-truncated (i.e., with first calvings before January 1, 1998) and right-censored data are also shown. Setting restrictions on the minimum number of cows in each HY inevitably led to a decrease in the number of cows in the analyses. In the case of a minimum of 5 cows per HY, only 13.2% (32,907 vs. 37,908 with no restrictions) of cow records were discarded from the data. The proportion of discarded records reached 50.0% (18,954 vs. 37,908 with no restrictions) when a minimum of 10 cows per HY was required. Setting restrictions on the minimum number of cow records per HY led to a larger decrease in number of herds (34.6% with 5 and 72.8% with 10 records at minimum per HY) and HY (43.2% with 5 and 77.6% with 10 records at minimum per HY). For the sire-MGS model, the decrease in the number of sires in the pedigree was 2.5% and 9.0% when setting a minimum of 5 or 10 records per HY, respectively. For the animal model, the decrease in number of animals in pedigree closely followed the reduction in number of cows: 11.0 or 42.2% with a restriction at 5 or 10 records at minimum per HY.

Table 1. Data characteristics under different restrictions on the minimum number of records in herd-year group

HY size ¹	Cow records	Left truncated (%)	Right censored (%)	Herd	Herd-years	Animals in pedigree	
						Sire-MGS model ²	Animal model
1	37,908	21.2	49.7	2,401	18,689	886	57,005
2	37,683	21.8	50.0	2,262	16,936	885	56,738
3	37,084	22.8	50.8	2,149	14,979	885	55,961
5	32,907	23.8	51.9	1,571	10,607	864	50,741
10	18,954	25.0	53.1	654	4,183	806	31,796

¹Minimum number of records per herd-year group.

²Sire-maternal grandsire model.

Computing Requirements

Computing time for the evaluation with the sire-MGS model was around 10 min for each of the models. With the animal model, computing time ranged from 40 min for the model with the highest restriction on a minimum number in HY class to approximately 2 h with the model with no restriction on a minimum HY class size. Sire-MGS models used approximately 0.16 GB, whereas animal models used around 25 GB of computer memory. This illustrates the unfeasibility of animal model evaluations with the Survival Kit for large populations.

Variance Components

With sire-MGS models, variance of contemporary group effects decreased with greater restrictions on minimum HY group size (Table 2). The decrease was highest between no restriction (0.296 for herd effect and 0.211 for HY effect) and at a minimum of 2 records per HY (0.193 for herd effect and 0.162 for HY effect). Surprisingly, the herd variance was always higher than the HY variance.

Changes in additive genetic variance with respect to restrictions on HY group size were small with sire-MGS models. There was a slight decrease (from 0.129 to

0.119 with herd effect and from 0.123 to 0.110 with HY effect) with the first restriction on herd size (minimum size of 2). Then, estimates were relatively stable up to the restriction of a minimum of 10 cows per HY, when slightly higher additive genetic variance was obtained (0.145 with herd effect and 0.129 with HY effect). Heritabilities were relatively stable to changes in variance of contemporary group effects and additive genetic variance. Estimates for heritabilities ranged from 9.1 to 11.9% (Table 2).

With the animal models, the contemporary group variance decreased with higher restriction on minimum HY group size in similar way as with sire-MGS models (Table 3). The herd variance was between 0.159 and 0.286 and comparable with estimates using the sire-MGS model. The HY variance was much smaller and ranged from 0.089 to 0.113.

Additive genetic variance estimates for the animal models were all higher compared with sire-MGS models. This was especially pronounced for the animal model with the HY effect. As a result, heritabilities in models with the herd effect were between 0.125 and 0.160, whereas in models with an HY effect, heritabilities varied between 0.171 and 0.210.

Variance component estimates between sire-MGS and animal models differed depending on the way contemporary group effect was defined. Estimates of herd

Table 2. Estimates of variance components obtained using a sire-maternal grandsire model with contemporary group defined as herd or herd-year combination¹

HY size ²	Herd			Herd-year		
	σ_c^2	σ_a^2	h^2	σ_c^2	σ_a^2	h^2
1	0.296	0.129 ± 0.020	0.096	0.211	0.123 ± 0.020	0.098
2	0.193	0.119 ± 0.019	0.097	0.162	0.110 ± 0.018	0.092
3	0.186	0.117 ± 0.019	0.096	0.159	0.108 ± 0.018	0.091
5	0.164	0.119 ± 0.020	0.099	0.146	0.108 ± 0.019	0.092
10	0.172	0.145 ± 0.028	0.119	0.134	0.129 ± 0.026	0.110

¹Where σ_c^2 = contemporary group variance; σ_a^2 = additive genetic variance and its standard error of estimation, $\sigma_a^2 = 4\sigma_s^2$, where σ_s^2 is sire additive genetic variance; h^2 = heritability.

²Minimum number of records per herd-year group.

MODELS FOR GENETIC EVALUATION OF LONGEVITY

8007

Table 3. Estimates of variance components obtained using an animal model with contemporary group defined as herd or herd-year combination¹

HY size ²	Herd			Herd-year		
	σ_c^2	σ_a^2	h^2	σ_c^2	σ_a^2	h^2
1	0.286	0.199 ± 0.024	0.134	0.113	0.295 ± 0.031	0.210
2	0.182	0.168 ± 0.022	0.125	0.095	0.229 ± 0.029	0.173
3	0.177	0.169 ± 0.022	0.125	0.095	0.227 ± 0.028	0.172
5	0.159	0.182 ± 0.024	0.136	0.090	0.225 ± 0.029	0.171
10	0.175	0.223 ± 0.033	0.160	0.089	0.232 ± 0.036	0.176

¹Where σ_c^2 = contemporary group variance; σ_a^2 = additive genetic variance and its standard error of estimation; h^2 = heritability.

²Minimum number of records per herd-year group.

variance were stable for sire-MGS and animal models, with a maximum change of 6% (from 0.193 to 0.182) with a minimum of 2 cows per HY class. On the other hand, HY variance was from 1.5 to 1.9 times higher with the sire-MGS model than with the animal model. Additive genetic variance estimates were higher with the animal model: 1.4 to 1.5 times higher for models with a herd effect and 1.8 to 2.5 times higher for models with an HY effect. As a result, heritability estimates were also higher with the animal model: 1.3 to 1.4 times higher for the model with herd effect and 1.6 to 2.1 times higher for the model with HY effect.

EBV

The average rank correlations between the EBV derived from the pedigree index based on the sire-MGS model and animal model EBV were 0.85 when a herd effect was fitted and 0.77 when an HY effect was fitted (Table A1 in the Appendix), denoting large reranking of cows. Correlations were the highest for restrictions to a minimum of 2 and 3 cows on HY group size when a herd effect was included and to a minimum of 10 cows when an HY effect was considered.

Rank correlations between the approximate animal model based on EBV from sire-MGS model with the animal model EBV were larger (Table 4) than with the pedigree index (Table A1 in the Appendix). In general, they were larger for sires (from 0.92 to 0.95) than for cows (from 0.88 to 0.94). This can be explained by the greater reliability of sire EBV. Similarity between cow EBV from an animal model and its approximation based on sire-MGS model was lower when an HY effect was considered instead of a herd effect. The reduction in rank correlation due to this change in the model was, on average, 0.04 for cows. This could be related to the large difference in variance component estimates between the 2 models. Whatever the type of contemporary group effects, higher restrictions on the number of cows per HY increased the correlation between EBV

for cows when HY effect was considered. The opposite was observed for sires.

To assess the effect of using quite different variances, the same rank correlations were computed when the animal model was implemented, assuming that the correct variance component estimates are those derived from the sire-MGS model (Table A2 in the Appendix). This time, correlations of 0.95 or greater were found in nearly all cases, underlying the similar EBV between the 2 models. A slight reduction was found only for sires in the case of higher restrictions on HY group size.

Animal model EBV when variance components estimates were obtained either from the animal or the sire-MGS model were compared. Rank correlations were almost unity for both cows and sires when a herd effect was fitted (on average 0.99 for cows and sires, Table A3 in the Appendix). As expected, given the change in variance estimates, the correlations were lower when an HY effect was fitted, but were still relatively high (on average, 0.97 for cows and 0.98 for sires). When restriction on HY group size was high, the difference in correlations was even smaller. These results illustrate again the consequences of the likely underestimation of HY variance and overestimation of the additive genetic variance with animal model due to confounding.

Table 4. Rank correlations for cow and sire EBV from an animal model and approximate animal model based on EBV from the sire-maternal grandsire model when contemporary group is defined as herd or herd-year combination

HY size ¹	Cows		Sires	
	Herd	Herd-year	Herd	Herd-year
1	0.94	0.88	0.94	0.95
2	0.94	0.90	0.94	0.93
3	0.94	0.90	0.94	0.93
5	0.94	0.91	0.93	0.92
10	0.94	0.92	0.92	0.92
Average	0.94	0.90	0.93	0.93

¹Minimum number of records per herd-year group.

Table 5. Rank correlations for 806 sire EBV from sire-maternal grandsire model and for 31,796¹ cow EBV obtained from an animal model with different minimum requirements on herd-year group size and contemporary group defined as herd or herd-year

Item	HY size X ²				
	1	2	3	5	10
Herd X vs. herd-year X					
Sires	0.94	0.96	0.96	0.96	0.97
Cows	0.91	0.94	0.94	0.95	0.96
Herd X vs. herd 10					
Sires	0.83	0.84	0.83	0.88	—
Cows	0.86	0.86	0.86	0.89	—
Herd-year X vs. herd-year 10					
Sires	0.76	0.81	0.80	0.86	—
Cows	0.83	0.86	0.86	0.88	—

¹Animals (cows and sires) must be present in the model with a minimum of 10 cows in herd-year group.

²Minimum number of records per herd-year group.

Rank correlations between EBV obtained from models fitting either a herd or an HY effect under various restrictions on HY group size are shown in Table 5 for sires (EBV from a sire-MGS model) and for cows (EBV from an animal model). Only animals included in the model with the restriction of a minimum of 10 cows in HY class were included. Within the same group size, rank correlations were always high (at least 0.94) for sires and increased when the minimum HY group size increased. Corresponding values were somewhat lower for cows but still reasonably high (at least 0.91). When EBV for the same model were compared under different HY group size restrictions, substantial reranking occurred (Table 5). Correlation between EBV under increasing minimum HY group sizes (from 1 to 5) and EBV under the highest restriction (at least 10 cows per HY) were always ≤ 0.89 . These correlations were lower for sires than for cows, which can be related to the loss of information from the excluded daughters of a particular sire. A lower correlation between EBV was found for the model including an HY effect than with a herd effect. This indicates sensitivity of genetic evaluation to minimum HY group size, especially when an HY effect is fitted.

Model validation based on daughters from 63 sires (Figure 1) showed that the correlations between sire EBV and daughter survival were systematically better for models with an HY effect than for models with a herd effect. With higher restriction in herd size, the predictive ability was decreasing for an early survival (183 d; i.e., half a year after first calving). For later survival (1, 2, or 3 yr after first calving), an increase in correlation was observed for the highest restriction in herd size. On the other hand, a decrease was found for the highest restriction in case of survival to 4 yr after first calving. When comparing different model types, on average a slightly higher (+0.01) correlation was ob-

served for sire-MGS models. On average, correction for an HY random effect increased the correlation between the sire-predicted breeding value and observed survival by 0.04 compared with models where only a herd effect was accounted for.

The raw survivor curves for the second-crop daughters from the validation data set (Figure 2) showed an absolute difference of 0.14 in survival between the extreme groups 5 yr after first calving. When a herd effect was applied, survival of daughters from bulls in the second quartile was the highest for animal models. However, survival of daughters from the sires from first and second quartiles was similar for animal models with HY effect and sire-MGS model, whatever the contemporary group effect.

DISCUSSION

An essential objective of genetic evaluations is to produce EBV that allow the ranking of males and females as correctly as possible. Some of our results using theoretically more-appropriate models were unexpected, and in some instances, counterintuitive. For example, the fact that estimated herd variance was always higher than HY variance was not anticipated, because HY groups are intuitively associated with a finer description of the within-herd heterogeneity in culling policy over years. Nevertheless, measures of predictive ability clearly showed that the models with time-dependent HY effects were better. Although the variance explained by smaller contemporary group effects was lower, the correlation between sire EBV and daughter survival was systematically higher and the raw survival curves from second-crop daughters of groups of bulls based on their EBV ranking was more appropriate. This shows that the proportion of the variance explained with varying contemporary group

MODELS FOR GENETIC EVALUATION OF LONGEVITY

8009

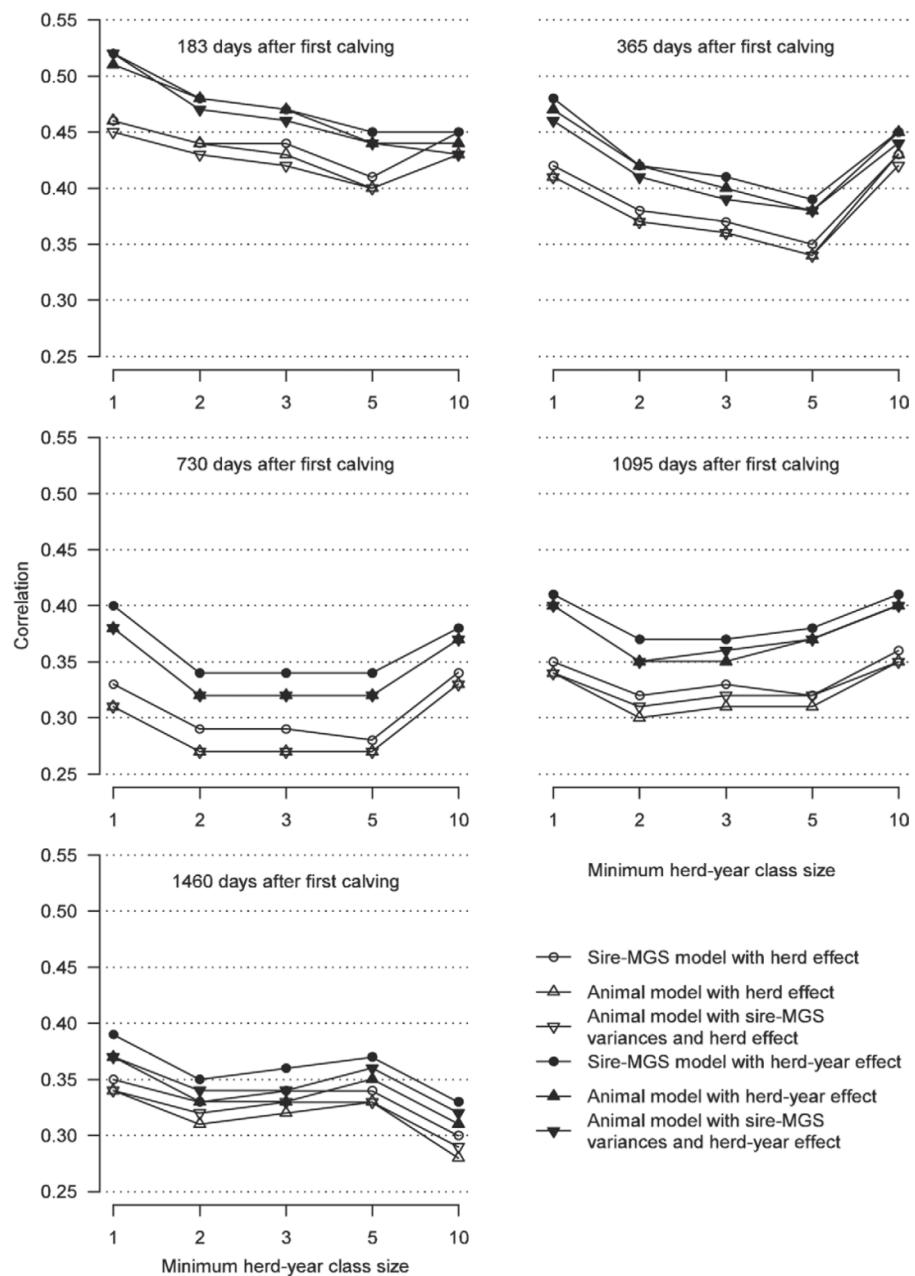


Figure 1. Correlation coefficients between sire EBV and observed survival of second-crop daughters from the validation data set when EBV were obtained from either a sire-maternal grandsire (MGS) model, an animal model, or an animal model with genetic variance derived from the sire-MGS variances. The contemporary group effect is either a herd or a herd-year effect.

8010

JENKO ET AL.

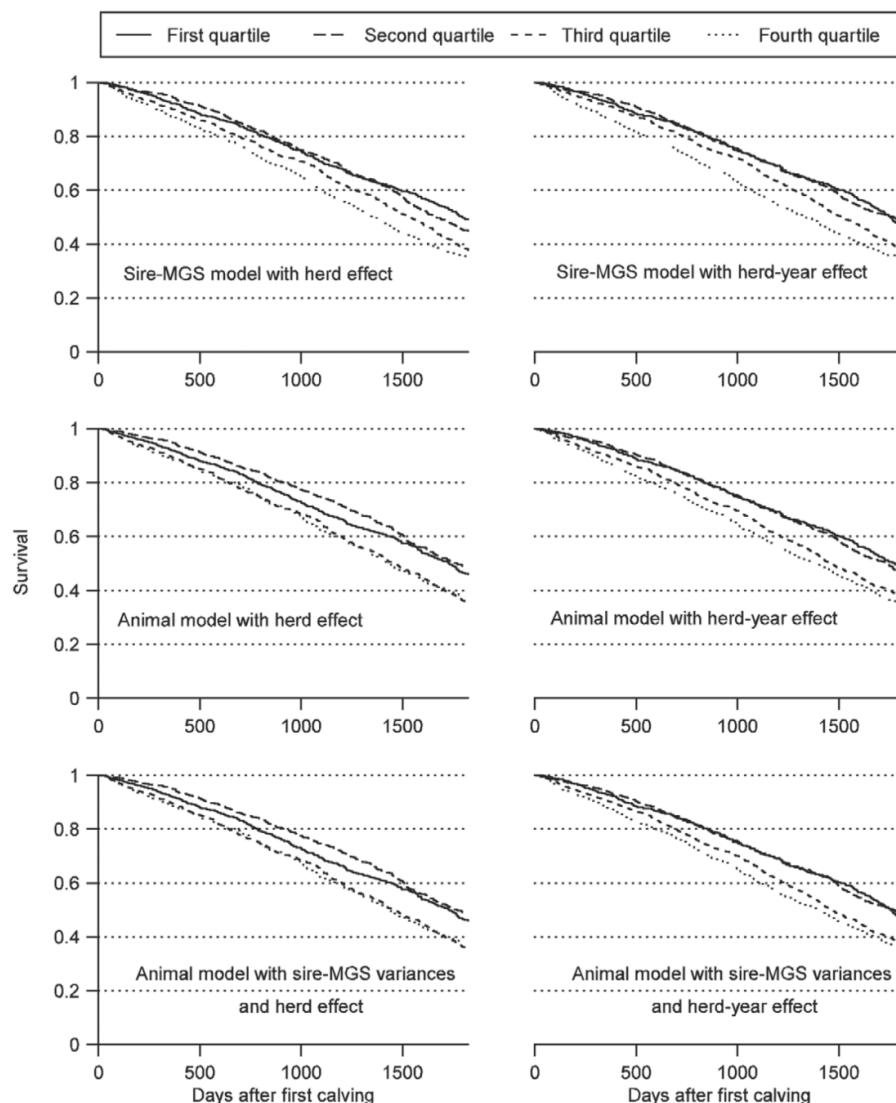


Figure 2. Raw survivor curves of the second-crop daughters from the validation data set, grouped into quartiles based on the EBV for length of productive life of their sire, computed under the following conditions: no restriction on herd-year group size, with either a herd or a herd-year contemporary effect and with a genetic part described by either a sire-maternal grandsire (MGS) effect, an animal effect, or an animal effect using a variance derived from a sire-MGS model.

effects does not reveal the real improvement in survival prediction when confounding with other components (genetic effects or residual) is likely. Compared with the results from Holtsmark et al. (2009), the obtained correlations between second-crop survival and sire EBV were lower, which may be the result of much smaller data set used in this study.

Modeling the additive genetic component of a trait is traditionally considered to be better with animal models: animal information from both the paternal and maternal sides of the pedigree as well as the individual (animal) Mendelian sampling term are taken into account. In contrast, in sire-MGS models, maternal information is only through the MGS, and the cow's Men-

delian sampling term is ignored. Consequently, only a part of the additive genetic variance ($0.3125 = 1/4 + 1/16$) is captured, with the remainder (0.6875) being included in the residual term of the model that follows a censored extreme value distribution. Damgaard et al. (2003) considered that sire or sire-MGS survival models are inconsistent with the additive genetic infinitesimal model by construction. However, some authors (e.g., Meuwissen et al., 2002) found very little effect due to this inconsistency, which was the source of a controversy (see Ducrocq, 2006). In dairy cattle, AI bulls have many daughters, leading to precise estimates of their breeding values, even for lowly heritable traits, whereas cows have only single observation and very few relatives. Given the usually low heritability of longevity, the contribution of (potentially censored) daughter performances to the breeding value of their dam is very limited. In other words, the longevity breeding value of a cow is mainly estimated using information from her male ancestors and her own (possibly censored) length of productive life.

Korsgaard et al. (1998) suggested the use of an alternative model where an extra residual term is explicitly included to account for the part of additive genetic variance ignored in sire-MGS model. However, estimation of this extra term and of its characteristics (e.g., variance) is very imprecise and heavily dependent on the a priori distribution assumed (Ducrocq, 2006), to such a point that its use is not recommended. Our situation makes the identifiability problem even worse because of the small HY groups. Results of variance component estimation suggest a large confounding effect between the additive genetic effect, the contemporary group effect, and the residual. Indeed, the high heritability estimates for longevity obtained with an animal model (up to 21%) are rather unusual. Assuming a too-large heritability would lead to overestimated EBV reliabilities. Most heritability estimates obtained from sire-MGS model were reported to be below 0.10 in longevity studies (Vollema, 1998; Chirinos et al., 2007; Mészáros et al., 2008), although some authors reported (theoretical) heritability up to 0.18 (Roxström and Strandberg, 2002; Potočnik et al., 2011). In our case, increased genetic variance with an animal model was compensated for by a large decrease in HY variance. The data structure may not be adequate to properly disentangle these 2 effects when genetic and HY variances are estimated. On the other hand, variance components appeared more stable with the sire-MGS model.

Another difficulty encountered with the animal survival model is its computational limitation. The repeated computation and inversion of a nearly dense matrix of a size larger than the total number of fixed

and random effects (Ducrocq and Casella, 1996) hinders the use of animal models for routine genetic evaluation and even more for the estimation of dispersion parameters. Approximations are therefore needed. Correlations between the animal model EBV and their approximation were much higher than those obtained with the pedigree estimate (Table A1 in the Appendix). However, whatever the model, these correlations were substantially lower than the correlations (almost unity) obtained by Ducrocq (2001) with the same approach but on a simulated data set and an idealized situation, where nearly no changes between sire and dam EBV were detected. The reasons for this might be the relatively large number of records in each HY-season group and of progeny per sire in Ducrocq (2001), but also the use of the same additive genetic variance in the sire-MGS and animal models. Here, the 2 additive genetic variances used were very different and, as mentioned before, the one obtained from the animal model appears overestimated to such a degree that the estimated additive genetic variance computed from the sire-MGS appears more appropriate.

For a given minimum size of HY class, the 2 options to model the contemporary group effect led to similar rankings. As larger contemporary group size increases the accuracy of sire evaluations (Meyer et al., 1989), it is not surprising that the higher the restriction, the more similar the ranking except that here, size restrictions led to fewer recorded daughters per sire. An alternative that needs to be studied is the definition of herd or HY class groups for small herds instead of excluding them from the analysis, as done in the current study. These classes could be formed according to similarity on milk production level. When dealing with HY groups, the clustering of similar HY groups within herd could be performed to increase the number of animals within a particular HY group (Van Bebber et al., 1997).

CONCLUSIONS

Genetic evaluation for the length of productive life of populations characterized by small herd size is possible but should be implemented with caution. Whatever the model used, when no restriction at all was imposed on the minimum HY group size, herd or HY variance was substantially inflated. Ranking of EBV was quite sensitive to these restrictions. When a herd effect was fitted, estimates of herd variance were similar whether a sire-MGS model or an animal model was used. In contrast, when an HY effect was used, estimates of HY variance were smaller, especially with animal model. This had an effect on the prediction of second-crop daughters' survival regarding the sires' EBV, where the inclusion of HY instead of herd effect was more

appropriate when an animal model was applied. Also, the correlation between the second-crop survival and sires' EBV was improved for both animal and sire-MGS models when an HY effect was used. Conclusions for the estimates of additive genetic variance were different. When a sire-MGS model was used, estimates were very similar whether a herd or an HY effect was fitted, whereas estimates were much larger with the animal model, especially when an HY effect was fitted. These findings suggest that in the case of small herds, the confounding between animal genetic effect, contemporary group effect and residual may be large. Variance component estimates derived from the sire-MGS model did not lead to more robust estimation of EBV when used in animal model. Regarding the model predictive ability, the most appropriate is the application of a sire-MGS model with HY contemporary group effect. Therefore, we recommend basing genetic evaluations of bulls and cows for longevity on the approximate animal model based on EBV from the sire-MGS model.

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APPENDIX

Table A1. Rank correlations for cow¹ EBV from an animal model and their pedigree index approximation from sire-maternal grand sire model (sire plus half the maternal grandsire EBV) with contemporary group defined as herd or herd-year

HY size ²	n	Herd	Herd-year
1	36,039	0.84	0.71
2	35,934	0.86	0.77
3	35,542	0.86	0.77
5	32,561	0.85	0.79
10	21,787	0.83	0.80
Average		0.85	0.77

¹For cows with known sire and maternal grandsire.

²Minimum number of records per herd-year group.

Table A3. Rank correlations between cow and sire EBV from an animal model using variance components estimated from a sire-maternal grandsire model or an animal model with contemporary group defined as herd or herd-year combination

HY size ¹	Cows		Sires	
	Herd	Herd-year	Herd	Herd-year
1	0.99	0.95	0.99	0.98
2	0.99	0.97	0.99	0.98
3	0.99	0.97	0.99	0.98
5	0.99	0.97	0.99	0.98
10	0.99	0.98	0.99	0.98
Average	0.99	0.97	0.99	0.98

¹Minimum number of records per herd-year group.

Table A2. Rank correlations for cow and sire EBV from an animal model [with variance components from a sire-maternal grandsire (sire-MGS) model] and approximate animal model based on EBV from the sire-MGS model, when contemporary group is defined as herd or herd-year combination

HY size ¹	Cows		Sires	
	Herd	Herd-year	Herd	Herd-year
1	0.96	0.95	0.94	0.98
2	0.96	0.95	0.95	0.95
3	0.96	0.95	0.95	0.95
5	0.96	0.95	0.94	0.94
10	0.95	0.95	0.93	0.95
Average	0.96	0.95	0.94	0.95

¹Minimum number of records per herd-year group.

2.4 GENETSKA POVEZAVA MED ŽIVLJENJSKO PRIREJO MLEKA, PRIREJO MLEKA V PRVI LAKTACIJI IN DOLGOŽIVOSTJO

Janez Jenko, Tomaž Perpar, Milena Kovač

Mljekarstvo, 2015, 65, 2: 111–120

Izvleček:

Analizirali smo genetsko povezavo med življenjsko prirejo mleka, količino mleka v prvi laktaciji in dolžino dobe prireje pri slovenski rjavi pasmi goveda. Skupno smo v analizo vključili 14389 krav. Za vse krave smo imeli na voljo podatek o količini mleka v prvi laktaciji, 12416 krav pa je imelo znano življenjsko prirejo mleka in dolžino dobe prireje. Podatke o življenjski prireji mleka in dolžini dobe prireje smo normalizirali tako, da smo njihove vrednosti korenili z dva. Pri vseh treh lastnostih so ocenjene vrednosti za sistematski vpliv sezone prve telitve nihale med različnimi sezonomi znotraj let. Za količino mleka v prvi laktaciji so bila ta nihanja ciklična. Krave s prvo telitvijo v hladnejšem delu leta so imele največjo prirejo mleka v prvi laktaciji, medtem ko so krave s prvo telitvijo v toplejšem delu leta priredile najmanjšo količino mleka v prvi laktaciji. Ocenjena heritabiliteta je znašala $0,12 \pm 0,017$ za življenjsko prirejo mleka, $0,09 \pm 0,015$ za dolžino dobe prireje in $0,15 \pm 0,001$ za količino mleka v prvi laktaciji. Genetska povezava med življenjsko prirejo mleka in dolžino dobe prireje je bila zelo močna ($0,96 \pm 0,008$), med življenjsko prirejo mleka in količino mleka v prvi laktaciji zmerna ($0,48 \pm 0,067$) ter šibka ($0,23 \pm 0,085$) med dolžino dobe prireje in količino mleka v prvi laktaciji. Povezava med skupnim okoljem v čredi je bila zmerna in negativna (- $0,41 \pm 0,052$) med dolžino dobe prireje in količino mleka v prvi laktaciji, šibka in pozitivna ($0,26 \pm 0,057$) med življenjsko prirejo mleka in količino mleka v prvi laktaciji in močna ter pozitivna med življenjsko prirejo mleka in dolžino dobe prireje ($0,74 \pm 0,025$). V zadnjih 40 letih je bil opazen pozitiven trend v genetski vrednosti živali za življenjsko prirejo mleka in količino mleka v prvi laktaciji, medtem ko za dolžino dobe prireje ni opaziti sprememb v genetski vrednosti živali.

Genetic relationship between the lifetime milk production, longevity and first lactation milk yield in Slovenian Brown cattle breed

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Janez Jenko¹, Tomaž Perpar¹, Milena Kovač²*

¹Agricultural Institute of Slovenia, Hacquetova ulica 17, 1000 Ljubljana, Slovenia

²Department of Animal Science, Biotechnical Faculty, University of Ljubljana, Groblje 3, 1230 Domžale, Slovenia

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Abstract

To study the genetic relationship between the lifetime milk production (LMP), first lactation milk yield (MY305), and length of productive life (PL) in the Slovenian Brown cattle population, first lactation records from 14,389 cows and lifetime performance records (LMP and PL) from 12,416 cows were used. Records of LMP and PL were normalised using the square root transformation of the raw values. The fixed effect of the first calving year-season oscillated between different seasons within a year for all the traits. These changes followed a seasonal pattern in MY305, where cows with first calving in colder seasons of a year had the highest MY305 and cows with first calving in the warmer seasons of a year had the lowest. The estimated heritability was 0.12 ± 0.017 for LMP, 0.09 ± 0.015 for PL, and 0.15 ± 0.001 for MY305. Genetic correlation between LMP and PL was very strong (0.96 ± 0.008), while it was moderate (0.48 ± 0.067) between LMP and MY305 and weak between PL and MY305 (0.23 ± 0.085). The common herd environment correlation between PL and MY305 was moderate and negative (-0.41 ± 0.052), whereas it was weak and positive between the LMP and MY305 (0.26 ± 0.057) and strong and positive between LMP and PL (0.74 ± 0.025). For the last 40 years, a positive genetic trend was observed for LMP and MY305, while the genetic trend for PL remained stable.

Key words: genetic evaluation, lifetime milk production, lactation milk yield, longevity, Brown cattle

Introduction

Lifetime milk production (LMP) is one of the traits of primary interest for dairy cattle breeders. It is important because the costs of rearing replacement cows represent a substantial part of the expenses in the dairy cattle production system. To decrease the costs, it is desirable that cows stay in a herd for a longer period of time and have a high level of milk production (Robertson and Rendel, 1950; Stott, 1994; Jenko et al., 2007). The combination of long productive life (PL) and high daily milk yield emerges

in a high level of LMP and increase in the profitability. Although LMP is one of the most important traits, direct selection for a high LMP is usually not performed in dairy cattle breeding programmes. There are various reasons for this, but mainly they are related to the time elapse between the sire's birth and the time of selection for LMP. When the LMP data are available, bulls are already too old and the selection for LMP cannot be performed anymore. One of possible solutions to overcome the problem of time elapse between the sire's birth and selection would be the application of other genetic evaluation

*Corresponding author/Dopisni autor: E-mail: janez.jenko@kis.si

methods e.g. survival analysis techniques (Ducrocq and Casella, 1996). Here, the application of hazard function enables the inclusion of records from cows that are still in the herd. One of the difficulties when using this method is the non-linearity in the increase of LMP function due to the different level of milk production and dry periods during the herd life of a cow. In contrast, this method was successfully applied to predict the breeding values for the length of productive life, which is known to be a linearly increasing trait.

Selection for high LMP through the selection of genetically strongly correlated traits is another way to overcome the problem. Different traits can be used to perform selection for this purpose (Hoque and Hodges, 1980; Tsuruta et al., 2004). Since genetic evaluation for PL using survival analysis techniques was shown to be successful in Slovenian Brown cattle (Jenko et al., 2013a), it is of a great interest to investigate the genetic relationship between the LMP and PL.

There were four objectives of the current study: i) estimation of the fixed effect on LMP, PL, and the first standard lactation milk yield (MY305), ii) estimation of the variance components for LMP, PL, and MY305, iii) estimation of the genetic correlation between LMP, PL, and MY305, and iv) estimation of the genetic trend for these three traits in the Slovenian Brown cattle population. Results showed that the range of correlations between pairs of LMP, PL, and MY305 varies substantially. The genetic trend clearly illustrated an emphasis on selection for the Slovenian Brown cattle during the past 40 years.

Material and methods

LMP, PL, and MY305 data from Slovenian Brown cattle breed were used to study the genetic relationship between the LMP, MY305, and PL. The PL was defined as the time period between the date of first calving and the date of culling. When culling date was missing a maximum date from the dates of calving, milk recording, or drying off was used instead. Records from 36,663 cows involved in the milk-recording scheme that had the first calving between 1 January 1998 and 31 December 2008 were used. As the lifetime performance records (LMP and PL) were collected up until 31 August 2014, all

the cows had the opportunity to stay in the herd for at least 68 months. Cows that were still alive on the last day of data collection (1,964 cows) were treated as culled on 31 August 2014. Cows younger than 20 months (104 cows) or older than 48 months (295 cows) at the day of first calving were excluded.

Because the study was performed on complete first standard lactation records, cows with first lactation shorter than 201 days were excluded (2,854 cows), as well as the records from cows that changed herds during the period of first lactation (1,137 cows). Due to the problems of model convergence only the records from herds with at least 20 cows that were progenies of sires with at least 30 daughters in the data records were kept. As small herds are typical for Brown cattle breed rearing systems in Slovenia, this restriction excluded 17,884 records.

After data filtering, there were 14,389 MY305 records included in the model to analyse MY305 variance components. As functional longevity was estimated, only cows with MY305 records were used to form the dataset for the analysis of LMP and PL. When the lifetime performance records of a single cow were collected from more than one herd, the records of a cow were excluded and the data were again updated for the minimum of 20 cows per herd and at least 30 daughters per sire. At the end, 12,416 cows were kept in the data set for the analysis of variance components for LMP and PL. For the purpose of genetic evaluation, the pedigree was prepared using the data from the last five generations. There were 25,468 animals in pedigree, from which 765 were sires and 165 of them were having progenies in the data.

A multivariate linear model was used for the estimation of variance components and the prediction of breeding values. A multivariate model overcomes the problem of the past selection for MY305, which is expected to be the problem in the data analysed. A single trait evaluation would not use all of the information to get good estimates, which may lead to biases in predicted breeding values, as well as an underestimation of the genetic trend when traits are correlated. Records for LMP and PL in which distribution was positively skewed were normalised using a square root transformation. Square root transformation is a proper solution for LMP and PL data, as all of the data are higher than 1 and no re-ranking within the data occurs. If data on the original scale were used, the convergence was not achieved.

Convergence was achieved with the normalised data used in the model. The fixed part of the model included the effect of region, calving-year season, age at first calving, first lactation length, and correction for the within herd first lactation milk yield. Cows were grouped into three regions (western, central, and eastern), based on the similarity in environmental conditions within each of the regions, as well as the presence of Brown cows in the territory of Slovenia.

The western region represents subpannonial Slovenia and part of Prealpine Hills, central Prealpine Hills with Dinaric Karst, and eastern sub-Mediterranean Slovenia. Due to the environmental factors, cattle breeding conditions are better in the central and western regions of Slovenia. The season in year-season interaction was formed through four seasons, with the periods from January to March, April to June, July to September, and October to December. To correct the model for the age at first calving, five classes were formed based on the age at first calving in months ($\geq 20 < 22$; $\geq 22 < 25$; $\geq 25 < 28$; $\geq 28 < 31$; $\geq 31 \leq 40$). The effect of lactation length was included only for MY305, and was grouped in 14 classes, each covering 15 days between the period of 201 and 410 days of lactation and one class for lactations longer than 410 days. The corrected within herd rank lactation milk yield effect was included only for the estimation of PL to correct the model for the effect of voluntary culling. The MY305 records were corrected for the effect of calving year, and subsequently, the average values for each of the herds were calculated and subtracted from a single record of a cow. Based on the standard Z score, deviations were grouped into 10 deciles (1 - low milk production, 10 - high milk production) forming the classes to correct for the effect of voluntary culling.

The following multivariate linear model was used to estimate the variance components and to predict the genetic trend:

$$y_{ijklmn} = \mu + R_i + CYS_j + AFC_k + LL_{I[MY305]} + MY_{m[PL]} + h_m + a_{ijklmn} + e_{ijklmn}$$

where:

y_{ijklmn} = trait (LMP, PL, and MY305); μ = general mean; R_i = fixed effect of region; CYS_j = fixed effect of year-season of first calving; AFC_k = fixed effect of age at first calving class; $LL_{I[MY305]}$ = fixed effect of lactation length class (only for MY305);

$MY_{m[PL]}$: fixed effect of corrected within herd rank lactation yield (only for PL); h_m = random effect of herd; a_{ijklmn} = random effect of animal; e_{ijklmn} = residual. Additive genetic variance (σ_a^2), common herd environment variance (σ_c^2), and residual variance (σ_e^2) were divided with phenotypic variance σ^2 to be expressed as heritability ($h^2 = \sigma_a^2 / \sigma^2$), variance ratio for common herd environment ($c^2 = \sigma_c^2 / \sigma^2$), and variance ratio for residual ($e^2 = \sigma_e^2 / \sigma^2$).

To estimate the linear genetic trend, yearly averages of breeding values for sires born between 1970 and 2000 were standardised using the following equation:

$$SBV_{ty} = \frac{\overline{BV}_{ty}}{\sigma_{ty}} \quad \text{where:}$$

SBV_{ty} = standardised breeding value for trait t (LMP, PL, and MY305) and year y (1970-2000);

\overline{BV}_{ty} = Average of predicted breeding values for trait t and year y ; σ_{ty} = standard deviation of breeding values for trait t for sires born in year 1970.

Data were prepared using the R software (R Development Core Team, 2008), while the Wombat (Meyer, 2007) software package was used for the estimation of variance components and the prediction of breeding values.

Results and discussion

Descriptive statistics

Descriptive statistics for LMP, PL, and MY305 are presented in Table 1. On average, cows were producing 5,109 kg of milk in the first lactation and 24,376 kg total in 1,544 days. As records from the cows culled before 201 days of first lactation were excluded from the analysis, the lifetime performance records were higher than those from the yearly report for Slovenia (Sadar et al., 2014). The range of herd averages was wide for LMP and PL, where the maximum herd average was around four times the minimum herd average. For MY305, this range was smaller, with a maximum herd average of 2.3 times the minimum herd average.

Table 1. Descriptive statistics for lifetime milk production (LMP), length of productive life (PL), and first standard lactation milk yield (MY305)

Trait	N ¹	Mean	SD ²	CV ³	Herd Min ⁴	Herd Max ⁵
LMP (kg)	12,416	24,376	15,083	61.9	10,765	43,436
PL (days)	12,416	1,544	878	56.9	725	2,702
MY 305 (kg)	14,389	5,109	1,101	21.5	3,174	7,190

¹Number of cows; ²Standard deviation; ³Coefficient of variation; ⁴Minimum herd average; ⁵Maximum herd average

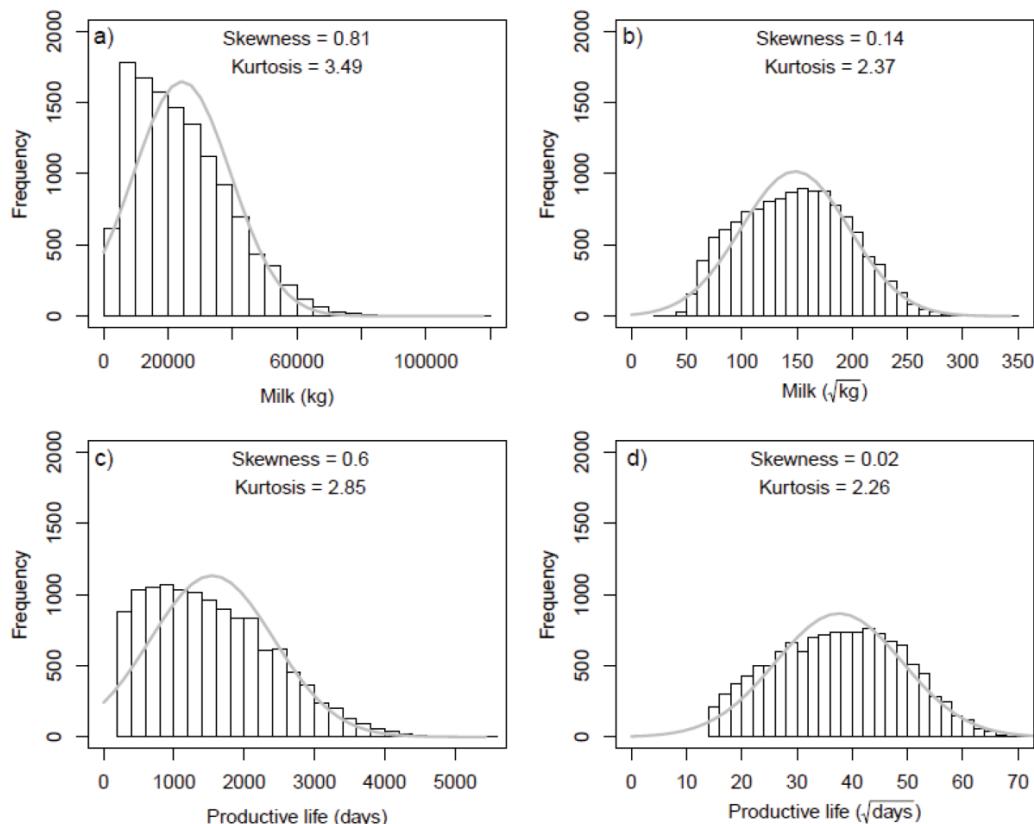


Figure 1. Distribution of lifetime milk yield a), square root of lifetime milk yield b), length of productive life c), and square root of length of productive life d) with curves of ideal normal distribution

Square root transformation decreased the skewness of distribution for both LMP and PL (Figure 1). With a skewness of 0.14 for LMP and 0.02 for PL, the transformation almost completely solved the problem of positive skewness in LMP and PL. The problem of kurtosis was not solved. Square root

transformation changed the distribution of LMP from leptokurtic to platykurtic, and made the distribution of PL even more platykurtic. In the rest of the paper LMP and PL will be used as a square root transformed data.

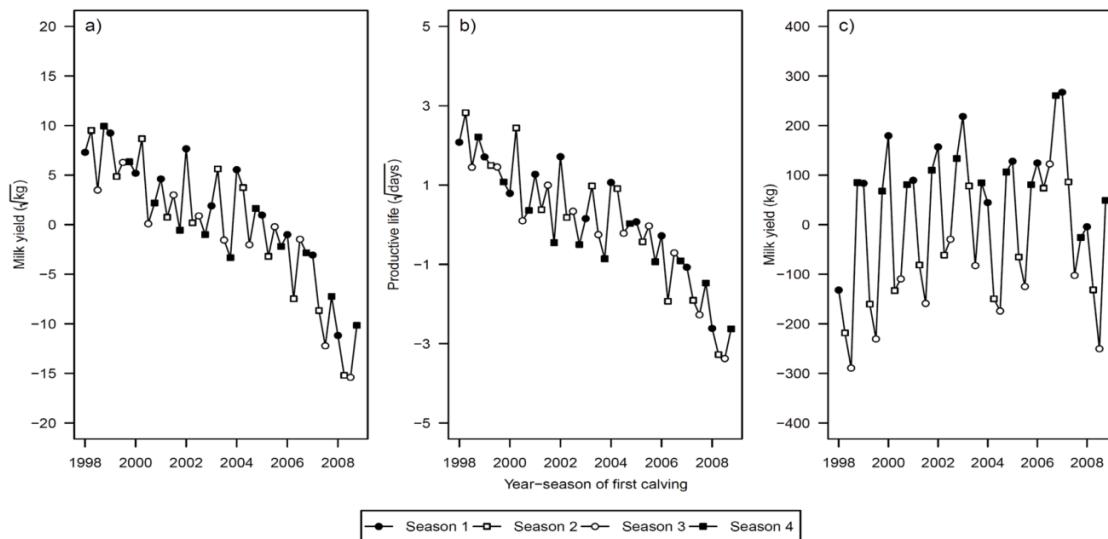


Figure 2. Estimates of year-season effect at first calving on the lifetime milk production a), length of productive life b), and first lactation milk yield c)

Table 2. Estimates of the effect of age at first calving on lifetime milk production (LMP), length of productive life (PL), and first lactation milk yield (MY305)

Age at first calving (months)	$\geq 20 < 22$	$\geq 22 < 25$	$\geq 25 < 28$	$\geq 28 < 31$	$\geq 31 \leq 40$
LMP ($\sqrt{\text{kg}}$)	-1.48	0.08	-0.72	2.82	-0.71
PL ($\sqrt{\text{days}}$)	0.40	0.22	-0.28	0.39	-0.72
MY 305 (kg)	-658	-41	90	232	378

Fixed effects

The effect of year-season oscillated between different seasons. Yearly peaks and bottoms of seasonal effect are rather random in LMP (Figure 2a) and PL (Figure 2b). Oscillations followed a seasonal pattern in MY305 (Figure 2c) where cows with first calving in seasons one and four had the highest MY305 and cows with first calving in seasons two and three had the lowest. This might be the consequence of heat stress, which decreases the feed intake during the period of high temperatures and can occur during seasons two and three.

Increased temperatures have big influence on the feed intake of cows in the first stage of lactation (West et al., 2003). Between the years 1998 and 2007, the environmental conditions improved the MY305, while after the year 2007, there was a

negative trend of environment effect on the MY305 observed. The general trend of the environmental effect on LMP and PL was negative throughout the whole observed period, which might be the consequence of a constant decrease of the population size in Brown cattle (Perpar et al., 2010). For this reason, cows did not have an opportunity to express their lifetime potential as they were culled for the reason of abandoned farming.

There was a stable trend observed for the effect of age at first calving on LMP and PL (Table 2). This is not surprising as the effect of age at first calving was found to be non-significant in a study of PL on the same breed (Jenko et al., 2013a). Older cows at first calving had a higher MY305. Differences between the extreme classes can be related to the differences in the maturity of first calving cows

Table 3. Estimates of the regional effect on the lifetime milk production (LMP) length of productive life (PL), and lactation milk yield (MY305)

	East	Central	West
LMP ($\sqrt{\text{kg}}$)	0.7	4.0	4.7
PL ($\sqrt{\text{days}}$)	1.0	1.	2.1
MY 305 (kg)	62	36	98

Table 4. Estimates of variance components, heritability (h^2), variance ratio for common herd environment (c^2), and variance ratio for the residual (e^2) for lifetime milk production (LMP), length of productive life (PL), and first standard lactation milk yield (MY305)

Variance components / ratios	LMP ($\sqrt{\text{kg}}$)	PL ($\sqrt{\text{days}}$)	MY 305 (kg)
Additive genetic (σ_a^2)	299±43	12.4±2.0	139,178±955
Herd (σ_e^2)	204±21	12.7±1.2	373,442±2,854
Residual (σ_e^2)	1,908±39	106.7±2.0	441,152±6,356
Phenotypic (σ^2)	2,411±36	132.0±2.0	953,773±6,350
h^2	0.12±0.017	0.09±0.015	0.15±0.001
c^2	0.08±0.008	0.09±0.008	0.39±0.003
e^2	0.79±0.018	0.81±0.016	0.46±0.004

or the growth rate before puberty, which were both reported to cause differences in the milk yield (Sejrøsen and Purup, 1997). Positive relationships between the age at first calving and the MY305 are in agreement with Moore et al. (1991).

Regional differences in the environmental conditions influenced management practices and culling reasons. Regional-specific characteristics are finally expressed as differences in LMP, PL, and MY305 (Table 3). In the eastern part of Slovenia, conditions were in favour of MY305, whereas in the western part, better conditions for LMP and PL existed. The longer life of Brown cows in the region with tougher conditions for cattle breeding was also confirmed by a study of functional traits (Jenko et al., 2013a).

Estimates of variance components

Estimated heritability for LMP was 0.12 (Table 2) and was practically the same as the estimates of

0.11 by Hoque and Hodges (1980) or 0.13 by Jairath et al. (1995) obtained in Canadian Holsteins. This shows that the selection of individuals for LMP is reasonable and can be performed. Heritability estimate for MY305 was 0.15 and was lower compared to the heritability estimate of 0.28 for the univariate repeatability model for Slovenian Brown cattle breed (Potočnik, 2001). The obtained heritability estimate was in the lower part of the reported heritabilities for milk yield, which can range from 0.13 to 0.48 (Hoekstra et al., 1994; Veerkamp and Goddard, 1998) and are usually higher for the higher milk production level (Hill et al., 1983). The estimated heritability for PL was 0.09 which is similar to the estimate obtained with the application of survival analysis techniques using a sire-maternal grand sire model for the same population (Jenko, et al., 2013b). Other studies reported heritability of PL in the interval of between 0.02 and 0.21

Table 5. Estimates of the phenotypic, genetic, common herd environment, and residual correlations between the lifetime milk production (LMP), length of productive life (PL), and first standard lactation milk yield (MY305)

Variance component	Trait	LMP ($\sqrt{\text{kg}}$)	PL ($\sqrt{\text{days}}$)
Phenotypic	PL ($\sqrt{\text{days}}$)	0.95±0.001	0.05±0.013
	MY305 (kg)	0.27±0.013	
Genetic	PL ($\sqrt{\text{days}}$)	0.96±0.008	0.23±0.085
	MY305 (kg)	0.48±0.067	
Common herd environments	PL ($\sqrt{\text{days}}$)	0.74±0.025	-0.41±0.052
	MY305 (kg)	0.26±0.057	
Residual	PL ($\sqrt{\text{days}}$)	0.98±0.001	0.16±0.015
	MY305 (kg)	0.26±0.014	

(Sasaki, 2013). This relatively wide range of heritability estimates depends on the data structure and the model applied (Jenko et al., 2013b; Raguž et al., 2014).

The variance of MY305 explained with the common herd environment was 2.7 times bigger compared to the variance explained with additive genetic variance. This means that the management practices are more important compared to the genetic effect for MY305. For PL and LMP, the variances explained by the common herd environment and additive genetic variance were close to each other. According to heritability and the proportion of phenotypic variance explained by the common herd environment, herd management is less important for lifetime performance traits than for MY305, which is in agreement with Zavadilová and Zink (2013). Residual variance remained the main part of the estimated phenotypic variance for all the traits. The proportions of total phenotypic variances that remained unexplained were 79 % for LMP, 81 % for PL, and 46 % for MY305.

Both the phenotypic and genetic correlations between LMP and PL were very strong (Table 5). This shows that LMP and PL are near identical traits and performing selection on one measure will increase the genetic values of the other measure. The phenotypic correlation between LMP and MY305 was much weaker (0.27), and even weaker between PL and MY305 (0.05). However, genetic correlations between MY305 and LMP or PL were stronger than were the phenotypic correlations. The genetic correlation between LMP and MY305 was 0.48,

which shows a moderate predictive ability of MY305 for LMP. A similar result of estimated genetic correlation between the LMP and MY305 (0.56) was obtained in the study of lifetime production traits in the Canadian Holstein population (Hoque and Hedges, 1980). A weak positive (0.23) genetic correlation between PL and MY305 indicates that cows with high potential for milk yield are also genetically superior for PL. Literature reports of genetic correlations between PL and MY305 or survival are in the range of between -0.53 and 0.84 (De Lorenzo and Everett, 1982; Jairath et al., 1995; Dematawewa and Berger, 1998; González-Recio and Alenda, 2007).

There are different reasons for the explanation of positive correlations obtained in the current study. One of them is the method used to analyse the longevity records, which can be analysed as continuous or as survival up to the specific point in time.

Another reason is the preferential treatment of cows with a higher milk yield that are receiving more health treatments compared to the cows with a lower milk yield.

The correlation between the common herd environment effect for PL and MY305 was moderately negative (-0.41). This shows that improvement in the herd environment for MY305 deteriorated the herd environment for PL (Table 5). Zavadilová and Zink (2013) also obtained a weak negative correlation (-0.28) for the common herd-year environment between PL and MY305. When looking at the residuals, there was a weak positive correlation of 0.16 between PL and MY305, meaning that the

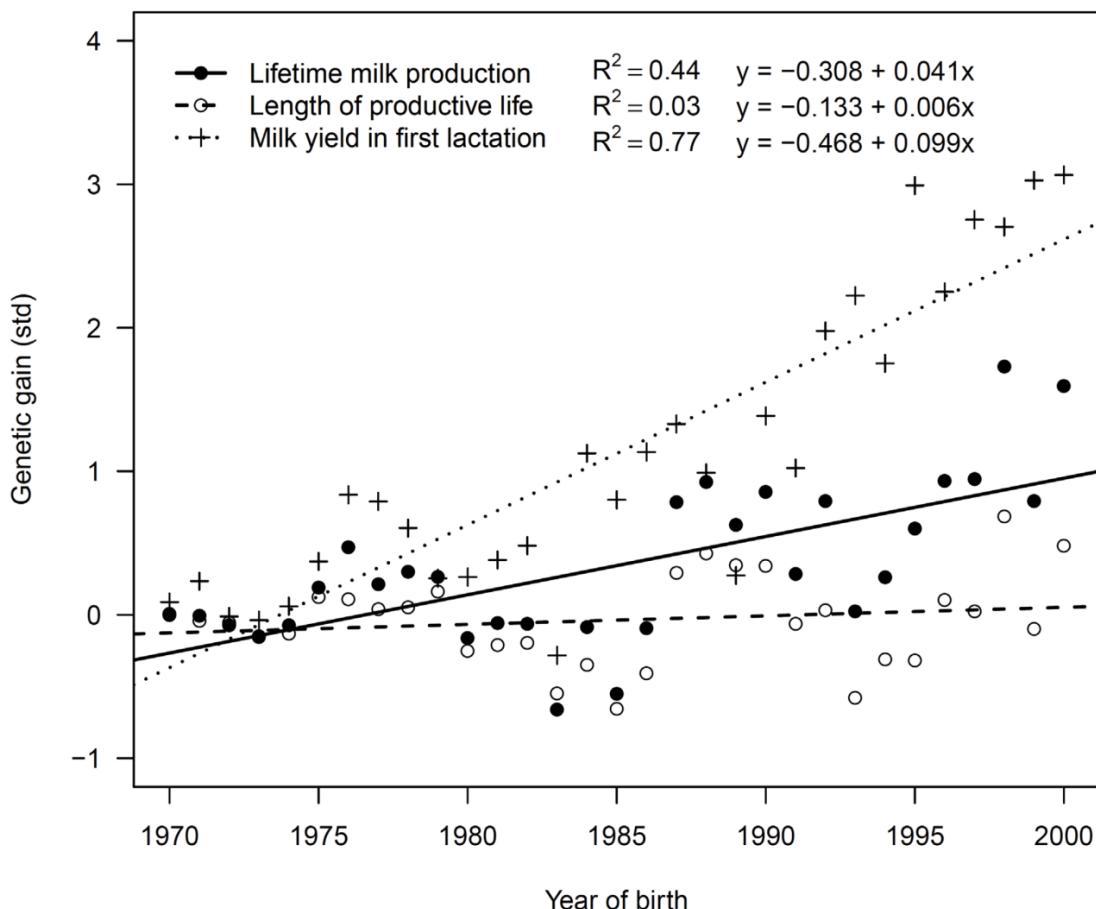


Figure 3. Genetic trend for lifetime milk production, length of productive life, and first lactation milk yield for sires born between 1970 and 2000

improvement in the cow microenvironment for one of the traits will also improve the cow's microenvironment for the other trait. Between the other trait combinations, the correlations in the common herd environments and residuals were always positive but of different strength. It was weak for the common herd environments and the residuals between LMP and MY305 (0.26), strong for the common herd environments between LMP and PL (0.74), and very strong for the residuals between LMP and PL (0.98).

Genetic trend

The linear regression coefficient of the standardised genetic trend for LMP was 0.041 ± 0.009 , whereas for MY305, it was more than two times steeper and was 0.099 ± 0.011 (Figure 3). Genetic trend for PL remained stable as selection on longevity was re-

cently implemented (Potočnik et al., 2011). The presented genetic trends confirm that in the past, the main emphasis in the selection of Brown cattle in Slovenia was on production traits. The first genetic evaluation on a smaller scale started in 1958 (Ferčej, 1965) and in 1974, two yearly breeding value estimation were introduced for milk and fat traits (Pogačar, 1978). Due to the moderate genetic correlation between MY305 and LMP, an improvement in genetic values for LMP was achieved indirectly with the selection for production traits.

Conclusions

It was shown that cows with first calving in a year's colder seasons had higher MY305 compared to the cows that had their first calving in the warmer seasons. This structured pattern of seasonal effect

was not detected for LMP and PL. Very strong genetic correlation (0.96) was found between LMP and PL in Slovenian Brown cattle breeds. This shows that LMP and PL are near identical traits, and performing selection on one of the traits would also affect the change in genetic values for the other trait. The genetic correlation between LMP and MY305 was moderate (0.48) and weak between PL and MY305 (0.23). Herd and residual correlations were, except for the common herd environment between PL and MY305 (-0.41), always positive. The linear regression coefficient of the standardised genetic trend for the last four decades was positive for MY305 (0.099) and LMP (0.041), whereas it was stable for PL.

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Genetska povezanost između životne proizvodnje mlijeka, dugovječnosti i proizvodnje mlijeka u prvoj laktaciji smeđe pasmine goveda u Sloveniji

Sažetak

Za proučavanje genetske povezanosti između životne proizvodnje mlijeka (LMP), količine mlijeka u standardnoj laktaciji (MY305) i dužine produktivnog života (PL) slovenske populacije smeđe pasmine goveda, korišteni su podaci prvih laktacija 14.389 krava kao i životne proizvodnje (LMP i PL) za 12.416 krava. U svrhu dobivanja normalne distribucije, prvobitne vrijednosti za LMP i PL transformirane su pomoću kvadratnog korijena. Fiksni utjecaj interakcije između godine i sezone prvog teljenja razlikovalo se između različitih sezona unutar godine za sva analizirana svojstva. Navedene promjene slijede sezonski uzorak proizvodnje mlijeka u standardnoj laktaciji (MY305) gdje krave koje se tele tijekom hladnijih sezona imaju najvišu MY305 proizvodnju, a krave koje se tele tijekom toplijih godišnjih razdoblja imaju najnižu MY305 proizvodnju. Procijenjeni heritabiliteti su iznosili $0,12 \pm 0,017$ za LMP,

$0,09 \pm 0,015$ za PL i $0,15 \pm 0,001$ za MY305. Genetska korelacija između LMP i PL je bila visoka i pozitivna ($0,96 \pm 0,008$), umjerena i pozitivna korelacija ($0,48 \pm 0,067$) između LMP i MY305, dok je slaba i pozitivna korelacija utvrđena između PL i MY305 ($0,23 \pm 0,085$). Korelacija za utjecaj stada između PL i MY305 bila je umjerena i negativna ($-0,41 \pm 0,052$), slaba i pozitivna između LMP i MY305 ($0,26 \pm 0,057$) te jaka i pozitivna između LMP i PL ($0,74 \pm 0,025$). Tijekom posljednjih 40 godina zabilježen je pozitivan genetski trend za LMP i MY305, dok genetski trend za PL nije moguće detektirati.

Ključne riječi: genetsko vrednovanje, životna proizvodnja mlijeka, količina mlijeka u standardnoj laktaciji, dužina produktivnog života, smeđa pasmina goveda

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2.5 GENETSKO VREDNOTENJE ŽIVLJENJSKE PRIREJE MLEKA GOVEDA V POPULACIJAH MAJHNIH ČRED Z UPORABO NAKLJUČNE REGRESIJE

Janez Jenko¹, Špela Malovrh², Milena Kovač²

¹Kmetijski inštitut Slovenije, Hacquetova 17, 1000 Ljubljana, Slovenija;

²Univerza v Ljubljani, Biotehniška fakulteta, Oddelek za zootehniko, Groblje 3, 1230 Domžale, Slovenija

Neobjavljeni delo

IZVLEČEK

Za napoved plemenskih vrednosti za življenjsko pirejo mleka smo uporabili podatke 638688 dnevnih kontrol mlečnosti, ki so bile opravljene v 131739 kontrolnih dneh med 1. 1. 1998 in 31. 12. 2008 pri 36604 kravah rjave pasme. Korelacijo med napovedanimi plemenskimi vrednostmi za življenjsko pirejo mleka in ostanki korigiranih fenotipskih vrednosti za življenjsko pirejo mleka njihovih hčera smo preverili na testnem nizu 3660 krav, ki so bile potomke 55 bikov. Plemenske vrednosti za življenjsko pirejo mleka smo napovedali v 12 različnih scenarijih, ki so se razlikovali glede vključitve napovedane plemenske vrednosti za količino mleka in mlečne vztrajnosti v prvih treh laktacijah. Za napoved plemenskih vrednosti dnevne količine mleka v prvih treh laktacijah smo uporabili trilastnostni model z naključno regresijo. Dnevno količino mleka smo korigirali za sistematski vpliv stadija brejosti, sezone znotraj leta prve telitve, regije ter (samo za količino mleka v prvi laktaciji) za vpliv starosti ob prvi telitvi. Kot naključni vpliv smo v model vključili vpliv skupnega okolja v čredi in vpliv živali. Sistematski vpliv sezone znotraj leta telitve, naključni vpliv skupnega okolja v čredi in živali, smo modelirali z uporabo Legendrovega polinoma tretje stopnje. Heritabiliteta za dnevno količino mleka se skozi celoten potek prve laktacije ni bistveno spremenila. V času trajanja druge in tretje laktacije je bila heritabiliteta najnižja na začetku laktacije. Povprečna, najnižja in največja ocenjena heritabiliteta za dnevno količino mleka v času prve laktacije je znašala 0,190, 0,175 in 0,200; v času druge laktacije: 0,140, 0,109 in 0,159; ter v času tretje laktacije 0,125, 0,099 in 0,143. Koeficienti korelacije med napovedanimi plemenskimi vrednostmi za življenjsko pirejo mleka očetov in ostanki korigiranih fenotipskih vrednosti življenjske

prireje mleka potomk iz testnega niza so bili nizki (med 0,07 in 0,09). Vključitev mlečne vztrajnosti ali uporaba različnih ekonomskih tež nista izboljšali napovedne moči modela.

UVOD

Razvoj statističnih modelov, ki omogočajo spreminjanje varianc in kovarianc s časom, in zbiranje zaporednih podatkov na ravni živali sta omogočila modeliranje proizvodnih krivulj v obliki analize časovnih vrst. V govedoreji podatki časovnih vrst najpogosteje predstavljajo mase rastočih živali izmerjene ob tehtanjih pri različni starosti, rezultate dnevnih kontrol prireje mleka in zauživanje krme skozi obdobje rasti ali laktacije. Modeli z naključno regresijo razdelijo prispevke k rastnim (Andersen in Pedersen, 1996; Malovrh, 2003; Nobre in sod., 2003; Cue in sod., 2012; Lopes in sod., 2012) oziroma laktacijskim krivuljam (Swalve, 1995, Swalve 2000; Jensen, 2001; Komprej in sod., 2013; Torshizi in sod., 2013; Tullo in sod., 2014) med sistematske vplive, ki oblikujejo splošno proizvodno funkcijo na ravni primerjalne skupine, in naključne vplive, ki opisujejo specifična odstopanja od splošne krivulje pričakovanih vrednosti za posamezne ravni naključnih vplivov. Uporabo modelov z naključno regresijo so prvi predlagali Henderson (1982) ter Laird in Ware (1982). Schaeffer in Dekkers (1994) sta predstavila uporabo naključne regresije za analizo dnevnih meritev količine mleka. Za modeliranje laktacijske krivulje lahko uporabimo različne funkcije. Najbolj poznane so Woodova (Wood, 1967), Wilminkova (Wilminck, 1987), Ali-Schaefferjeva (Ali in Schaeffer, 1987) in Guo-Swalvejeva (Guo in Swalve, 1995). Poskusi vključitve laktacijskih krivulj kot funkcije časovne spremenljivke stadija laktacije so se zaradi prevelike korelacije med parametri naključne regresije, počasne konvergencije in slabšega modeliranja vrha laktacije izkazali za neuspešne (Schaeffer, 2004). V primeru uporabe ortogonalnih polinomov (Legendrovi polinomi, polinomi Čebiševa) so korelacije med parametri precej manjše. S tem je ocena parametrov računsko enostavnejša in število iteracij za doseg konvergencije manjše (Pool in sod., 2000). Kot najenostavnnejši in hkrati najbolj uporabljeni za modeliranje laktacijske krivulje so se izkazali Legendrovi polinomi (Jamrozik in sod., 2001; López-Romero in sod., 2004) in linearni zlepki (White in sod., 1999; Silvestre in sod., 2005; Druet in sod., 2005). Primerjava v prileganju laktacijski krivulji med Legendrovimi polinomi in

linearnimi zlepki je pokazala, da so razlike majhne (Bohmanova in sod., 2008; Pereira in sod., 2013).

Uporaba večlastnostne naključne regresije omogoča napoved plemenskih vrednosti v več laktacijah hkrati za več različnih parametrov. Kanadski model (Schaeffer in sod., 2000) dnevnih meritev za lastnost mlečnosti tako vsebuje 12 lastnosti, s katerimi so napovedane plemenske vrednosti za količino mleka, maščob, beljakovin in število somatskih celic za vsako od prvih treh laktacij. Togashi in Lin (2008) sta za napoved genetskih vrednosti dnevne količine mleka v prvih treh laktacijah za japonsko črno-belo pasmo goveda uporabila trilastnostni model.

Cilj raziskave je napoved plemenskih vrednosti za življenjsko priejo mleka slovenske rjave pasme goveda, za katerega je značilna reja v manjših čredah. Za modeliranje dnevnih meritev za lastnost mlečnosti smo uporabili trilastnostni model z naključno regresijo. Plemensko vrednost za življenjsko priejo mleka smo napovedali z različnimi scenariji, ki se razlikujejo glede vključitve plemenskih vrednosti za različno število laktacij, mlečne vztrajnosti in ekonomskimi težami. Najprimernejši model smo izbrali na podlagi dveh kriterijev. Pri prvem kriteriju smo ocenili korelacije med napovedmi plemenskih vrednosti očetov in ostanki fenotipskih vrednosti hčera iz testnega niza podatkov za življenjsko priejo mleka. Pri drugem kriteriju smo bike glede na njihovo plemensko vrednost razvrstili v štiri razrede in analizirali razlike v ostankih za življenjsko priejo mleka njihovih hčera iz testnega niza podatkov.

MATERIAL IN METODE

Podatki

Podatke o dnevni prieji mleka smo pridobili iz centralno podatkovne zbirke Govedo (Jeretina in sod., 1997). Zajeli smo podatke kontrole prieje mleka opravljene pri kravah rjave pasme, ki so imele prvo kontrolno mlečnost v prvi laktaciji opravljeno po 1. 1. 1998. Podatki so vsebovali 1487304 zapisov dnevnih kontrol prieje mleka, ki so bile opravljene v času od 1. 1. 1998 do 31. 12. 2008 pri 50959 kravah rjave pasme. Iz podatkov smo izločili meritve pridobljene v četrti ali poznejših laktacijah (581321 meritev) ter kontrole

opravljene pred 5. dnem laktacije (1993 meritov) ali po dopolnjenem 314. dnevu laktacije (128654). V nadaljevanju smo izločili 8895 dnevnih kontrol prireje mleka, ki so bile opravljene pri 831 kravah, za katere ni bil znan datum prve telitve in tako nismo mogli izračunati starosti ob prvi telitvi. Starost krav ob prvi telitvi smo navzdol omejili na 20 mesecev, čemur ni zadostilo 108 krav s 1830 dnevnimi kontrolami mlečnosti, in navzgor na 48 mesecev, ko smo izločili 319 krav s 4595 podatki iz dnevnih kontrol prireje mleka. Izločili smo 32 dnevnih kontrol pri štirih kravah, kjer je laktacija sledila brejosti, ki je trajala manj kot 140 dni in 422 dnevnih kontrol pri 51 kravah, ki naj bi bile glede na podatke breje več kot 310 dni. Pri 586 dnevnih kontrolah je od predhodne kontrole minilo manj kot 22 dni, zato smo podatke teh kontrol izločili. Zaradi problema ocenjevanja komponent variance v majhnih čredah smo izločili še 120288 zapisov iz let, kjer sta bili v povprečju na kontrolni dan opravljeni manj kot dve meritvi. Po opravljenem prečiščevanju podatkov smo imeli podatke o dnevni prireji mleka iz 638688 kontrol mlečnosti, ki so bile opravljene v 131739 kontrolnih dneh. Na kontrolni dan je bilo tako v čredi povprečno opravljenih 4,84 kontrole prireje mleka.

Za namen genetskega vrednotenja smo oblikovali poreklo, v katerega smo zajeli živali z meritvami in največ pet generacij prednikov. Skupno je bilo v poreklu zajetih 54746 živali, od tega 1180 bikov in 53566 krav.

Testni niz podatkov

Napovedane plemenske vrednosti za življenjsko prirejo mleka smo preverjali na podatkovnem nizu, kamor smo uvrstili krave, ki so bile rojene po dopolnjenem četrtem letu starosti očeta. Očetje izbranih krav so morali imeti vsaj 20 hčera, ki so bile rojene pred dopolnjenim četrtim letom starosti očeta ter vsaj 20 hčera, ki so bile rojene po dopolnjenem četrtem letu očeta. Krave so morale prihajati iz čred, kjer je bila količina mleka na kontrolni dan v povprečju izmerjena pri več kot petih kravah in so v času od prve telitve do izločitve ostale v isti čredi. Skupaj je tem kriterijem zadostilo 4509 krav, ki so bile potomke 55 bikov in so prihajale iz 373 čred. Izmed teh smo naključno izbrali 3660 krav tako, da je bilo po vsakem biku izbranih vsaj 20 hčera in je iz vsake črede prihajalo vsaj pet hčera. Te krave so predstavljale 10 % vseh krav (3660) in so imele 65078 zapisov

dnevnih kontrol mlečnosti. Testni niz podatkov smo uporabili za analizo razlik pri napovedi življenjske priteje mleka na podlagi različnih scenarijev. Podatke o življenjski priteji mleka smo zbrali iz kontrol priteje mleka, ki so bile opravljene do konca leta 2014.

Statistični model za napoved plemenskih vrednosti

Uporaba večlastnostne naključne regresije omogoča napoved plemenskih vrednosti za več laktacij v enem koraku. Po zgledu Togashi in Lin (2008) smo oblikovali trilastnostni model, s katerim smo napovedali plemenske vrednosti za količino mleka v prvih treh laktacijah (l). Znotraj vsake laktacije smo oblikovali 14 intervalov (t), v katere smo uvrstili izmerjene količine mleka glede na stadij laktacije. Vsak interval je zajemal obdobje 22 dni med 5. in 313. dnem laktacije. Rezultate dnevnih kontrol priteje mleka smo opisali s sistematskimi in naključnimi vplivi. Sistematski del modela za lastnost dnevne količine mleka v prvi laktaciji sestavljajo širje vplivi oziroma trije za dnevno količino mleka v drugi in tretji laktaciji. Vse vplive iz sistematskega dela modela smo predhodno preverili z metodo najmanjših kvadratov v programske paketu R (R Development Core Team, 2008). Vključene vplive smo zaradi lažje primerjave oblikovali podobno kot v analizah dolgoživosti. Starost ob prvi telitvi (P_i) smo vključili kot sistematski vpliv samo za lastnost količine mleka v prvi telitvi. Glede na starost ob prvi telitvi smo krave razvrstili v pet razredov (1: $\geq 20 - 22$ mesecev; 2: $\geq 22 - 25$ mesecev, 3: $\geq 25 - 28$ mesecev, 4: $\geq 28 - 31$ mesecev, 5: $\geq 31 - 40$ mesecev). Zaradi reje govedi rjave pasme na območjih, ki se med seboj razlikujejo glede pogojev reje, smo oblikovali tri območja (R_{lj}) in jih vključili kot sistematski vpliv pri vseh laktacijah. Krave s kmetij na območju vzhodne Slovenije smo uvrstili v prvo regijo, v drugo regijo smo uvrstili krave iz osrednjega dela Slovenije in v tretjo krave iz zahodnega dela Slovenije. Vpliv stadija brejosti (B_{lk}) smo kombinirali z dolžino poporodnega premora in oblikovali šest razredov (Preglednica 1). V prvi razred smo uvrstili meritve iz dnevnih kontrol: (i) pri katerih krave na kontrolni dan niso bile breje ali (ii) so bile breje manj kot 20 tednov ali (iii) je bil poporodni premor daljši od 24 tednov in je bila kontrola opravljena po 44. tednu laktacije. Poporodni premor krajši od 17 tednov je skupen trem razredom, pri katerih so bile krave breje več kot 20 tednov. Zadnja dva razreda za vpliv stadija brejosti sta vključevala dnevne kontrole priteje mleka pri

laktacijah z dolžino poporodnega premora med 17 in 24 tedni ter dolžino brejosti med 20 in 28 tedni. Za oblikovanje vpliva sezone smo leto razdelili na štiri trimesečja (1: januar–marec; 2: april–junij; 3: julij–september; 4: oktober–december) in jih oblikovali kot interakcijo med letom in trimesečji telitve z m razredi. Sezono smo vključili v obliki sistematske regresije kot Legendrov polinom tretje stopnje.

Preglednica 1: Kombinacije vpliva poporodnega premora in stadija brejosti

Dolžina poporodnega premora (tedni)	Dolžina brejosti (tedni)			
	< 20	$\geq 20 - 24$	$\geq 24 - 28$	≥ 28
< 17	1	2	3	4
$\geq 17 - 24$	1	5	6	/
≥ 24	1	1	/	/

Za napoved plemenskih vrednosti smo uporabili naslednji večlastnostni model z vključeno sistematsko in naključno regresijo:

$$\begin{aligned}
y_{ltijkmno} = & [P_i] + R_{lj} + B_{lk} \\
& + \sum_{x=0}^3 S_{lxm} \phi_{lx} (q_{ltijkmno}) \\
& + \sum_{x=0}^3 h_{lxjn} \phi_{lx} (q_{ltijkmno}) \\
& + \sum_{x=0}^3 p_{lxijkmno} \phi_{lx} (q_{ltijkmno}) \\
& + \sum_{x=0}^3 a_{lxijkmno} \phi_{lx} (q_{ltijkmno}) \\
& + e_{ltijkmno}
\end{aligned}$$

kjer pomeni:

$y_{ltijkmno}$ – izmerjena dnevna količina mleka

S_{lxm} – sistematski regresijski koeficient x -te stopnje za vpliv sezone telitve m

$\phi_{lx} (q_{ltijkmno})$ – vrednost standardiziranega Legendrovega polinoma x -te stopnje v stadiju laktacije q

h_{lxjn} – naključni regresijski koeficienti x -te stopnje Legendrovega polinoma za naključni vplivi skupnega okolja v čredi n

$p_{lxijkmno}$ – naključni regresijski koeficienti x -te stopnje Legendrovega polinoma za vpliv permanentnega okolja v laktaciji

$a_{lxijkmo}$ – naključni regresijski koeficienti x -te stopnje Legendrovega polinoma za vpliv živali o

$e_{ltijkmno}$ – nepojasnjeni ostanek

Za modeliranje vpliva sezone in naključnih vplivov smo uporabili Legendrove polinome tretje stopnje. Stadij laktacije smo transformirali v neodvisno spremenljivko z vrednostmi med -1 in +1:

$$q_{ltijkmno} = -1 + 2 \left(\frac{d_{ltijkmno} - d_{min}}{d_{max} - d_{min}} \right)$$

kjer pomeni:

$q_{ltijkmno}$ – standardiziran stadij laktacije

$d_{ltijkmno}$ – stadij laktacije (dni)

d_{min} – najkrajša dolžina laktacije (5 dni)

d_{max} – najdaljša dolžina laktacije (313 dni)

Model lahko zapišemo tudi v matrični obliki:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_h\mathbf{h} + \mathbf{Z}_p\mathbf{p} + \mathbf{Z}_a\mathbf{a} + \mathbf{e}$$

kjer pomeni:

\mathbf{y} – vektor opazovanj

\mathbf{X} – matrika dogodkov za sistematski del modela

$\boldsymbol{\beta}$ – vektor parametrov za sistematski del modela

\mathbf{Z}_h – matrika dogodkov za naključni vpliv skupnega okolja črede in \mathbf{h} pripadajoči vektor regresijskih koeficientov

\mathbf{Z}_p – matrika dogodkov za naključni vpliv permanentnega okolja v laktaciji in \mathbf{p} pripadajoči vektor regresijskih koeficientov

\mathbf{Z}_a – matrika dogodkov za naključni vpliv živali (direktni aditivni genetski vpliv) in \mathbf{a}

pripadajoči vektor parametrov za naključni vpliv živali

e – vektor ostankov

Glede na standardni mešani model matrike dogodkov za sistematski vpliv sezone in naključne vplive namesto 1 vsebujejo vektorje ϕ , medtem ko vrednost 0 nadomeščajo ničelni vektorji.

Pričakovane vrednosti opazovanj:

$$E \begin{bmatrix} \mathbf{y} \\ \mathbf{h} \\ \mathbf{p} \\ \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} X\beta \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}$$

Oblika strukture varianc in kovarianc:

$$\text{var}(\mathbf{y}) = \mathbf{Z}_h \mathbf{K}_h \mathbf{Z}'_h + \mathbf{Z}_p \mathbf{K}_p \mathbf{Z}'_p + \mathbf{Z}_a \mathbf{K}_a \mathbf{Z}'_a + \mathbf{e}$$

$$\text{var} \begin{bmatrix} \mathbf{h} \\ \mathbf{p} \\ \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{K}_h & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{K}_p & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{K}_a & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{R} \end{bmatrix} = \begin{bmatrix} \mathbf{I}_h \otimes \mathbf{K}_{0h} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_p \otimes \mathbf{K}_{0p} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{A} \otimes \mathbf{K}_{0a} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \Sigma^{\otimes} \mathbf{R}_{0i} \end{bmatrix}$$

kjer pomeni:

K_h – matrika varianc in kovarianc za naključne regresijske koeficiente za vpliv skupnega okolja v čredi

K_p – matrika varianc in kovarianc za vpliv permanentnega okolja v laktaciji

K_a – matrika varianc in kovarianc za aditivni genetski vpliv

I_h – identična matrika za vpliv skupnega okolja v čredi

A – matrika sorodstva

R – matrika varianc za ostanek

Ker smo uporabili Legendrov polinom tretje stopnje, je splošna struktura matrike varianc in kovarianc naključnih regresijskih koeficientov za vpliv skupnega okolja v čredi dimenzijsi 4×4 . Za kovariance skupnega okolja v čredi med laktacijami smo predpostavili, da so enake 0.

$$K_h = \begin{bmatrix} K_{h1} & 0 & 0 \\ sim & K_{h2} & 0 \\ sim & K_{h3} \end{bmatrix} = var \begin{bmatrix} h_{1,0} \\ h_{1,1} \\ h_{1,2} \\ h_{1,3} \\ h_{2,0} \\ h_{2,1} \\ h_{2,2} \\ h_{2,3} \\ h_{3,0} \\ h_{3,1} \\ h_{3,2} \\ h_{3,3} \end{bmatrix} = \begin{bmatrix} \sigma_{h1,0}^2 & \sigma_{h1,01} & \sigma_{h1,02} & \sigma_{h1,03} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \sigma_{h1,1}^2 & \sigma_{h1,12} & \sigma_{h1,13} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \sigma_{h1,2}^2 & \sigma_{h1,23} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \sigma_{h1,3}^2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & \sigma_{h2,0}^2 & \sigma_{h2,01} & \sigma_{h2,02} & \sigma_{h2,03} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & \sigma_{h2,1}^2 & \sigma_{h2,12} & \sigma_{h2,13} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & \sigma_{h2,2}^2 & \sigma_{h2,23} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & \sigma_{h2,3}^2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ & & \sigma_{h3,0}^2 & \sigma_{h3,01} & \sigma_{h3,02} & \sigma_{h3,03} & & & & & & \\ & & \sigma_{h3,1}^2 & \sigma_{h3,12} & \sigma_{h3,13} & & & & & & & \\ & & \sigma_{h3,2}^2 & \sigma_{h3,23} & & & & & & & & \\ & & \sigma_{h3,3}^2 & & & & & & & & & \end{bmatrix}$$

kjer pomeni:

K_{h1} , K_{h2} in K_{h3} – matrike varianc in kovarianc naključnih regresijskih koeficientov za vpliv skupnega okolja v čredi znotraj laktacije

Splošna oblika strukture matrik varianc in kovarianc za naključne regresijske koeficiente za vpliv permanentnega okolja v laktaciji in aditivni genetski vpliv je dimenzije 12×12 . Zapis za naključne regresijske koeficiente za vpliv permanentnega okolja je (za aditivni genetski vpliv indeks p zamenjamo z indeksom a):

$$K_s = \begin{bmatrix} K_{p1} & K_{p12} & K_{p13} \\ & K_{p2} & K_{p23} \\ sim & & K_{p3} \end{bmatrix} = var = \begin{bmatrix} p_{1,0} & \left[\begin{array}{cccccccccccc} \sigma_{p1,0}^2 & \sigma_{p1,01} & \sigma_{p1,02} & \sigma_{p1,03} & \sigma_{p12,0} & \sigma_{p12,01} & \sigma_{p12,02} & \sigma_{p12,03} & \sigma_{p13,0} & \sigma_{p13,01} & \sigma_{p13,02} & \sigma_{p13,03} \\ \sigma_{p1,1}^2 & \sigma_{p1,1} & \sigma_{p1,12} & \sigma_{p1,13} & \sigma_{p12,10} & \sigma_{p12,1} & \sigma_{p12,12} & \sigma_{p12,13} & \sigma_{p13,10} & \sigma_{p13,1} & \sigma_{p13,12} & \sigma_{p13,13} \\ \sigma_{p1,2}^2 & & \sigma_{p1,2} & \sigma_{p1,23} & \sigma_{p12,20} & \sigma_{p12,21} & \sigma_{p12,22} & \sigma_{p12,23} & \sigma_{p13,20} & \sigma_{p13,21} & \sigma_{p13,22} & \sigma_{p13,23} \\ \sigma_{p1,3}^2 & & & \sigma_{p1,3} & \sigma_{p12,30} & \sigma_{p12,31} & \sigma_{p12,32} & \sigma_{p12,3} & \sigma_{p13,30} & \sigma_{p13,31} & \sigma_{p13,32} & \sigma_{p13,3} \\ p_{2,0} & & & & \sigma_{p2,0}^2 & \sigma_{p2,01} & \sigma_{p2,02} & \sigma_{p2,03} & \sigma_{p23,0} & \sigma_{p23,01} & \sigma_{p23,02} & \sigma_{p23,03} \\ p_{2,1} & & & & & \sigma_{p2,1}^2 & \sigma_{p2,12} & \sigma_{p2,13} & \sigma_{p23,10} & \sigma_{p23,1} & \sigma_{p23,12} & \sigma_{p23,13} \\ p_{2,2} & & & & & & \sigma_{p2,2}^2 & \sigma_{p2,23} & \sigma_{p23,20} & \sigma_{p23,21} & \sigma_{p23,2} & \sigma_{p23,23} \\ p_{2,3} & & & & & & & \sigma_{p2,3}^2 & \sigma_{p23,30} & \sigma_{p23,31} & \sigma_{p23,32} & \sigma_{p23,3} \\ p_{3,0} & & & & & & & & \sigma_{p3,0}^2 & \sigma_{p3,01} & \sigma_{p3,02} & \sigma_{p3,03} \\ p_{3,1} & & & & & & & & & \sigma_{p3,1}^2 & \sigma_{p3,12} & \sigma_{p3,13} \\ p_{3,2} & & & & & & & & & & \sigma_{p3,2}^2 & \sigma_{p3,23} \\ p_{3,3} & & & sim & & & & & & & & \sigma_{p3,3}^2 \end{array} \right] \end{bmatrix}$$

kjer pomeni:

K_{p1} , K_{p2} in K_{p3} – matrike varianc in kovarianc naključnih regresijskih koeficientov za vpliv permanentnega okolja znotraj laktacije

K_{p12} , K_{p13} , K_{p21} , K_{p23} , K_{p31} in K_{p32} – matrike kovarianc naključnih regresijskih koeficientov za vpliv permanentnega okolja med laktacijami z dimenzijami 4×4

Matrika varianc za ostanek (\mathbf{R}) je direktna vsota (\sum^{\otimes}) varianc za ostanek pri meritvah merjenih na isti živali (\mathbf{R}_{00}).

$$\mathbf{R}_{00} = \begin{bmatrix} \sigma_{eo11}^2 & 0 & \cdots & 0 \\ & \sigma_{eo12}^2 & \cdots & 0 \\ & & \ddots & 0 \\ sim & & & \sigma_{eolt}^2 \end{bmatrix} = diag(\sigma_{eolt}^2)$$

Izpeljane napovedi genetskih vrednosti za plemensko vrednost na dan laktacije, standardno laktacijo in vztrajnost.

Matrika koeficientov Legendrovih polinomov tretje stopnje je dimenzije 308×12 in jo lahko za vse tri laktacije skupaj zapišemo kot:

$$\Phi = [\Phi_1 \Phi_2 \Phi_3]$$

kjer pomeni:

Φ_1 , Φ_2 in Φ_3 – matrike vrednosti Legendrovih polinomov za posamezno laktacijo.

Za izračun matrike komponent varianc in kovarianc za skupno okolje v čredi (\mathbf{C}_h), permanentno okolje v laktaciji (\mathbf{C}_p) in aditivni genetski vpliv (\mathbf{C}_p) smo uporabili splošno enačbo za izračun komponent varianc in kovarianc (\mathbf{C}_s):

$$\mathbf{C}_s = \Phi \mathbf{K}_s \Phi'$$

Vektor napovedi plemenskih vrednosti (\mathbf{npv}_{lo}) za dnevno količino mleka med 5. in 313. dnem laktacije za posamezno žival smo izračunali kot:

$$\mathbf{npv}_{lo} = \Phi_1 \mathbf{a}_{lo}$$

Z množenjem vektorja napovedi plemenskih vrednosti za dnevno količino mleka med 5. in 309. dnem laktacije z vektorjem enk dimenzije 1×305 smo napovedali plemensko vrednost za količino mleka v standardni laktaciji (\mathbf{snpv}_l):

$$\text{snpv}_l = \mathbf{1}' \mathbf{n} \mathbf{p} \mathbf{v}_l$$

Plemensko vrednost za mlečno vztrajnost znotraj vsake laktacije (V_l) smo izračunali tako, da smo od napovedi plemenskih vrednosti za dnevno količino mleka na 280. dan laktacije ($\text{snpv}_{l,280}$) odšteli plemensko vrednost za dnevno količino mleka na 30. dan laktacije ($\text{snpv}_{l,30}$):

$$V_l = \text{snpv}_{l,280} - \text{snpv}_{l,30}$$

Na podlagi napovedanih plemenskih vrednosti za količino mleka in mlečno vztrajnost smo oblikovali 12 scenarijev napovedi plemenskih vrednosti za življenjsko prirejo mleka (Preglednica 2). Pri štirih scenarijih (Sce_1, Sce_4, Sce_7 in Sce_{10}) smo plemenske vrednosti za življenjsko prirejo mleka napovedali samo na podlagi plemenskih vrednosti za količino mleka, pri osmih scenarijih smo dodali 50-kratnik (Sce_2, Sce_5, Sce_8 in Sce_{11}) oziroma 305-kratnik (Sce_3, Sce_6, Sce_9 in Sce_{12}) napovedi plemenske vrednosti za mlečno vztrajnost, pri treh scenarijih (Sce_{10}, Sce_{11} in Sce_{12}) smo za napovedi plemenske vrednosti za količino mleka znotraj posamezne laktacije uporabili različne ekonomske teže.

Preglednica 2: Scenariji za napoved plemenskih vrednosti za življenjsko prirejo mleka

Napoved plemenske vrednosti za mlečno vztrajnost	Napoved plemenske vrednosti za količino mleka			
	snpv_l	$\sum_{l=1}^L \text{snpv}_l$	$\sum_{l=1}^L \text{snpv}_l$	$1,1 \cdot \text{snpv}_l + 1,05 \cdot \text{snpv}_2 + \text{snpv}_3$
Število laktacij (L)	1	2	3	3
$0 \cdot \sum_{l=1}^L V_l$	Sce_1	Sce_4	Sce_7	Sce_{10}
$50 \cdot \sum_{l=1}^L V_l$	Sce_2	Sce_5	Sce_8	Sce_{11}
$305 \cdot \sum_{l=1}^L V_l$	Sce_3	Sce_6	Sce_9	Sce_{12}

Napovedane plemenske vrednosti za življenjsko prirejo mleka pri 55 bikih, katerih potomke smo uvrstili v testni niz, smo primerjali s povprečno življenjsko prirejo mleka

potomk iz testnega niza. Živiljenjsko prirejo mleka potomk iz testnega niza (y_{mno}) smo predhodno korigirali za sistematski vpliv sezone znotraj leta telitve (S_m) ter za sistematski vpliv skupnega okolja v čredi (H_n):

$$y_{mno} = \mu + S_m + H_n + e_{mno}$$

Za namen analize povezave med ostanki fenotipskih vrednosti živiljenjske prireje mleka krav (e_{mno}) iz testnega niza in plemenskih vrednosti za živiljenjsko prirejo mleka njihovih očetov, pridobljeno iz scenarijev za napoved živiljenjske prireje mleka, smo bike glede na napovedano plemensko vrednost razvrstili v štiri kvartile. Na podlagi razvrstitve bikov smo njihove potomke uvrstili v enega izmed štirih razredov. V prvem razredu so bile tako potomke bikov z najmanjšo plemensko vrednostjo za živiljenjsko prirejo mleka, medtem ko so bile v četrtem razredu potomke bikov z največjo plemensko vrednostjo za živiljenjsko prirejo mleka. Vse potomke posameznega bika so bile tako razvrščene v isti razred. Razlike med srednjimi vrednostmi ostankov posameznih razredov znotraj različnih scenarijev smo testirali z uporabo kontrastov.

Komponente varianc in kovarianc za regresijske koeficiente Legendrovih polinomov smo ocenili z uporabo metode največje zanesljivosti v programu VCE 6 (Groeneveld in sod., 2010). Izračun ocen komponent varianc in kovarianc za dnevno količino mleka, napovedi plemenske vrednosti in primerjavo med scenariji za napoved živiljenjske prireje mleka smo opravili v programskem paketu R (R Development Core Team, 2014).

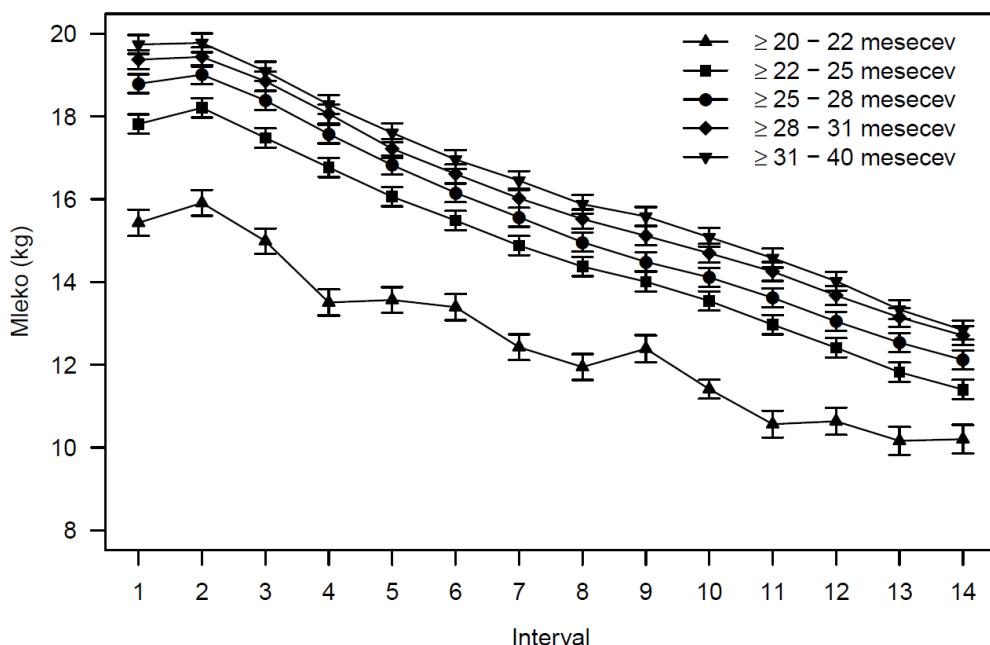
REZULTATI IN RAZPRAVA

Za nastavitev sistema enačb in izračun komponent parametrov disperzije (varianc in kovarianc) smo porabili 11,3 GB delovnega spomina. Konvergenčni kriterij je bil dosežen po 96 iteracijah v 2 dneh in 16 urah na računalniku opremljenim s procesorjem Intel Xeon X5650, katerih jedra delujejo pri hitrosti 2,66 GHz.

Sistematski vplivi

Za vsakega od sistematskih vplivov smo najprej izračunali povprečno vrednost za prirejo mleka znotraj vsake ravni vpliva in časovnega intervala znotraj laktacije. V nadaljevanju smo navedli razlike med nivoji znotraj vsakega vpliva ocenjene z večlastnostnim modelom z vključeno naključno regresijo.

Starost ob prvi telitvi smo kot sistematski vpliv vključili samo pri lastnosti dnevne količine mleka v prvi laktaciji. Starejše kot so bile krave ob prvi telitvi, večja je bila dnevna količina mleka v prvi laktaciji (Slika 1). Negativen vpliv manjše starosti ob prvi telitvi na prirejo mleka v prvi laktaciji je dobro znan. Za vsak mesec dni nižja starost ob prvi telitvi naj bi tako zmanjšala količino mleka v prvi laktaciji za med 56 in 60 kg (Pirlo in sod., 2000; Berry in Cromie, 2009), kar se ujema z našo ugotovitvijo za starost krav ob prvi telitvi med 22 in 25 meseci (Preglednica 3). Čeprav se lahko negativen učinek prenizke starosti ob prvi telitvi na količino mleka v prvi laktaciji zmanjša s hitrejšo rastjo in posledično večjo maso živali ob prvi telitvi (Dobos in sod., 2004), prehitra rast v predpubertetnem obdobju negativno vpliva na razvoj mlečne žleze in ima za posledico manjšo prirejo mleka (Sejrsen in sod., 2000; Le Cozler in sod., 2008). Največja razlika v dnevni količini mleka je bila opažena med razredoma, kjer so bile krave ob prvi telitvi najmlajše. Razlika med srednjo vrednostjo za starost ob prvi telitvi med prvim in drugim razredom je znašala 2,5 meseca, torej se je za 1 mesec zmanjšanja starosti ob prvi telitvi dnevna prireja mleka zmanjšala za 0,84 kg, kar je nekoliko več, kot poroča Haworth (2008) za krave mlajše od 2 let ob prvi telitvi (0,6 kg).

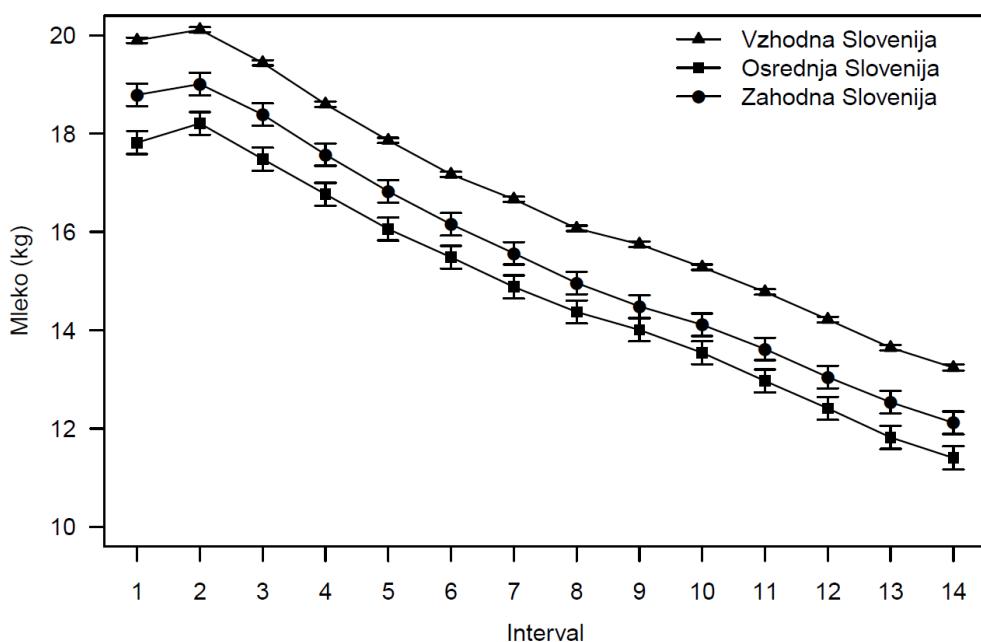


Slika 1: Povprečna prireja mleka na kontrolni dan glede na starost ob prvi telitvi (v mesecih) v prvi laktaciji.

Preglednica 3: Razlike v prireji mleka glede na starost ob prvi telitvi

Razred starosti prve telitve (mesec)	$\geq 22 - 25$	$\geq 25 - 28$	$\geq 28 - 31$	$\geq 31 - 40$
Odstopanje od prvega razreda (kg) za različna obdobja	1 dan	2,10	2,68	3,14
	30 dni	63	80,4	94,2
	305 dni	641	818	958
				1071

V povprečju so največjo količino mleka na kontrolni dan namolzli rejci na območju vzhodne Slovenije (Slika 2). Nekoliko manjšo količino mleka po kravi so priredili v osrednji Sloveniji in najmanj na območju zahodne Slovenije. Razlike v prirejeni količini mleka so se v višjih laktacijah povečevale (Preglednica 4). Razloge za razlike v povprečni dnevni prireji mleka med posameznimi območji gre iskati v različnih pogojih reje. Za območje zahodne Slovenije so značilni težji pogoji prireje, kar se kaže tudi preko večjega deleža območij z omejenimi možnostmi za kmetijstvo (Ministrstvo za kmetijstvo in okolje RS, 2007). Za zahodni del Slovenije so značilna kraška tla, ki nimajo visoke kapacitete zadrževanja vode, kar otežuje pridelavo kakovostne krme.



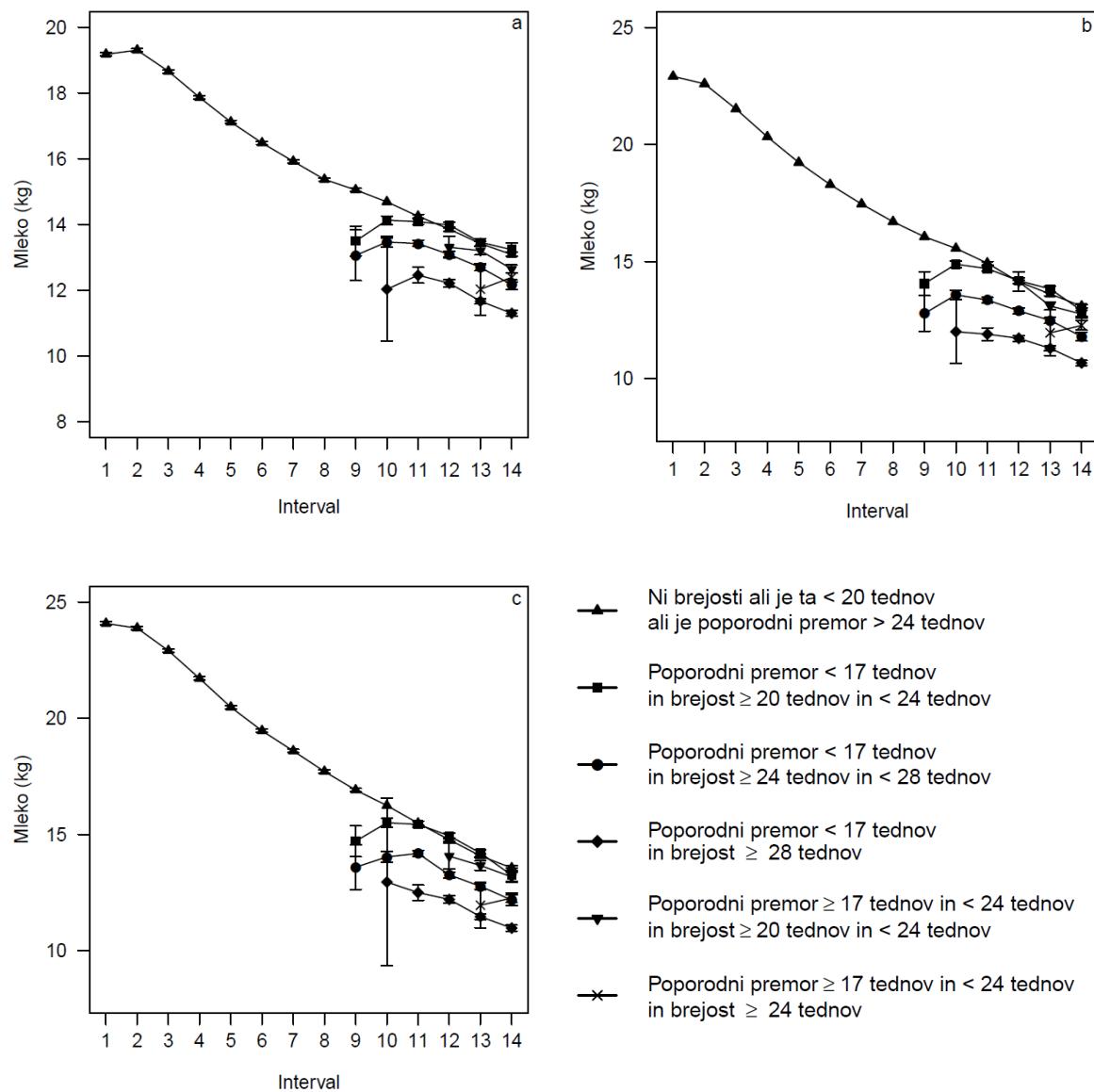
Slika 2: Povprečna prireja mleka na kontrolni dan glede regijo za prve tri laktacije.

Preglednica 4: Vpliv regije na prirejo mleka (kg) v prvih treh laktacijah kot odstopanje od vpliva vzhodne regije za različno dolga obdobja

Laktacija	Regija					
	Osrednja			Zahodna		
	1 dan	30 dni	305 dni	1 dan	30 dni	305 dni
1	-0,82	-24,6	-250	-1,48	-44,4	-451
2	-1,20	-36,0	-366	-1,76	-52,8	-537
3	-1,23	-36,9	-375	-1,75	-52,5	-534

Dnevna količina mleka se je s poznejšim stadijem brejosti zmanjšala (Slika 3). Padec količine mleka zaradi brejosti je posledica povečanih potreb ploda po hranih za rast in razvoj predvsem v zadnjih 4 mesecih brejosti (Olori in sod., 1997; Haile-Mariam in sod., 2003). Krajši kot je bil poporodni premor in daljša kot je bila brejost, manjša je bila dnevna količina mleka. Vpliv brejosti je bil še posebej izražen pri kravah z izrazito kratkim poporodnim premorom (Preglednica 5). V primeru, da dnevnih kontrol prireje mleka ne bi korigirali za vpliv brejosti, bi se to najbolj izrazilo v nižji plemenski vrednosti za mlečno vztrajnost pri živalih s kratkim servisnim intervalom in visoko uspešnostjo osemenitev (Pereira in sod., 2011). Brejost je imela najmanjši vpliv na dnevno količino mleka v prvi

laktaciji. Z vsako naslednjo laktacijo se je vpliv brejosti povečeval znotraj vseh razredov brejosti in dolžine poporodnega premora.



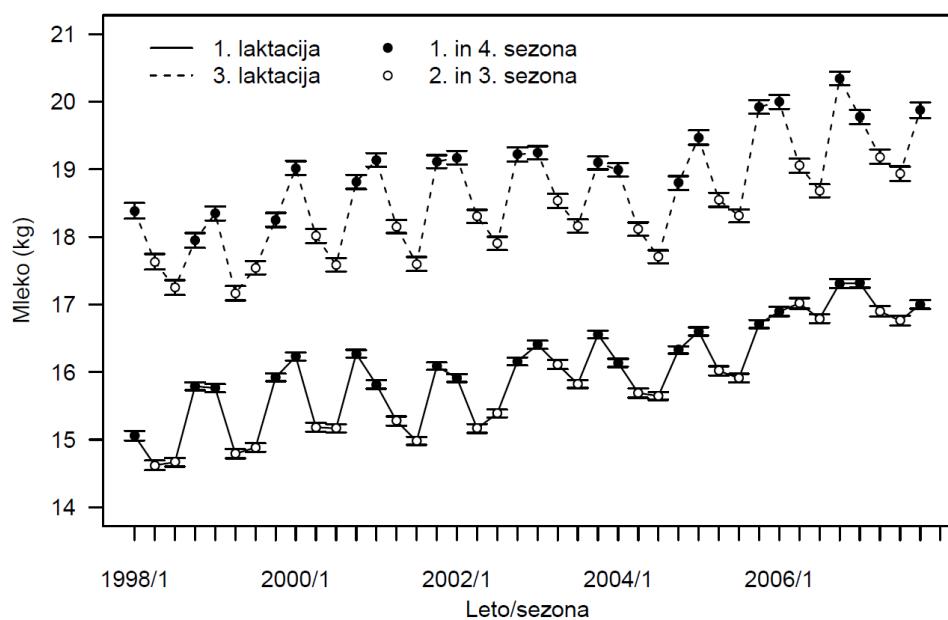
Slika 3: Povprečna prireja mleka na kontrolni dan glede na stadij brejosti in dolžino poporodnega premora za prve tri laktacije.

Preglednica 5: Vpliv stadija brejosti in dolžine poporodnega premora na dnevno količino mleka (kg) v prvih treh laktacijah kot odstopanje od prvega razreda brejosti

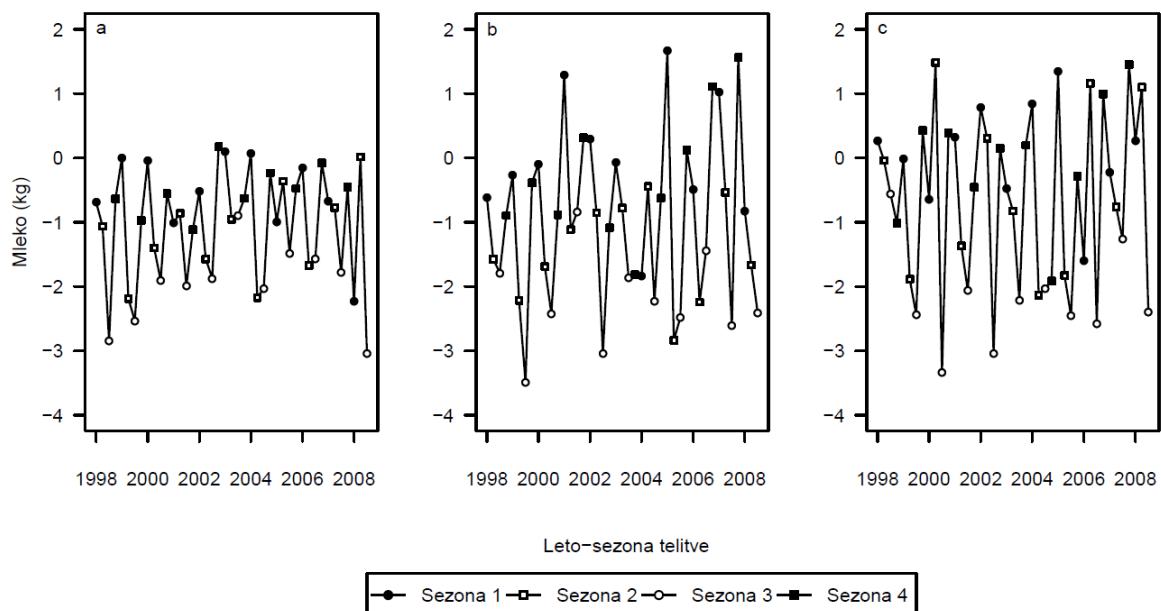
Laktacija	Razred brejosti in dolžine poporodnega premora*				
	2	3	4	5	6
1	-2,30	-3,16	-4,19	-3,30	-3,86
2	-3,44	-4,87	-6,60	-4,76	-5,50
3	-3,79	-5,40	-7,30	-5,29	-6,32

*Razredi brejosti in dolžine poporodnega premora: 1: ni brejosti ali brejost < 20 tednov ali poporodni premor > 24 tednov in kontrola opravljena po 44. tednu laktacije; 2: poporodni premor < 17 tednov in brejost ≥ 20 in < 24 tednov; 3: poporodni premor < 17 tednov in brejost ≥ 24 in < 28 tednov; 4: poporodni premor < 17 tednov in brejost ≥ 28 tednov; 5: brejost ≥ 20 in < 24 tednov in poporodni premor ≥ 17 in < 24 tednov; 6: brejost ≥ 24 tednov in poporodni premor ≥ 17 in < 24 tednov

Povprečna priteja mleka na kontrolni dan se je z leti povečevala (Slika 4), kar je predvsem posledica genetskega napredka, saj v modelu za oceno dnevnih mlečnosti med posameznimi leti ni opazen trend rasti oziroma padca v dnevni količini mleka (Slika 5). Okolje se v opazovanem obdobju torej ni izboljšalo. Glede na to, da glavni vir krme krav rjave pasme v času poletja predstavlja paša in pozimi travna silaža in mrva ter v manjšem obsegu koruzna silaža, je tak rezultat tudi pričakovani, saj se energijska vrednost travnih silaž in mrve v obdobju med leti 2000 in 2010 ni izboljšala (Perpar in sod., 2010; Verbič in sod., 2011). Vpliv sezone telitve znotraj let kaže na pozitiven vpliv prve in četrte sezone. V primeru, da je bila telitev v obdobju tretje sezone, je bila dnevna količina mleka najmanjša. Glavni razlog za razlike v dnevni priteji mleka gre iskati v negativnem vplivu vročinskega stresa na krave molznice, ki zmanjša sposobnost zauživanja krme, otežuje dihanje in oddajanje toplotne ter poveča izločanje slin, kar vodi v zmanjšano pritejo mleka, plodnostne motnje in zdravstvene težave (Bohmanova, 2006). Najmanjši vpliv je imela sezona telitve na dnevno količino mleka v prvi laktaciji, kar je delno posledica nižje priteje mleka v prvi laktaciji. Vpliv sezone bi lahko vključili tudi v obliki sezone, ko je bila opravljena kontrola priteje mleka. Ker je poznan vpliv sezone telitve na življenjsko pritejo mleka (Jenko in Perpar, 2013), smo ga vključili v obliki sezone telitve.



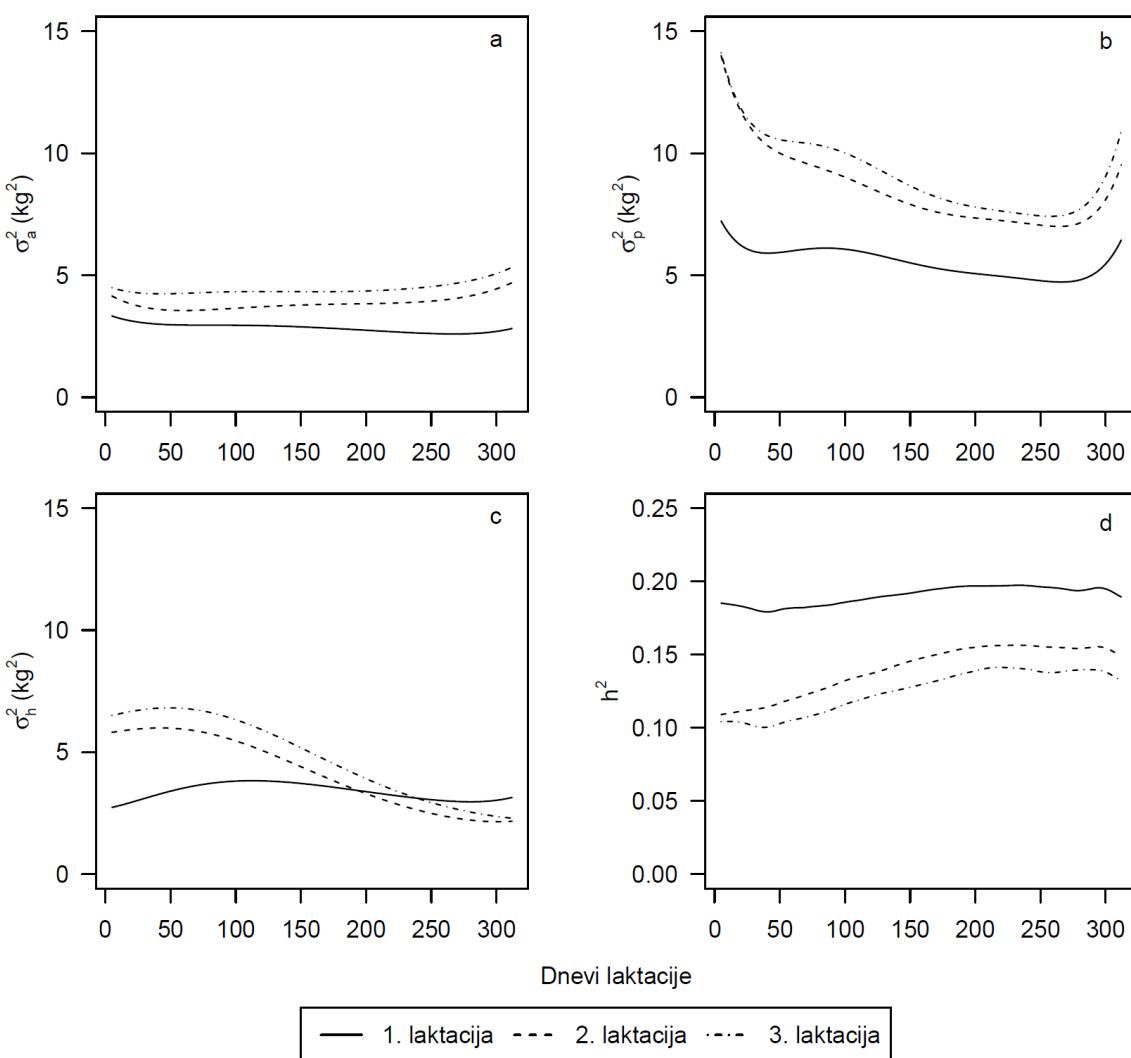
Slika 4: Povprečna prireja mleka na kontrolni dan glede na leto in mesec prve telitve za prvo in tretjo laktacijo.



Slika 5: Vpliv sezone telitve na dnevno količino mleka v prvi (a), drugi (b) in tretji (c) laktaciji kot odstopanje od vpliva zadnje sezone v letu 2008.

Ocena komponent varianc

Aditivna genetska varianca za lastnost dnevne količine mleka v laktaciji je bila najmanjša v prvi laktaciji (Slika 6a). Znotraj vseh laktacij je zaznati rahel padec aditivne genetske variance v prvih dneh in porast v zadnjih dneh laktacije. Posebej izrazite razlike v padcu oziroma porastu variance na začetku oziroma koncu laktacije so opazne pri vplivu permanentnega okolja v laktaciji. Za vse laktacije je značilno, da je varianca permanentnega okolja v laktaciji večja, kot je varianca aditivnega genetskega vpliva (Slika 6b). Varianca za vpliv skupnega okolja v čredi se v času prve laktacije ni bistveno spremojala, medtem ko je za lastnosti dnevne količine mleka v drugi in tretji laktaciji proti koncu laktacije padla (Slika 6c). Heritabiliteta za dnevno količino mleka se skozi prvo laktacijo ni bistveno spremenila, v drugi in tretji laktaciji je bila heritabiliteta nižja na začetku laktacije (Slika 6d). Do dvestotega dne se je povečevala ter do konca laktacije ostala na podobni ravni. Povprečno, najnižje in najvišje ocenjena heritabiliteta za dnevno količino mleka v času prve laktacije je znašala 0,190, 0,175 in 0,200. Glede na to, da lahko zasledimo raziskave, ki navajajo oceno za heritabiliteto tudi do 0,59 (Jamrozik in Schaeffer, 1997), so ocnjene heritabilitete za dnevno količino mleka v prvi laktaciji nizke, vendar se ujemajo z ocenami iz podobnih raziskav (Druet in sod., 2003; McCarthy in Veerkamp, 2012). Razloge za nizke heritabilite lahko iščemo v veliki varianci permanentnega okolja v laktaciji, kar kaže na velike spremembe okolja v času poteka laktacije. Heritabiliteta za dnevno količino mleka v času druge in tretje laktacije je bila nekoliko nižja. Ocena se je gibala med 0,109 in 0,159 za dnevno količino mleka v času druge laktacije ter med 0,099 in 0,143 za dnevno količino mleka v času tretje laktacije. Padec heritabilitete v poznejših laktacijah se ujema z ugotovitvami raziskave, ki sta jo opravila Lindauer in Mäntysaari (1999). Nasprotno pa nekateri drugi raziskovalci ugotavljamjo, da so razlike v heritabiliteti med posameznimi laktacijami majhne (Jamrozik in sod., 1997; Muir in sod., 2007).



Slika 6: Aditivna genetska varianca (a), varianca za vpliv permanentnega okolja laktacije (b), varianca za skupno okolje v čredi (c) in heritabiliteta za dnevno količino mleka v prvih treh laktacijah (d).

Povezava med plemensko vrednostjo očetov za živiljenjsko prirejo mleka in povprečno živiljenjsko prirejo mleka potomk testnega niza

Koeficienti korelacije med napovedanimi plemenskimi vrednostmi za živiljenjsko prirejo mleka za očete in ostanki korigiranih fenotipskih vrednosti živiljenjske prireje mleka potomk iz testnega niza so bili nizki (Preglednica 6). Dodatek plemenskih vrednosti druge in tretje laktacije (Sce_4, Sce_7 in Sce_{10}) ni spremenil vrednosti korelacijskega koeficiente, kakor tudi ne vključitev mlečne vztrajnosti v obliki 50-kratnika razlike med plemensko

vrednostjo za dnevno količino mleka na 280. in 30. dan v laktaciji (Sce_2, Sce_5, Sce_8 in Sce_{11}). Vključitev mlečne vztrajnosti, v obliki 305-kratnika razlike med plemensko vrednostjo za dnevno količino mleka na 280. in 30. dan v laktaciji, je zmanjšala vrednost koeficienta korelacji za scenarije, kjer je bila življenska priteja mleka napovedana na podlagi plemenskih vrednosti več laktacij (Sce_6, Sce_9 in Sce_{12}). V primeru uporabe plemenske vrednosti prve laktacije (Sce_3) pa je le-ta ostala nespremenjena. Sprememba ekonomskih tež z večjim poudarkom na plemenskih vrednostih prve in druge laktacije (Sce_{10}, Sce_{11} in Sce_{12}) je glede na scenarije z enakim prispevkom vseh laktacij (Sce_7, Sce_8 in Sce_9) povečala vrednost koeficienta korelacji za 0,01 za scenarij, kjer je bil velik poudarek na mlečni vztrajnosti (Sce_{12}). Nizka vrednost korelacijskih koeficientov kaže na šibko napovedno točnost uporabljenih scenarijev za napoved življenske priteje mleka. Glede na podobne vrednosti koeficientov korelacji ne moremo določiti scenarija, s katerim bi najbolje napovedali plemenske vrednosti za življensko pritejo mleka.

Preglednica 6: Korelacije med plemensko vrednostjo za življensko pritejo mleka očetov in ostanki za korigirano življensko pritejo mleka njihovih potomk vključenih v testni niz glede na scenarij napovedi življenske priteje mleka

Scenarij	Sce_1	Sce_2	Sce_3	Sce_4	Sce_5	Sce_6	Sce_7	Sce_8	Sce_9	Sce_{10}	Sce_{11}	Sce_{12}
Koeficient korelacji	0,09	0,09	0,09	0,09	0,09	0,08	0,09	0,09	0,07	0,09	0,09	0,08

Srednje vrednosti za ostanke življenske priteje mleka so bile v desetih izmed dvanajstih scenarijev najnižje v 1. razredu, kamor so bile uvrščene potomke bikov z najnižjo plemensko vrednostjo za življensko pritejo mleka (Preglednica 7). Potomke bikov z največjo plemensko vrednostjo za življensko pritejo mleka (4. razred) so dosegla največjo pritejo mleka v življenju v desetih izmed dvanajstih scenarijev. V scenarijih, v katerih je bil velik poudarek pri izračunu plemenske vrednosti za življensko pritejo mleka na mlečni vztrajnosti in je bila ekomska teža za plemensko vrednost posamezne laktacije enaka (Sce_6 in Sce_9), so največjo pritejo mleka v življenju dosegale potomke bikov, ki so se glede na plemensko vrednost uvrstile v 3. razred. Prevelik poudarek na mlečno vztrajnost ima tako negativen vpliv na življensko pritejo mleka. Največja razlika med razredi za srednje vrednosti ostankov je bila dosežena v scenariju Sce_1 in najmanjša v scenariju Sce_9 .

Preglednica 7: Srednje vrednosti ostankov za korigirano življenjsko pritejo mleka potomk testnega niza glede na plemensko vrednost očetov in scenarij napovedi življenjske priteje mleka*

Scenarij	1. razred	2. razred	3. razred	4. razred
Sce ₁	-1312 ± 528 ^a	-697 ± 716 ^{ab}	-22 ± 648 ^b	1481 ± 684 ^c
Sce ₂	-1343 ± 485 ^a	-547 ± 716 ^{ab}	510 ± 638 ^b	720 ± 624 ^b
Sce ₃	-1278 ± 486 ^a	-158 ± 486 ^b	434 ± 657 ^b	623 ± 628 ^b
Sce ₄	-1312 ± 528 ^a	-697 ± 528 ^{ab}	510 ± 671 ^{bc}	720 ± 658 ^c
Sce ₅	-1343 ± 485 ^a	-547 ± 485 ^{ab}	510 ± 638 ^b	720 ± 624 ^b
Sce ₆	-1488 ± 479 ^a	-206 ± 479 ^b	709 ± 651 ^b	556 ± 617 ^b
Sce ₇	-1312 ± 528 ^a	-697 ± 528 ^{ab}	510 ± 671 ^{bc}	720 ± 658 ^c
Sce ₈	-1343 ± 485 ^a	-547 ± 485 ^{ab}	510 ± 638 ^b	720 ± 624 ^b
Sce ₉	-823 ± 508 ^a	-901 ± 508 ^a	672 ± 707 ^b	597 ± 624 ^b
Sce ₁₀	-1312 ± 528 ^a	-697 ± 528 ^{ab}	510 ± 671 ^{bc}	720 ± 658 ^c
Sce ₁₁	-1343 ± 485 ^a	-547 ± 485 ^{ab}	510 ± 638 ^b	720 ± 624 ^b
Sce ₁₂	-823 ± 507 ^{ab}	-901 ± 507 ^a	493 ± 696 ^{bc}	702 ± 628 ^c

*Vrednosti z različnimi črkami v vrstici so statistično značilno različne

ZAKLJUČEK

Uporaba večlastnostne naključne regresije na rezultatih dnevnih kontrol priteje mleka prvih treh laktacij v majhnih čredah je mogoča, vendar bo učinek na povečanje življenjske priteje mleka v populaciji majhen. Korelacija med napovedmi plemenskih vrednosti za življenjsko pritejo mleka očetov in ostanki korigiranih vrednosti za življenjsko pritejo mleka potomk testnega niza je bila majhna. Primerjava med različnimi scenariji za napoved življenjske priteje mleka je pokazala, da vključitev plemenskih vrednosti druge in tretje laktacije ter mlečne vztrajnosti ne izboljša korelacije. Prevelik poudarek na mlečno vztrajnost vrednost korelacijskega koeficienta celo zmanjša. Primerjava srednjih vrednosti ostankov življenjske priteje mleka potomk testnega niza razvrščenih v štiri skupine glede na plemensko vrednost očetov je to potrdila. Razlika v srednjih vrednostih ostankov med skupinami je bila največja v scenariju, kjer je bila v model vključena samo količina mleka v prvi laktaciji.

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3 RAZPRAVA IN SKLEPI

3.1 RAZPRAVA

Čeprav se je odbira govedi z namenom izboljšanja dolgoživosti z uporabo analize preživetja v svetu pričela že v 80. letih 19. stoletja (Ducrocq in sod., 1988), se ta v Sloveniji izvaja šele od leta 2010 (Logar in sod., 2009; Potočnik in sod., 2011). Razlogov za pozno uvedbo je več. Eden izmed glavnih je verjetno relativna dobra dolgoživost krav v slovenski populaciji. Primerjava dolgoživosti krav v slovenski populaciji, ki so imele prvo telitev v času od 1. 1. 1995 do 31. 12. 2000 glede na populacijo krav v ZDA, ki so imele prvo telitev med 1. 1. 1980 in 2. 3. 2005, je pokazala boljšo preživitveno sposobnost krav v slovenski populaciji. Delež krav, ki dočakajo peto laktacijo, je bil v Sloveniji 40,7 % za rjavo in 32,5 % za črno-belo pasmo, medtem ko je ta delež v ZDA znašal 20,9 % za rjavo oziroma 18,4 % za črno-belo pasmo (Hare in sod., 2006; Jenko in sod., 2007). Zaradi precej manjše mlečnosti v standardni laktaciji, je razumljivo, da rejci v Sloveniji še vedno želijo izboljšati predvsem mlečnost. V primerjavi z ZDA je bila prirejena količina mleka v standardni laktaciji v Sloveniji v letu 2013 manjša za 35,3 % pri rjavi pasmi in 32,7 % pri črno-beli pasmi (Sadar in sod., 2014; ICAR, 2015).

Posebno težavo pri genetskem ovrednotenju dolgoživosti v slovenski populaciji predstavlja velikost čred. V Sloveniji je bila leta 2014 povprečna velikost črede v kontroli prieje mleka 20,8 krave, medtem ko so na primer v ZDA v povprečni čredi leta 2014 redili 230 krav (Sadar in sod., 2015; ICAR, 2015). Glede na to, da genetsko ovrednotenje običajno opravimo znotraj ene pasme, so črede dejansko še manjše, saj so v posamezni čredi pogosto krave različnih pasem. Korekcija za vpliv skupnega okolja v čredi je zato v majhnih čredah lahko problematična zaradi otežene porazdelitve fenotipske variance na aditivni genetski del in vpliv skupnega okolja v čredi. Dodatno težavo v majhnih čredah predstavlja korekcija plemenskih vrednosti dolgoživosti za vpliv prostovoljnih izločitev, ki se običajno opravi z vključitvijo relativne mlečnosti glede na preostale krave v čredi (Durr in sod., 1999; Ducrocq, 2005). Kot rešitev slednjega problema v majhnih čredah obstajata vsaj dve možnosti. Prva je oblikovanje primerjalnih skupin znotraj večjega števila čred, ki so si podobne glede na priejo, geografsko lego (Vukasinovic in sod., 1995) ali pa glede na velikost. Druga možnost je vključitev podatkov o vzrokih izločitev, ki so se v Sloveniji bolj sistematično pričeli zbirati po letu 2003. Analiza vzrokov za izločitev je pokazala, da

pri 29,2 % izločitvah točen vzrok zanje ni poznan (vzrok izločitve je naveden kot: zakol – vzrok ni poznan, neznan ali drugo). Izmed krav, katerih vzrok izločitve je bil znan, jih je bilo 11 % izločenih na podlagi odločitve rejca (Jenko in Perpar, 2009). Velik delež nepojasnjenih vzrokov izločitev tako poraja dvome o smotrnosti vključitve vzrokov izločitev za namen korekcije prostovoljnih izločitev. V analizi, ki smo jo opravili v poglavjih 2.1, 2.2 in 2.3, vključitev vzroka izločitve niti ni bila mogoča, saj so bile v analizo zajete tudi krave, ki so bile izločene še pred letom 2003.

Glede na dejstvo, da je obračun plemenskih vrednosti za dolgoživost v populaciji z majhnimi čredami mogoč z uporabo uniformne Weibullove porazdelitve (Potočnik in sod., 2011), predstavlja analiza modela z uporabo te porazdelitve po delih naslednjo stopnjo v razvoju napovedi plemenskih vrednosti v prej omenjenih populacijah. Oceno uporabe modela sorazmernih ogroženosti za napoved plemenskih vrednosti, kjer smo funkcijo ogroženosti modelirali z uporabo Weibullove porazdelitvene funkcije znotraj laktacije in znotraj nje za različne stadije laktacije, smo opravili na populacijah slovenske rjave in črno-bele pasme govedi. Smotrnost uporabe Weibullove porazdelitve po delih smo utemeljili z različnim naklonom premic dvojnega logaritma preživitvene funkcije glede na logaritem števila dni v laktaciji, ki je bila predhodno uporabljena tudi na populaciji švedskega rdeče-belega goveda (Roxström in sod., 2003). Število in dolžino stadijev znotraj laktacij smo določili glede na spremembo oblike neparametrične funkcije ogroženosti. Znotraj vsakega stadija smo uporabili različne izhodiščne funkcije ogroženosti, ki so se razlikovale v vrednostih parametrov oblike in merila. Najmanjša verjetnost izločitve krave iz črede je bila v prvi laktaciji, medtem ko je bila znotraj laktacij najmanjša v prvih dveh stadijih, kar se ujema z ugotovitvami drugih raziskav (Ducrocq, 2005; Terawaki in sod., 2006). Razlike v ogroženosti za izločitev krav so pričakovane in jih lahko pripisemo razlikam v obravnavi starejših in mlajših krav ozziroma krav na začetku ozziroma koncu laktacije v primeru bolezni in plodnostnih motenj.

Model za napoved plemenskih vrednosti smo korigirali za vpliv naslednjih sistematskih časovno odvisnih spremenljivk: sprememba velikosti črede, interakcija med območjem in letom ter interakcija med sezono in letom. V primeru, da smo napovedovali funkcionalno dolgoživost, smo v model vključili tudi vpliv mlečnosti, medtem ko v modelu za oceno

prave dolgoživosti vpliva mlečnosti ni (Ducrocq, 1987). Testiranje, ki smo ga opravili v obliki preživetja 4212 potomk po 63 bikih na populaciji rjavega goveda, je pokazalo, da je bila povprečna korelacija med plemensko vrednostjo bikov in preživetjem njihovih potomk v različnih obdobjih po prvi telitvi za 0,04 % večja v primeru, ko je bil za napoved plemenskih vrednosti uporabljen model za oceno funkcionalne dolgoživosti. Podrobno analizo sistematskih vplivov smo opravili v poglavju 2.1 na populaciji govedi rjave pasme, ker sta se kot statistično neznačilna izkazala vpliva starosti ob prvi telitvi in vpliv interakcije med letom in količino mleka. Glede na precejšen vpliv rejcev si posebno pozornost zasluži neznačilnost vpliva starosti ob prvi telitvi, kar si lahko razložimo z različno hitrostjo rasti telic do prve telitve, ki se med čredami zaradi različnih sistemov rejcev razlikuje (Bielfeldt in sod., 2006). Ugotovitev analiz dolgoživosti v drugih populacijah so si glede vpliva starosti ob prvi telitvi različne. Kot primer, kjer se je učinek starosti ob prvi telitvi izkazal za statistično značilnega, lahko navedemo analizo dolgoživosti v kanadski populaciji črno-belega goveda (Durr in sod., 1999), slovaški populaciji pincgavskega goveda (Mészáros in sod., 2008) ter švicarski populaciji rjavega in lisastega goveda (Vukasinovic in sod., 2001). Nasprotno se je starost ob prvi telitvi izkazala kot neznačilna pri analizi dolgoživosti francoske normandijske kombinirane pasme govedi (Ducrocq, 1994).

Spremembo v velikosti črede smo lahko ustrezno korigirali v čredah, ki so imele v posameznem letu v čredi vsaj pet krav. Relativna sprememba pri vključitvi oziroma izločitvi ene molznice je v majhnih čredah prevelika, da bi razlog zanjo lahko pripisali odločitvi rejca o povečevanju oziroma zmanjševanju črede. V primeru, da se je število živali v čredi zmanjševalo, se je verjetnost izločitve povečala in nasprotno zmanjšala, ko se je čreda povečevala. Ugotovitev drugih raziskav o vplivu spremembe velikosti črede na tveganje izločitve krave iz črede si niso povsem enotne. Nekatere so se ujemale z rezultati naše raziskave (Ducrocq, 1994, 2005; Mészáros in sod., 2008), vendar je mogoče zaslediti tudi takšne, kjer se je tveganje za izločitev povečalo tudi v primeru, ko se je velikost črede povečevala (Durr in sod., 1999; Sewalem in sod., 2005). Zadnje lahko pripišemo težavam v menedžmentu, kot posledico prilagajanja na večje število krav v čredi.

Vpliv interakcije leta in sezone je imel ciklično obliko s spremembami znotraj enega leta. Najnižje tveganjem za izločitev molznic iz črede je bilo v času med aprilom in junijem ter najvišje med oktobrom in novembrom. Oblika nihanj nakazuje, da rejci velikost črede prilagajajo krmi, ki je na voljo. V poletnem obdobju je krme običajno dovolj, poleg tega se 37,5 % krav rjave pasme poleti pase (Perpar in sod., 2010), kar predstavlja pomemben prihranek pri strojnem delu potrebnem za pripravo krme. V zimskem času rejci, razen z nakupom, ne morejo povečati zalog voluminozne krme, tako da že v jeseni ocenijo, koliko živali morajo izločiti glede na trenutne zaloge krme. Odstopanje od pričakovanih trendov, ki ga lahko opazimo med leti 2001 in 2003, lahko razložimo z uvedbo mlečnih kvot in sušo poleti leta 2003.

Vpliv regije na tveganje za izločitev molznic iz črede je morda nekoliko nepričakovan. Molznice na območju Primorske in Krasa imajo namreč manjše tveganje za izločitev, čeprav so pogoji za govedorejo na tem območju zaradi geografskih dejavnikov težji. Do sprememb v tveganju izločitve krav iz črede med regijami je prišlo med leti 2002 in 2003, ko je suša najbolj prizadela prav območje Primorske in Krasa, ki že zaradi naravnih lastnosti nima velike kapacitete zadrževanja vode (Ceglar in Kajfež-Bogataj, 2008). Čeprav je bilo v tem obdobju pomanjkanje voluminozne krme zaznati po vsej državi, so rejci zaradi uvedbe mlečnih kvot, predvsem na območju osrednje in vzhodne Slovenije, povečali količino močne krme in v čredi zadržali tudi krave, ki bi jih v razmerah pomanjkanja voluminozne krme izločili iz črede.

Razvrščanje živali glede na mlečnost znotraj črede, leta in laktacije je za populacije govedi z majhnimi čredami zaradi majhnih primerjalnih skupin neustrezno. Za namen razvrščanja smo zato združili črede podobnih velikosti in ocenili rang mlečnosti posebej za prvesnice in krave v drugi in poznejših laktacijah. Mlečnosti smo ocenili na podlagi maksimalne količine mleka v prvih dveh kontrolah prieje mleka, ki sta morali biti opravljeni znotraj 120 dni po telitvi. Tako pridobljena mlečnost dobro ponazarja potencial za priejo mleka (Beaudeau in sod., 1995; Roxström in Strandberg, 2002). Tveganje za izločitev je bilo najmanjše v prvem stadiju prve laktacije za krave razvrščene zunaj razreda z najmanjšo količino prirejenega mleka in najvišje v drugem stadiju prve laktacije za krave z najmanjšo prirejo mleka. Glede na dosežena nižja tveganja za izločitve v poznejših laktacijah lahko

sklepamo, da so bile krave z izrazito nizko mlečnostjo izločene že v prvi laktaciji. Ugotovitve o večjem tveganju za izločitev krav z nizko prirejo mleka se ujemajo z drugimi raziskavami o funkcionalni dolgoživosti (Vukasinovic in sod., 2001; Roxström in Strandberg, 2002; Ducrocq, 2005), kar kaže, da je razvrščanje glede na mlečnost znotraj čred podobnih velikosti primerno za napoved plemenskih vrednosti za funkcionalno dolgoživost v populacijah govedi z majhnimi čredami.

Analizo variance, za naključne vplive vključene v model za oceno prave in funkcionalne dolgoživosti, smo opravili za slovensko rjavo in črno-belo pasmo govedi. V model za napoved plemenskih vrednosti za dolgoživost smo vključili okoljski in genetski naključni vpliv. Čreda oziroma interakcija med letom in čredo, porazdeljena v obliki logaritemske gama porazdelitve s parametrom oblike in merila enakim 1, predstavljata naključni vpliv okolja, medtem ko vpliv očeta in materinega očeta oziroma vpliv živali, porazdeljen v obliki večrazsežne normalne porazdelitve, pojasnjujeta genetski vpliv. Razlike v ocenah komponent variance, med modeloma za oceno prave in funkcionalne dolgoživosti za slovensko rjavo in črno-belo pasmo govedi, so pokazale, da je varianca naključnih vplivov večja v primeru modela za oceno funkcionalne dolgoživosti. Varianca interakcije med letom in čredo je bila tako v modelu za oceno funkcionalne dolgoživosti večja za 42 % pri slovenski rjavi pasmi oziroma kar za 74 % pri slovenski črno-beli pasmi in kaže na zmanjšanje variance znotraj črede po opravljeni korekciji za vpliv priejene količine mleka. Manjši porast variance je bil zaznan za naključni genetski vpliv očeta in materinega očeta, kjer je bila varianca v modelu za oceno funkcionalne dolgoživosti večja za 11 % pri slovenski rjavi oziroma 12 % pri slovenski črno-beli pasmi. Glede na rezultate podobnih analiz takšen porast variance ni pričakovani. Van der Linde in sod. (2007) namreč ugotavljajo, da se varianca naključnega vpliva interakcije med letom in čredo skoraj ni spremenila, medtem ko se je genetska varianca za vpliv očeta zmanjšala za 19 % modelu za oceno funkcionalne dolgoživosti glede na model za oceno prave dolgoživosti pri nizozemski črno-beli pasmi goveda. Čeprav so bile razlike ocen varianc precejšnje, so bile spremembe v heritabiliteti majhne. Heritabiliteta za pravo dolgoživost je bila 0,094 in 0,084 za rjavo in črno-belo pasmo oziroma 0,099 in 0,085 za funkcionalno dolgoživost pri rjavi in črno-beli pasmi. Nekoliko nižja vrednost heritabilitete v modelu za oceno prave dolgoživosti se ne ujema z ugotovitvami primerljivih raziskav (Vollema in Groen, 1996;

Van der Linde in sod., 2007), vendar se ocene nahajajo v mejah ocen držav članic Interbulla (Forabosco in sod., 2009). Napovedi plemenskih vrednosti za pravo in funkcionalno dolgoživost so bile visoko korelirane. Vrednost korelacijskega koeficienta med napovedanimi plemenskimi vrednostmi za pravo in funkcionalno dolgoživost je znašala 0,94 pri rjavi in 0,87 pri črno-beli pasmi in je bila višja glede na oceno (0,80) pridobljeno v nizozemski populaciji črno-belega goveda (Van der Linde in sod., 2007).

Učinek vključitve različnih naključnih vplivov (vpliv skupnega okolja v čredi oziroma interakcije med letom in čredo in genetski vpliv očeta in materinega očeta oziroma vpliv živali) ter različne omejitve v najmanjši velikosti črede, smo analizirali na modelu za napoved plemenskih vrednosti funkcionalne dolgoživosti pri slovenski rjavi pasmi govedi. Varianca okoljskega vpliva je bila večja za 40 % (model brez omejitve v minimalni velikosti črede) v primeru, ko je bil v model vključen vpliv skupnega okolja v čredi, kot pa interakcija med vplivom skupnega okolja v čredi in letom, kar ni pričakovano, saj naj bi se varianca okoljskega vpliva povečala takrat, ko v modelu uporabimo vpliv z več nivoji. V primeru, ko smo za oceno komponent variance uporabili model živali, so bile te razlike samo še večje, tako da je bila varianca za vpliv skupnega okolja v čredi večja kar za 153 % (model brez omejitve v minimalni velikosti črede). Z vključeno omejitvijo za najmanjšo velikost črede se je varianca okoljskih vplivov zmanjšala. Zmanjšanje je bilo podobno, tako pri modelu očetov in materinih očetov, kakor pri modelu živali. Prav tako je opazna manjša razlika med varianco za vpliv skupnega okolja v čredi oziroma interakcija med letom in skupnim okoljem v čredi, ki ob minimalni omejitvi 10 krav v letu znaša 28 % za model očetov in materinih očetov in 97 % za model živali. Primerjava modela očetov in materinih očetov z modelom živali je pokazala, da je bila največja razlika v vrednosti variance za vpliv skupnega okolja v čredi med modeli z enako spodnjo mejo za velikost črede znotraj leta 6 %, medtem ko je bila v modelu očetov in materinih očetov glede na model živali varianca za vpliv interakcije med skupnim okoljem v čredi in letom večja za med 50 % in 87 %. Sprememba okoljskega vpliva ima relativno majhen učinek na spremembo aditivne genetske variance v modelu očetov in materinih očetov. Razlike med modeli z enako spodnjo mejo za velikost črede znotraj leta ne presegajo 12 %, medtem ko se je le-ta v modelu živali zmanjšala za do 33 %, ko je bila kot okoljski vpliv vključena interakcija med skupnim okoljem v čredi in letom. Aditivna genetska varianca je bila v

modelu živali glede na model očetov in materinih očetov, med modeli z enako spodnjo mejo za velikost črede znotraj leta, večja za med 141 % in 154 % v primeru, da je bil v model vključen vpliv skupnega okolja v čredi oziroma za med 180 % in 240 %, ko je model vseboval naključni vpliv interakcije med skupnim okoljem v čredi in letom. Heritabilitete so bile znotraj modela očetov in materinih očetov podobne, ne glede na spodnjo mejo za velikost črede oziroma različno vključitev naključnega vpliva okolja. V modelu živali so bile heritabilitete, med modeli z enako spodnjo mejo za velikost črede znotraj leta, večje za med 10 % in 57 %, ko je model vseboval interakcijo med letom in skupnim okoljem v čredi. Razlike med modeli so se zmanjševale z večjo spodnjo mejo za velikost črede znotraj leta. To kaže na dejstvo, da je model živali manj primeren za oceno komponent variance v majhnih čredah z vključenim vplivom interakcije med skupnim okoljem v čredi in letom. Heritabilitete za oceno funkcionalne dolgoživosti so bile vedno večje za model živali. V primeru, da je bil v model vključen vpliv skupnega okolja v čredi, so se razlike med modeli z enako spodnjo mejo za velikost črede znotraj leta gibale med 28 % in 40 % oziroma za modele z vključeno interakcijo med letom in čredo med 60 % in 114 %.

Kot že omenjeno, je bila povprečna korelacija med plemensko vrednostjo bikov in preživetjem njihovih potomk iz testnega niza v različnih obdobjih po prvi telitvi za 0,04 % večja v primeru, ko je bil za napoved plemenskih vrednosti uporabljen model za oceno funkcionalne dolgoživosti. Prav iz tega razloga smo korelacije med plemenskimi vrednostmi, napovedane z uporabo različnih modelov, opravili samo za funkcionalno dolgoživost. Korelacijske smo izračunali med plemenskimi vrednostmi napovedanimi na podlagi porekla (plemenska vrednost očeta in polovica plemenske vrednosti materinega očeta), modela očetov in materinih očetov ter modela živali. Zaradi ocene vpliva velikosti črede na napovedi plemenskih vrednosti smo velikost črede omejili na vsaj 2, 3, 5 oziroma 10 krav v čredi. Z namenom analize vpliva leta in različne velikosti primerjalnih skupin smo v model vključili vpliv skupnega okolja v čredi oziroma vpliv interakcije med skupnim okoljem v čredi in letom. S tako zasnovano primerjavo smo skušali oceniti vpliv različnih modelov ter vpliv velikosti črede za napoved plemenskih vrednosti za dolgoživost. Podobnih primerjav v literaturi nismo zasledili.

Model živali velja za primernejšega glede na model očetov in materinih očetov, saj ta vključuje tako informacije obeh staršev kot vpliv mendelskega vzorčenja. Model očetov in materinih očetov vključuje informacije po materini strani le preko materinega očeta, medtem ko vpliv mendelskega vzorčenja ni ocenjen. Model očetov in materinih očetov tako oceni le 31,25 % ($(1/4 + 1/16)*100$) skupne genetske variance, medtem ko je preostanek, 68,75 %, zajet v ostanku. Prav iz tega razloga nekateri avtorji menijo, da je uporaba modela očetov in materinih očetov neprimerena za napoved plemenskih vrednosti dolgoživosti z uporabo modela preživetja (Damgaard in sod., 2003). Nasprotno Meuwissen in sod. (2002) ugotavljajo, da so bile točnosti napovedanih plemenskih vrednosti za dolgoživost med modelom ogroženosti, linearnim modelom in binarnim logit modelom podobne. Razlog za podobnost gre iskati v visoki točnosti napovedanih plemenskih vrednosti očetov, ki imajo večje število hčera. Glede na nizko heritabiliteto za dolgoživost, manjše število hčera po kravi pomeni nizko točnost napovedanih plemenskih vrednosti za mater. Napovedana plemenska vrednost hčera je tako odvisna predvsem od napovedane plemenske vrednosti očeta in lastnega podatka, ki je v primeru, da je krava še živa, okrnjen. Visoka korelacija (0,94 [naključni vpliv skupnega okolja v čredi] oziroma 0,90 [naključni vpliv interakcije skupnega okolja v čredi in leta] za krave in 0,93 [ne glede na vključitev naključnega vpliva skupnega okolja v čredi] za bike) med napovedanimi plemenskimi vrednosti pridobljenimi z modelom živali oziroma z modelom očetov in materinih očetov za bike ter aproksimativnega modela živali za krave, nakazuje, da je model očetov in materinih očetov primeren za napoved plemenskih vrednosti v populacijah govedi z majhnimi čredami. Ker je za napoved plemenskih vrednosti z modelom živali potrebnega več delovnega spomina (model živali je potreboval 25 GB RAM-a, model očetov in materinih očetov 0,16 GB RAM-a) in izračun traja bistveno dlje (model živali je potreboval med 40 minut in 2 uri za različne omejitve v najmanjši velikosti črede, model očetov in materinih očetov pa 10 minut), lahko za napoved plemenskih vrednosti krav uporabimo aproksimativno metodo, kjer je napoved plemenskih vrednosti krav izračunana na podlagi plemenske vrednosti očetov v modelu očetov in materinih očetov. Ne glede na visoko korelacijo med modelom živali in modelom očetov in materinih očetov, so bile ocene komponent variance zelo različne. Ocena heritabilitete za model živali je tako znašala tudi do 0,21, kar lahko vodi v precenitev točnosti napovedanih plemenskih vrednosti. Večina raziskav poroča o heritabiliteti za dolgoživost, ki je manjša od 0,10

(Vollema, 1998; Chirinos in sod., 2007; Mészáros in sod., 2008), čeprav lahko zasledimo tudi raziskave, kjer ocene heritabilitet dosegajo večje vrednosti (Roxström in Strandberg, 2002; Potočnik in sod., 2011). Heritabiliteta ocenjena z uporabo modela očetov in materinih očetov se je gibala med 0,091 in 0,119 in se je ujemala s podatki iz literature.

Vključitev naključnega vpliva okolja v obliki skupnega okolja v čredi oziroma interakcije med skupnim okoljem v čredi in letom je imela pomemben vpliv na ocenjene vrednosti komponent varianc. V primeru vključitve vpliva skupnega okolja v čredi je bila ocenjena varianca za vpliv okolja zelo podobna, ne glede na model, s katerim je bila ocenjena. Nasprotno je bila varianca v modelu z interakcijo med skupnim vplivom okolja v čredi in letom za med 1,5- in 1,9-krat večja ob uporabi modela očetov in materinih očetov glede na model živali. Varianca za naključni vpliv skupnega okolja v čredi je bila večja od variance za naključni vpliv interakcije med skupnim okoljem v čredi in letom. Takšen rezultat ni pričakovani, saj interakcija med skupnim okoljem v čredi in letom opisuje tudi heterogenost znotraj črede. Ne glede na to, se je za boljšega še vedno izkazal model z vključeno interakcijo med skupnim okoljem v čredi in letom, saj je bila korelacija med plemenskimi vrednostmi očetov in preživetjem potomk večja kot v modelu z vključenim vplivom skupnega okolja v čredi.

Testiranje modelov opravljeno na hčerah 63 bikov je pokazalo, da se korelacija med napovedanimi plemenskimi vrednostmi in preživetjem hčera spreminja z različno omejitvijo najmanjše velikosti črede. Glede na dejstvo, da večje primerjalne skupine povečajo točnost napovedanih plemenskih vrednosti (Meyer in sod., 1989), čeprav obenem omejitve v velikosti črede tudi zmanjšajo število potomk po bikih, kar vodi v manjšo točnost napovedanih plemenskih vrednosti, so te spremembe tudi pričakovane. Korelacija med napovedanimi plemenskimi vrednostmi in zgodnjim preživetjem hčera (pol leta po prvi telitvi) se je z večanjem omejitve v velikosti črede zmanjševala. V poznejšem obdobju (1, 2 oziroma 3 leta po prvi telitvi) se je korelacija med napovedanimi plemenskimi vrednostmi in preživetjem hčera v primeru omejitve najmanjše velikosti črede na vsaj 10 krav povečala, medtem ko se je v primeru preživetja do 4. leta po prvi telitvi zmanjšala.

Analize so pokazale, da je genetsko vrednotenje za dolgoživost v majhnih čredah govedi mlečnih pasem mogoče. Podaljšana doba prireje sama po sebi še ne zagotavlja ekonomske učinkovitosti. Poleg dolge dobe prireje je pomembna tudi mlečnost. Ekonomsko najbolj učinkovite so krave, ki imajo visoko prirejo mleka in proizvajajo mleko daljše obdobje (Robertson in Rendel, 1950; Stott, 1994; Jenko in sod., 2007). Življenjska prireja mleka je tako kot dolgoživost znana šele po izločitvi krave iz črede. Modeliranje življenjske prireje mleka z uporabo analize preživetja zaradi zahtevnosti še ni bilo opravljeno. Težava uporabe analize preživetja za življenjsko prirejo mleka je predvsem v analiziranem parametru. Prireja mleka se v času spreminja, kar predstavlja težavo pri vključitvi časovno odvisnih spremenljivk. Zaradi kompleksnosti uporabe analize preživetja za življenjsko prirejo mleka smo analizirali dve potencialni možnosti za izboljšanje življenjske prireje mleka. Kot prvo možnost smo analizirali genetsko povezavo med življenjsko prirejo mleka, dolžino dobe prireje in prirejene količine mleka v prvi laktaciji. Glede na to, da so napovedi plemenskih vrednosti za dolžino dobe prireje in prirejeno količino mleka v prvi laktaciji mogoče, bi lahko živali odbirali na podlagi genetsko povezanih lastnosti. Kot drugo možnost smo analizirali uporabo večlastnostne naključne regresije za napoved plemenskih vrednosti za življenjsko prirejo mleka.

V analizo genetske povezave med življenjsko prirejo mleka, dolžino dobe prireje in prirejene količine mleka v prvi laktaciji smo vključili podatke krav slovenske rjave pasme, ki so imele prvo telitev med 1. 1. 1998 in 31. 12. 2008. Za izbrane krave smo zbrali podatke o prireji in dolžini dobe prireje do 31. 8. 2014. Vse krave so imele tako možnost v čredi ostati vsaj 68 mesecev. Pri kravah, ki so bile 31. 8. 2014 še vedno aktivne, smo predpostavili, da so bile izločene prav takrat. Tako pripravljeni podatki so omogočili uporabo večlastnostnega linearnega modela. Ker v primeru vključitve osnovnih podatkov konvergenčni kriterij ni bil dosežen, smo podatke o življenjski prireji mleka in dolžini dobe prireje normalizirali z uporabo kvadratnega korena. Kot sistematske vplive smo v model vključili vpliv območja, interakcije med letom in sezono ter starost ob prvi telitvi. Samo za količino mleka v prvi telitvi smo v model vključili še vpliv dolžine laktacije. Ker smo želeli oceniti funkcionalno dolgoživost, smo dolžino dobe prireje korigirali za očiščen vpliv količine mleka v laktaciji znotraj črede. Kot naključne vplive smo v model vključili

vpliv skupnega okolja v čredi in žival. Črede so bile med seboj neodvisne, medtem ko so bile živali med seboj povezane glede na stopnjo sorodstva.

Vpliv sezone prve telitve se je spreminjal znotraj let. Nihanja so imela ciklično obliko za količino mleka v prvi telitvi, medtem ko so bila nesistematska za dolžino dobe prireje in življenjsko prirejo mleka. Krave, ki so telile v toplejšem delu leta, so imele manjšo prirejo mleka glede na krave s prvo telitvijo v hladnejšem delu leta. To lahko pripisemo vplivu vročinskega stresa, ki v prvi vrsti predvsem zmanjša zauživanje krme (West, 2003). Vpliv let se je izkazal kot negativen za življenjsko prirejo mleka in dolžino dobe prireje. Razloge za to lahko iščemo tudi v zmanjševanju števila krav rjave pasme v Sloveniji (Perpar in sod., 2010). Do leta 2007 je bil vpliv let na količino mleka v prvi laktaciji rahlo pozitiven. Po letu 2007 se je trend obrnil v negativno smer. Starost ob prvi telitvi ni izkazala pozitivnega oziroma negativnega trenda za lastnosti dolgoživosti in življenjske prireje mleka. Glede na dejstvo, da njen vpliv ni bil značilen niti v modelu z uporabo analize preživetja, je bilo to tudi pričakovati. Starost ob prvi telitvi je imela pozitiven vpliv na količino mleka ob prvi telitvi. Razloge za to lahko iščemo v različni stopnji rasti krav do prve telitve, saj krave, ki ob prvi telitvi ne dosegajo primerne telesne mase, priredijo manjšo količino mleka (Moore in sod., 1991; Sejrsen in Purup, 1997). Razlike med območji so se pri dolžini dobe prireje ujemale z rezultati modela z uporabo sorazmernih ogroženosti. Temu so sledile tudi spremembe življenjske prireje mleka. V zahodni Sloveniji, kjer so pogoji za rejo težji, so krave imele daljšo dobo prireje in večjo prirejo mleka v življenju. Nasprotno je bila prireja mleka v prvi laktaciji večja v vzhodni Sloveniji.

Ocena heritabilitete za dolžino dobe prireje se je ujemala z oceno pridobljeno iz modela sorazmernih ogroženosti (0,09). Nekoliko višja (0,11) je bila ocena heritabilitete za življenjsko prirejo mleka, kar nakazuje na dejstvo, da je selekcija na večjo življenjsko prirejo mleka možna. Zelo podobno oceno heritabilitete za življenjsko prirejo mleka so pridobili tudi drugi raziskovalci. Hoque in Hodges (1980) poročata o oceni 0,11, medtem ko so jo Jairath in sod. (1995) ocenili na 0,13. Ocena heritabilitete za prirejo mleka v prvi laktaciji je znašala 0,15. To je nekoliko nižje od pričakovanj, saj so Potočnik in sod. (2001) z uporabo modela s ponovitvami ocenili, da je heritabiliteta za laktacijsko mlečnost 0,28.

Ocene heritabilitet v literaturi se sicer gibljejo med 0,13 in 0,59 (Hoekstra in sod., 1994; Veerkamp in Goddard, 1998) in so običajno večje v populacijah z večjo pritejo (Hill in sod., 1983).

Če so imele razlike v okolju med čredami 2,7-krat večji vpliv kot aditivni genetski učinek na pritejeno količino mleka v prvi laktaciji, je bil njun vpliv enak za lastnosti dolžine dobe priteje in življenske priteje mleka. Manjši vpliv razlik v okolju med čredami na razlike v dolžine dobe priteje in življenske priteja mleka se ujema z ugotovitvami, ki sta jih podala Zavadilová in Zink (2013). Z izboljšanjem pogojev reje bi največji napredek dosegli pri količini mleka v prvi laktaciji. Največji delež variabilnosti je še vedno ostal nepojasnjen. Ostanki tako pojasnijo 79 % variabilnosti za življensko pritejo mleka, 81 % za dolžino dobe priteje in 46 % za količino mleka v prvi laktaciji.

Fenotipska in genetska korelacija med življensko pritejo mleka in dolžino dobe priteje je bila visoka (0,95 oziroma 0,96). Visoke korelacije nakazujejo, da selekcija na eno od lastnosti vodi k izboljšanju druge lastnosti. Fenotipska korelacija s količino mleka v prvi laktaciji je bila nizka (0,27 z življensko pritejo mleka in 0,05 z dolžino dobe priteje). Nekoliko višja je bila genetska korelacija količine mleka v prvi laktaciji z življensko pritejo mleka (0,48), kar je zelo podobno oceni (0,56), o kateri poročata Hoque in Hodges (1980). Genetska korelacija med količino mleka v prvi laktaciji in dolžino dobe priteje je bila majhna in pozitivna (0,23). Ocene korelacije med količino mleka v prvi laktaciji in dolžino dobe priteje se v literaturi močno razlikujejo in se nahajajo med -0,53 in 0,84 (De Lorenzo in Everett, 1982; Jairath in sod., 1995; Dematawewa in Berger, 1998; González-Recio in Alenda, 2007). Korelacija med skupnim okoljem v čredi za dolžino dobe priteje in količino mleka v prvi laktaciji je bila -0,41 in je nekoliko večja od -0,28, o kateri poročata Zavadilová in Zink (2013). Izboljšanje skupnega okolja v čredi, ki bi povzročilo večjo pritejo mleka v prvi laktaciji, bi torej skrajšalo dobo priteje.

Genetski trend za življensko pritejo mleka in količino mleka v prvi laktaciji je bil pozitiven in je znašal 0,041 oziroma 0,099 standardne deviacije plemenskih vrednosti. Pozitiven genetski trend potrjuje uspešnost selekcije živali na proizvodne lastnosti, ki se je v Sloveniji začelo v letu 1958 (Ferčej, 1965). Genetski trend za dolžino dobe priteje je bil

nevtralen. Glede na to, da se je odbira živali za izboljšanje dolgoživosti pričela šele v letu 2010 (Logar in sod., 2009; Potočnik in sod., 2011), je tak rezultat tudi pričakovani.

Večlastnostna naključna regresija je drugi pristop, s katerim smo napovedali plemenske vrednosti za živiljenjsko prirejo mleka. Naključna regresija omogoča spremembo varianc in kovarianc s časom. Parametre disperzije in plemenske vrednosti tako lahko ocenimo za vsak dan znotraj laktacije. Živiljenjsko prirejo mleka smo napovedali na podlagi plemenske vrednosti za količino mleka in mlečno vztrajnost v prvih treh laktacijah pri slovenski rjavi pasmi goveda.

Trilastnostni model za dnevne količine mleka v prvih treh laktacijah je vključeval tako sistematske kot naključne vplive. Sistematski del modela so sestavljali vpliv območja, stadija brejosti in sezone telitve, medtem ko je bila dnevna količina mleka v prvi laktaciji korigirana še za vpliv starosti ob prvi telitvi. Naključni del modela sta sestavljala vpliv skupnega okolja v čredi ter vpliv živali. Ker smo vpliv skupnega okolja v čredi ugnezdili znotraj laktacije, smo predpostavili, da je kovarianca med laktacijami znotraj črede enaka 0. Predhodne analize so pokazale, da v primeru, ko vpliva skupnega okolja v čredi nismo ugnezdili znotraj laktacije, računalniku ni uspelo nastaviti enačb modela. Vpliv sezone telitve in oba naključna vpliva smo vključili v obliki Legendrovega polinoma tretje stopnje.

Starost ob prvi telitvi je tako kot pri večlastnostni linearni analizi tudi tu izkazala pozitivno povezavo s količino mleka v prvi laktaciji. Prav tako so se ujemale ugotovitve o večji količini mleka v vzhodni Sloveniji. Razlike v količini mleka med območji so se v drugi in tretji laktaciji še povečale. Poznejši stadij brejosti je zmanjšal količino mleka. Učinek stadija brejosti se je z zaporedno laktacijo povečeval. Največji vpliv je imel stadij brejosti na količino mleka pri kravah z najkrajšim poporodnim premorom. Zaradi negativnega učinka vročinskega stresa so krave s telitvijo v poletnem obdobju priredile manj mleka.

Povprečna ocena heritabilitete za dnevno količino mleka v prvi laktaciji je znašala 0,19 in je za 0,04 večja, kot je bila ocena heritabilitete za mlečnost v 305 dneh prve laktacije. Še nižja je bila povprečna ocena heritabilitete za dnevno količino mleka v drugi (0,15) in tretji (0,13) laktaciji. Padec heritabilitete v poznejših laktacijah se ujema z ugotovitvami

raziskave, ki sta jo opravila Lindauer in Mäntysaari (1999). Nasprotno nekateri drugi raziskovalci ugotavljajo, da so razlike v heritabiliteti med posameznimi laktacijami majhne (Jamrozik in sod., 1997; Muir in sod., 2007).

Korelacije med napovedanimi plemenskimi vrednostmi za življenjsko prirejo mleka za bike in ostanki za korigirano življenjsko prirejo mleka njihovih potomk vključenih v testni niz so bile med 0,07 in 0,09. Dodatek plemenskih vrednosti druge in tretje laktacije ali različna oblika vključitve mlečne vztrajnosti nista imela bistvenega vpliva na vrednost koeficiente korelacije. Prav tako ni imela večjega učinka uporaba različnih ekonomskih tež. Za analizo razlik v življenjski prireji mleka smo krave testnega niza razvrstili v štiri razrede glede na napovedano plemensko vrednost za življenjsko prirejo mleka njihovih očetov. V desetih od dvanajstih scenarijev so potomke bikov z najnižjo plemensko vrednostjo priredile tudi najmanj mleka. V enakem številu scenarijev so krave priredile največ mleka v primeru, ko so bili njihovi očetje razvrščeni v razred z največjo plemensko vrednostjo.

Nizke korelacije med napovedanimi plemenskimi vrednostmi za življenjsko prirejo mleka za bike in ostanki za korigirano življenjsko prirejo mleka njihovih potomk vključenih v testni niz nakazujejo, da uporaba samo proizvodnih lastnosti ni najbolj primerna za napoved plemenskih vrednosti življenjske prireje mleka. Glede na to, da je življenjska prireja mleka kompleksna lastnost, ki je odvisna od več dejavnikov, je De Jong (2014) razvil indeks, ki vključuje tako napoved plemenskih vrednosti za proizvodne kot funkcionalne lastnosti. Testiranje veljavnosti indeksa življenjske prireje je bilo opravljeno pri bikih s tisoč ali več izločenimi potomkami, ki so imele možnost dočakati vsaj 10 let. Korelacija med plemensko vrednostjo 62 bikov črno-bele pasme in življenjsko prirejo mleka je bila 0,79. Razlogi za velike razlike v vrednosti koeficiente korelacije glede na analizo, opravljeno v tej raziskavi, so predvsem trije: uporaba indeksa z vključenimi proizvodnimi in funkcionalnimi lastnostmi, razlike v točnost napovedanih plemenskih vrednosti in oblikovanje testnega niza. Plemenske vrednosti bikov s tisoč izločenimi potomkami so zelo zanesljive. Točnost napovedanih plemenskih vrednosti bikov z 20 potomkami je bistveno nižja. De Jong (2014) je opravil oceno korelacije na povprečni vrednosti za življenjsko prirejo vseh hčera bika s plemensko vrednostjo bika. Test je bil

pristranski, saj so vključene krave prispevale podatke tudi za napoved plemenskih vrednosti. Testni niz podatkov v naši analizi so sestavljale krave, ki niso bile vključene v model za napoved plemenskih vrednosti.

3.2 SKLEPI

- (1) Analiza preživetja, z uporabo vključitve Weibullove izhodiščne funkcije ogroženosti po delih, je primerna za napoved plemenskih vrednosti v populaciji majhnih čred. Njeno uporabo smo pokazali na primeru slovenske rjave in črno-bele pasme govedi. Plemensko vrednost za dolgoživost smo napovedali za pravo in funkcionalno dolgoživost. Korekcijo za prostovoljne izločitve smo opravili z vključitvijo vpliva mlečnosti. Ker so bile primerjalne skupine znotraj čred majhne, smo mlečnost krav primerjali v skupini čred podobnih velikosti. Ocene heritabilitet za pravo in funkcionalno dolgoživost so se ujemale z ocenami heritabilitet v populacijah z velikimi čredami.
- (2) Primerjava med modelom očetov in materinih očetov z modelom živali je pokazala, da model živali ne izboljša napovedi plemenskih vrednosti za dolgoživost. Vključitev naključnega vpliva skupnega okolja v čredi oziroma interakcije med skupnim okoljem v čredi in letom, je imela velik vpliv na oceno komponent variance v modelu živali. Ocene komponent variance so se v modelu živali spremenjale ob različnih spodnjih omejitvah za najmanjšo velikost črede. Model očetov in materinih očetov se je izkazal kot bolj robusten ob različnih vključitvah naključnega vpliva skupnega okolja v čredi in omejitvi v najmanjši velikosti črede. Kot najboljši se je izkazal model očetov in materinih očetov z vključeno interakcijo med naključnim vplivom skupnega okolja v čredi in letom. Aproksimativni model živali, z uporabo ocen iz modela očetov in materinih očetov, je primeren za napoved plemenskih vrednosti funkcionalne dolgoživosti krav.
- (3) Genetska korelacija med dolžino dobe prireje in življensko prirejo mleka je visoka. Visoka genetska korelacija omogoča posredno odbiro živali z visoko plemensko vrednostjo za življensko prirejo mleka. Genetska korelacija med količino mleka v prvi laktaciji in življensko prirejo mleka je manjša. V primeru posredne odbire živali za lastnost življenske prireje mleka bomo bolj uspešni pri odbiri krav z visoko plemensko vrednostjo za dolgoživost, kot pri odbiri krav z visoko plemensko vrednostjo za količino mleka v prvi laktaciji.
- (4) Dokazali smo, da je v majhnih populacijah možna uporaba večlastnostne naključne regresije za napoved plemenske vrednosti prireje mleka v prvih treh laktacijah.

Selekcija na količino mleka v prvih treh laktacijah je pokazala pozitivno, vendar šibko povezavo z živiljenjsko prirejo mleka. Vključitev mlečne vztrajnosti ni izboljšala korelacije med napovedanimi plemenskimi vrednostmi za živiljenjsko prirejo mleka za bike in ostanki za korigirano živiljenjsko prirejo mleka njihovih potomk vključenih v testni niz.

4 POVZETEK (SUMMARY)

4.1 POVZETEK

Dolgoživost govedi je ena od najpomembnejših lastnosti v rejah usmerjenih v prirejo mleka. Dolgoživost izboljšamo z boljšim okoljem in odbiro živali z visoko plemensko vrednostjo za dolgoživost. Napoved plemenskih vrednosti za dolgoživost opravimo s pomočjo genetskih modelov. Najbolj razširjen pristop napovedi plemenskih vrednosti za dolgoživost je uporaba analize preživetja, ki za modeliranje podatkov o dolgoživosti uporablja model sorazmernih ogroženosti. Analize preživetja temelji na uporabi funkcije ogroženosti, ki opisuje dolgoživost v obliki verjetja, da bo žival, ki je dočakala določeno starost, izločena v naslednjem trenutku svojega življenja. Bistvena prednost modela sorazmernih ogroženosti je v možni vključitvi podatkov tako živih kot izločenih živali. Za podatke krav, ki še niso bile izločene, pravimo, da so krnjeni. Vključitev krav s krnjenimi podatki o dolgoživosti izboljša točnost napovedi plemenskih vrednosti. Dodatno uporaba analize preživetja omogoča korekcijo modela za vpliv časovno odvisnih spremenljivk.

Analizo preživetja za napoved plemenskih vrednosti za dolgoživost je prvi uporabil Famula (1981). Razširitev napovedovanja plemenskih vrednosti za dolgoživost z uporabo analize preživetja v praksi je omogočil programski paket „The Survival Kit“ (Ducrocq in Sölkner, 1998). V letu 2015 so tako napoved plemenskih vrednosti za dolgoživost izvajali v 21 državah članicah Interbulla. Prvo genetsko vrednotenje za dolgoživost govedi v Sloveniji je bilo opravljeno v letu 2011 (Potočnik in sod., 2011).

Dolgoživost krav molznic določata prva telitev in izločitev. Vzroke izločitev delimo na prostovoljne in neprostovoljne. Glede na korekcijo dolgoživosti za vpliv prostovoljnih izločitev ločimo med pravo in funkcionalno dolgoživostjo. V primeru, da napovedi plemenskih vrednosti za dolgoživost korigiramo za prostovoljne vzroke izločitev, govorimo o funkcionalni dolgoživosti. O pravi dolgoživosti govorimo takrat, ko te korekcije ne opravimo. Korekcijo za vpliv prostovoljnih izločitev bi najbolj natančno določili z vzroki izločitev molznic iz črede, vendar zaradi prepogosto netočnih vzrokov izločitve to običajno opravimo s korekcijo na količino mleka. Količino mleka vključimo v obliki odstopanja od povprečne količine mleka v čredi. Zaradi majhnih primerjalnih skupin bi bila lahko v majhnih čredah korekcija za prostovoljne izločitve glede na količino mleka

problematična. Oblikovanje primerjalnih skupin znotraj čred podobnih velikosti predstavlja možno rešitev za krave, ki jih redimo v majhnih čredah.

Trenutno se za napoved plemenskih vrednosti za dolgoživost z analizo preživetja uporablja model očetov in materinih očetov. Glavna razloga neuporabe modela živali za napoved plemenskih vrednosti za dolgoživost sta računska zahtevnost in potreben čas za napoved plemenskih vrednosti. Prav zaradi teh omejitev je Ducrocq (2001) za napoved plemenskih vrednosti pri kravah razvil aproksimativno metodo.

Namen te doktorske disertacije je bil razvoj modela za napoved plemenskih vrednosti za dolgoživost pri govedu mlečnih pasem v populacijah z majhnimi čredami. Za objekt raziskave smo izbrali govedo slovenske rjave in črno-bele pasme vključeno v kontrolo prireje mleka v Sloveniji, za katere je značilna reja v majhnih čredah. Disertacijo lahko razdelimo v štiri tematske sklope. V prvem sklopu smo razvili modela za oceno prave in funkcionalne dolgoživosti pri slovenski rjavi in črno-beli pasmi. Korekcijo za vpliv prostovoljnih izločitev v modelu funkcionalne dolgoživosti smo opravili z vključitvijo vpliva mlečnosti, kjer smo mlečnost krav primerjali znotraj čred podobnih velikosti posebej za prvesnice in starejše krave. V drugem sklopu smo preverili ustreznost aproksimativne metode za napoved plemenskih vrednosti dolgoživosti pri kravah. Komponente variance smo ocenili znotraj različnih omejitev za najmanjšo velikost črede za model očetov in materinih očetov ter model živali. Glede na to, da rejci želijo povečati prirejo mleka v življenju, smo v tretjem sklopu z uporabo večlastnostnega linearnega modela ocenili genetsko povezavo med dolgoživostjo, življenjsko prirejo mleka in prirejo mleka v prvi laktaciji. Z ocenjevanjem genetskih korelacij smo ocenili možnost odbire živali z veliko življenjsko prirejo mleka posredno preko odbire živali za dolgoživost oziroma mlečnost v prvi laktaciji. V zadnjem sklopu disertacije smo življenjsko prirejo mleka napovedali z uporabo večlastnostne naključne regresije. Na podlagi dnevnih količin mleka v prvih treh laktacijah smo oblikovali trilastnostni model. Glede na različne kombinacije, napovedi plemenskih vrednosti za mlečnost v prvih treh laktacijah in mlečno vztrajnost, smo oblikovali več možnih modelov za napoved življenjske prireje mlela.

Za analizo dolgoživosti pri govedu slovenske rjave pasme smo zajeli podatke prvih petih laktacij 42120 krav, ki so imele vsaj eno od prvih petih telitev v času od 1. 1. 1998 in

31. 12. 2008. Zaradi različnih vzrokov smo podatke 20963 krav okrnili, medtem ko so bili podatki 21157 krav končni. Podatke o dolgoživosti 37908 krav smo vključili v trening niz kjer smo ocenili sistematske vplive, napovedali naključne vplive ter ocenili komponente variance. Podatke o dolgoživosti 4212 krav, ki so bile potomke 63 bikov, smo vključili v testni niz, kjer smo ocenili povezavo med napovedanimi plemenskimi vrednostmi za dolgoživost bikov in preživetjem njihovih potomk. Mediana dolžine dobe prireje je znašala 1192 dni za krave v trening nizu in 1131 dni za krave v testnem nizu. Glede na to, da smo uporabili model očetov in materinih očetov, smo v poreklo vključili smo bike. Skupno je bilo v poreklo vključenih 886 bikov.

Prav tako smo pri slovenski črno-beli pasmi zajeli podatke krav, ki so imele vsaj eno od prvih petih telitev v času med 1. 1. 1998 in 31. 12. 2008. Skupno smo v analizo vključili 89808 krav. Podatke o dolgoživosti smo okrnili pri 39509 kravah. Mediana dolžine dobe prireje je znašala 987 dni in je bila nekoliko manjša kot pri slovenski rjavi pasmi. Skupno je bilo v poreklo vključenih 1682 bikov. Podatke smo uporabili za napoved naključnih vplivov in oceno komponent variance.

Dolgoživost smo modelirali z uporabo analize preživetja in znotraj nje z modelom sorazmernih ogroženosti. Za oceno parametrov v modelu sorazmernih ogroženosti smo uporabili Weibullovo porazdelitev z različnimi izhodiščnimi funkcijami znotraj laktacij in stadijev laktacije. Oceno sistematskih vplivov, napoved plemenskih vrednosti in oceno komponent variance smo opravili v statističnem paketu »The Survival Kit«. Model za napoved plemenskih vrednosti za dolgoživost smo korigirali za naslednje sistematske vplive: spremembu velikosti črede med posameznimi leti, interakcija med območjem in letom, interakcija med letom in sezono ter v modelu za oceno prave dolgoživosti tudi za vpliv prireje mleka. Kot naključni aditivni genetski vpliv smo v model vključili vpliv očetov in materinih očetov in kot naključni vpliv okolja interakcijo med skupnim okoljem v čredi in letom.

V čredah, ki so se glede na preteklo leto zmanjševale, je bila verjetnost za izločitev molznice večja. Nasprotno se je verjetnost za izločitev molznic zmanjšala v čredah, kje se je velikost črede glede na preteklo leto povečala. Glede na območje je bila večja verjetnost izločitve za krave, ki so prihajale iz vzhodnega in osrednjega dela Slovenije. Znotraj let je

značilen cikličen vzorec verjetnosti izločitve živali. Verjetnost za izločitev je bila najnižja med aprilom in junijem in največja med oktobrom in decembrom. Te razlike lahko pripisemo prilagajanju rejcev na količino krme, ki je bila v določenem obdobju na voljo. Pri kravah z veliko pritejo mleka je bila verjetnost izločitve iz črede manjša. Verjetnost izločitve je bila velika predvsem za krave, pri katerih je bila priteja mleka zelo majhna.

Oceni heritabilitet za pravo in funkcionalno dolgoživost sta bili nekoliko nižji pri črno-beli pasmi glede na oceni heritabilitet pri rjavi pasmi govedi. Pri rjavi pasmi je ocena heritabilitete za pravo dolgoživost znašala 0,094, medtem ko je bila ocena heritabilitete za funkcionalno dolgoživost 0,099. Pri črno-beli pasmi je ocena heritabilitete za pravo dolgoživost znašala 0,084, medtem ko je bila ocena heritabilitete za funkcionalno dolgoživost 0,085. Korelacija med napovedmi plemenskih vrednosti bikov za pravo in funkcionalno dolgoživost je bila 0,94 pri rjavi pasmi in 0,87 pri črno-beli pasmi. Pri rjavi pasmi smo ocenili tudi korelacijo med napovedmi plemenskih vrednosti bikov in preživetjem njihovih potomk v testnem nizu podatkov, ki je znašala 0,39 pri modelu za pravo dolgoživost in 0,43 pri modelu za funkcionalno dolgoživost.

Podatke o dolgoživosti krav molznic rjave pasme smo uporabili tudi za primerjavo napovedi plemenskih vrednosti med modelom očetov in materinimi očetovi z modelom živali znotraj različnih omejitev za najmanjšo velikost črede znotraj leta. Najmanjšo velikost znotraj črede in leta smo omejili na: 2, 3, 5 in 10 molznic. Z omejitvijo najmanjše velikosti črede znotraj leta smo osnovno število meritev, v scenariju brez omejitve najmanjše velikosti črede oz. števila krav, s 37908 zmanjšali na: 37683 (2), 37084 (3), 32907 (5) in 18954 (10) krav. Pri modelu očetov in materinim očetov se je število bikov v poreklu z 886 zmanjšalo na 885 (2), 885 (3), 864 (5) in 806 (10) bikov. Poreklo v modelu živali je sestavljalo 57005 živali, medtem ko se je s spodnjimi omejitvami glede števila živali v čredi njihovo število zmanjšalo na 56738 (2), 55961 (3), 50741 (5) in 31796 (10) živali. Dodatno smo testirali razlike glede na to, ali smo v model vključili vpliv skupnega okolja v čredi ali interakcijo med skupnim okoljem v čredi in letom.

Računski čas, potreben za oceno komponent variance in napoved plemenskih vrednosti, je bil ne glede na spodnjo omejitev v velikosti črede v modelu očetov in materinim očetov okoli 10 minut. Pri modelu živali se je računski čas podaljšal in je znašal glede na različno

omejitev za najmanjše število krav v čredi od 40 minut do 2 uri. Različni modeli očetov in materinih očetov so za izračun porabili 0,16 GB delovnega spomina, medtem ko so modeli živali porabili 25GB delovnega spomina. Model živali je prav zato manj primeren za napoved plemenskih vrednosti velikih populacij.

Ocene heritabilitet za funkcionalno dolgoživost so se v modelu očetov in materinih očetov gibale med 0,096 in 0,119 za model z vključenim vplivom skupnega okolja v čredi in med 0,098 in 0,110 za model z vključeno interakcijo med vplivom skupnega okolja v čredi in leta. Ocene heritabilitet v modelu živali so se gibale med 0,125 in 0,160 za model z vključenim vplivom skupnega okolja v čredi in med 0,171 in 0,210 za model z vključeno interakcijo med vplivom skupnega okolja v čredi in letom. Vključitev naključnega vpliva skupnega okolja v čredi, oziroma interakcije med vplivom skupnega okolja v čredi in letom je imela pomemben vpliv na ocenjene vrednosti varianc. V primeru vključitve vpliva skupnega okolja v čredi, je bila ocenjena varianca za naključni vpliv skupnega okolja v čredi zelo podobna, ne glede na model, s katerim je bila ocenjena. Nasprotno je bila varianca za naključni vpliv skupnega okolja v čredi znotraj leta v modelu z interakcijo med skupnim okoljem v čredi in letom za med 1,5- in 1,9-krat večja ob uporabi modela očetov in materinih očetov glede na model živali. Aditivna genetska varianca je bila večja pri modelu živali za med 1,4- in 1,5-krat ob vključenem vplivu skupnega okolja v čredi ter za med 1,8- in 2,5-krat ob vključeni interakcije med skupnim okoljem v čredi in letom.

Korelacija med rangi plemenskih vrednosti krav za funkcionalno dolgoživost v primeru, ko smo plemensko vrednost krav napovedali na podlagi plemenske vrednosti očetov in materinih očetov glede na plemenske vrednosti napovedane z uporabo modela živali, je bila med 0,83 in 0,86 v modelih z vključenim naključnim vplivom skupnega okolja v čredi in med 0,71 in 0,80 v modelih z vključenim naključnim vplivom interakcije med skupnim okoljem v čredi in letom. V primeru uporabe aproksimativne metode je bila korelacija med rangi plemenskih vrednosti napovedanimi z uporabo modela živali večja. Za model z vključenim naključnim vplivom skupnega okolja v čredi je bila korelacija 0,94 ter za model z vključenim naključnim vplivom interakcije med vplivom skupnega okolja v čredi in letom 0,90. Korelacija med rangi plemenskih vrednosti bikov v primeru uporabe modela očetov in materinih očetov glede na plemenske vrednosti napovedane z uporabo modela

živali je bila večja in je ne glede na razlike v vključitvi naključnega vpliva skupnega okolja v čredi znašala 0,93. Najvišja je bila korelacija med plemenskimi vrednostmi napovedanimi z modelom živali, v katerem smo uporabili komponente varianc ocenjene z modelom živali oziroma z modelom očetov in materinih očetov. Vrednost koeficiente korelacije se je v tem primeru, glede na različne omejitve v najmanjši velikosti črede, gibal med 0,95 in 0,99.

Korelacija med rangi plemenskih vrednosti znotraj enakih spodnjih mej za najmanjšo velikost črede, med modelom z vključenim vplivom skupnega okolja v čredi in modelom z vključeno interakcijo med vplivom skupnega okolja v čredi in letom je bila visoka in se je povečevala z večjo spodnjo mejo za velikost črede. Korelacija med modeli glede na različne omejitve v najmanjši velikosti črede z modelom, kjer je bila spodnja meja vsaj 10 krav v čredi letno, je bila med 0,83 in 0,89 za modele z vključenim vplivom skupnega okolja v čredi in med 0,76 in 0,88 za modele z vključenim vplivom interakcije med skupnim okoljem v čredi in letom. Korelacija med plemenskimi vrednostmi 63 bikov in preživetjem 4212 njihovih potomk iz testnega niza je bila večja v modelih, kjer smo kot okoljski vpliv uporabili interakcijo med skupnim okoljem v čredi in letom. Krivulja preživetja krav testnega niza podatkov je pokazala, da je preživitvena sposobnost potomk bikov, ki so imeli višjo plemensko vrednost, boljša. Razlika v preživetju pet let po prvi telitvi med skupino potomk bikov z največjo plemensko vrednostjo in skupino potomk bikov z najmanjšo plemensko vrednostjo znaša 0,14.

V tretjem sklopu disertacije smo z uporabo večlastnostnega linearnega modela ocenili genetsko povezavo med dolgoživostjo izraženo v obliki dolžine dobe prireje, življenjsko prirejo mleka in prirejo mleka v prvi laktaciji. Skupno smo zajeli podatke 36663 krav slovenske rjave pasme, ki so imele prvo telitev v času od 1. 1. 1998 do 31. 12. 2008. Podatke o dolžini dobe prireje in življenjski prireji mleka smo zajeli do 31. 8. 2014, ko je bilo aktivnih še 1964 krav. Po prečiščevanju podatkov smo pridobili končni niz 14389 krav z znano količino mleka v prvi laktaciji. Pri 12416 kravah z znano količino mleka v prvi laktaciji smo vključili tudi podatke o dolžini dobe prireje in življenjski prireji mleka. Poreklo je vsebovalo 25468 živali. Krave vključene v analizo so v povprečju v prvi

laktaciji priredile 5109 kg mleka, 24376 kg mleka v življenju pri povprečni dolžini dobe prieje 1544 dni.

Večlastnostni linearni model je vseboval naslednje sistematske vplive: območje, interakcijo med letom in sezono prve telitve, starost ob prvi telitvi, dolžino laktacije (samo za lastnost količine mleka v prvi laktaciji) in korekcijo za priejo mleka v prvi laktaciji znotraj črede (samo za lastnost dolžine dobe prieje). Vpliv sezone prve telitve se je spremenjal znotraj let. Nihanja so imela ciklično obliko za količino mleka v prvi telitvi in niso bila sistematska za dolžino dobe prieje in življenjsko priejo mleka. Krave, ki so telile v toplejšem delu leta, so imele manjšo priejo mleka v prvi laktaciji, glede na krave s prvo telitvijo v hladnejšem delu leta. Starost ob prvi telitvi ni izkazala pozitivnega oziroma negativnega trenda za dolžino dobe prieje in življenjsko priejo mleka, medtem ko je imela pozitiven vpliv na količino mleka v prvi laktaciji. Razlike med območji so se pri dolžini dobe prieje in življenjski prieji mleka ujemale z rezultati modela z uporabo sorazmernih ogroženosti. V zahodni Sloveniji, kjer so pogoji za rejo težji, so imele krave daljšo dobo prieje, večjo priejo mleka v življenju in manjšo priejo mleka v prvi laktaciji.

Ocene heritabilitet so bile: 0,15 za priejeno količino mleka v prvi laktaciji, 0,12 za priejeno količino mleka v življenju in 0,09 za dolžino dobe prieje. Razlike v okolju med čredami so imele 2,7-krat večji vpliv kot aditivni genetski učinek na priejeno količino mleka v prvi laktaciji. Aditivni genetski vpliv in vpliv razlik v okolju med čredami sta bila podobna za lastnost dolžine dobe prieje in življenjske prieja mleka. Delež nepojasnjene variabilnosti je znašal 79 % za življenjsko priejo mleka, 81 % za dolžino dobe prieje in 46 % za količino mleka v prvi laktaciji. Fenotipska in genetska korelacija med življenjsko priejo mleka in dolžino dobe prieje je bila visoka (0,95 oziroma 0,96), kar nakazuje, da selekcija na eno od lastnosti vodi k izboljšanju druge lastnosti. Fenotipska korelacija s količino mleka v prvi laktaciji je bila nizka (0,27 z življenjsko priejo mleka in 0,05 z dolžino dobe prieje). Nekoliko višja je bila genetska korelacija količine mleka v prvi laktaciji z življenjsko priejo mleka (0,48). Genetska korelacija med količino mleka v prvi laktaciji in dolžino dobe prieje je bila nizka in pozitivna (0,23). Korelacija med skupnim okoljem v čredi za dolžino dobe prieje in količino mleka v prvi laktaciji je bila -0,41. Izboljšanje okolja v čredi, ki bi povzročilo večjo priejo mleka v prvi laktaciji bi torej

skrajšalo dobo prireje.

V četrtem sklopu disertacije smo za napoved življenjske prireje mleka uporabili trilastnostni model z naključno regresijo za napoved plemenskih vrednosti za količino mleka v prvih treh laktacijah. Naključna regresija omogoča spremembo varianc in kovarianc s časom. Parametre disperzije in plemenske vrednosti tako lahko napovemo za vsak dan znotraj laktacije. Življenjsko prirejo mleka smo napovedali v 12 različnih scenarijih, kjer smo vključili različne kombinacije napovedi plemenskih vrednosti za količino mleka in mlečno vztrajnost v prvih treh laktacijah govedi slovenske rjave pasme.

V analizo smo zajeli krave slovenske rjave pasme, ki so imele prvo kontrolo mlečnosti v prvi laktaciji opravljeno po 1. 1. 1998. Analizo smo opravili na podatkih dnevnih kontrol prireje mleka opravljenih v obdobju med 1. 1. 1998 in 31. 12. 2008. Po prečiščevanju smo pridobili podatke o dnevni prireji mleka iz 638688 kontrol mlečnosti, ki so bile opravljene v 131739 kontrolnih dneh pri 36604 kravah. Napovedane plemenske vrednosti smo preverjali na podatkovnem nizu, kamor smo uvrstili 3660 krav, ki so potomke 55 bikov.

Sistematski del modela so sestavljali: vpliv območja, interakcija med stadijem brejosti in stadijem laktacije ter sezone telitve. Dnevna količina mleka v prvi laktaciji je bila korigirana še za vpliv starosti ob prvi telitvi. Naključni del modela sta sestavljala vpliv skupnega okolja v čredi ter vpliv živali. Vpliv sezone telitve in oba naključna vpliva smo vključili v obliki Legendrovega polinoma tretje stopnje. Starost ob prvi telitvi je tako kot pri večlastnostni linearni analizi tudi tu izkazala pozitivno povezavo s količino mleka v prvi laktaciji. Prav tako so se ujemale ugotovitve o večji količini mleka v vzhodni Sloveniji. Razlike v količini mleka med območji so se v drugi in tretji laktaciji še povečale. Stadij brejosti je imel negativen vpliv na prirejeno količino mleka. Enako, kot je bilo ugotovljeno že pri večlastnostni linearni analizi, so krave s telitvijo v poletnem obdobju priredile manj mleka.

Povprečna ocena heritabilitete za dnevno količino mleka je znašala 0,19 v prvi laktaciji, 0,15 v drugi laktaciji in 0,13 v tretji laktaciji. Razlike med dvanajstimi scenariji za napoved plemenskih vrednosti za življenjsko prirejo mleka so bile majhne. Korelacije med napovedanimi plemenskimi vrednostmi za življenjsko prirejo mleka za bike in življenjsko

prirejo mleka njihovih potomk vključenih v testni niz, so bile med 0,07 in 0,09. Dodatek plemenskih vrednosti druge in tretje laktacije ter različna oblika vključitve mlečne vztrajnosti nista imela bistvenega vpliva na vrednost koeficienta korelacije. Prav tako ni imela večjega učinka uporaba različnih ekonomskih tež. Nizke korelacije med napovedanimi plemenskimi vrednostmi za življenjsko prirejo mleka za bike in življenjsko prirejo mleka njihovih potomk vključenih v testni niz nakazujejo, da uporaba izključno proizvodnih lastnosti ni najbolj primerna za napoved plemenskih vrednosti za življenjsko prirejo mleka.

4.2 SUMMARY

Longevity is one of the most important traits in a dairy cattle system. Longevity can be improved through better rearing conditions and selection of individuals with a higher breeding value for longevity. Prediction of longevity breeding values is performed using genetic models. Survival analysis is the most common genetic model for the prediction of longevity breeding values. To predict breeding values, survival analysis uses a proportional hazard model, where the hazard function is applied. Hazard function describes longevity as the probability of a cow being culled in the next instant upon reaching a certain point in life. There are two main advantages of using the proportional hazard model for the prediction of longevity breeding values. The first advantage is the possibility to include data from culled and live animals. The data from live cows is treated as censored, and their inclusion improves the accuracy of predicted breeding values. The second advantage of using the proportional hazard model is a possible correction for time-dependant variables.

Survival analysis was first used to predict longevity breeding values by Famula (1981). The application of survival analysis in routine genetic evaluation became possible only with the release of "The Survival Kit" software (Ducrocq in Sölkner, 1998). In 2015, longevity breeding values were estimated in 21 countries, including Slovenia, where the first genetic evaluation for longevity was performed in 2011 (Potočnik et al., 2011).

Longevity is determined with the first calving and culling. Culling reasons can be both voluntary and involuntary. With regard to correcting for voluntary culling reasons,

functional and true longevity are defined. Functional longevity is estimated with the model when correction for voluntary culling is included. When this correction is not included in the model, longevity is defined as true longevity. Correction for voluntary calving would be most accurate with the inclusion of culling reasons. Because culling reasons cannot be reliably collected, the effect of voluntary culling is corrected with milk yield. The effect of milk yield is included as a deviation from the average milk yield within a herd, which could pose a problem in a population with small herds. For this reason, merging herds of a similar size and comparing milk yield within each group is a possible solution for the estimation of functional longevity in small herds.

Currently, the sire-maternal grandsire model is used for the prediction of longevity breeding values. Due to its high demand on computing resources and long computational time, the animal model is not used. To solve this problem, Ducrocq (2001) developed an approximation method wherein the breeding values for cows are predicted.

The purpose of this thesis was to develop a model for the prediction of longevity breeding values for dairy cattle systems with small herds of different cattle breeds. The analysis was performed on Slovenian Brown and Slovenian Black and White cattle breeds included in the dairy milk recording scheme. In the Slovenian dairy cattle system, small herds with cattle of different breeds are common. This thesis can be separated into four parts. In the first part, the model for predicting true and functional longevity is outlined. The effect of voluntary culling was removed, and the milk yield effect was included. Instead of within each herd, milk yield was compared within herds of similar size for cows in first calving, with older cows compared separately. In the second part, an approximate animal model was used for the estimation of breeding values for cows. Variance components were estimated with different restrictions on minimum herd size separately for the sire-maternal grand sire and animal models. The aim of the third part was to estimate the genetic correlation between longevity, lifetime milk production, and milk yield in first lactation using a multivariate linear model. The obtained genetic covariances estimated the potential to perform selection for lifetime milk production through selection for longevity or first lactation milk yield. In the final part, genetic values for lifetime milk production were predicted using a multivariate random regression model using daily milk yields in the first

three lactations. Different models for lifetime milk production were created. They were defined with different combinations of milk yield and lactation persistency.

For the analysis of longevity for Brown cattle, records from 42120 milk recorded cows with at least one of their first five calvings occurring between 1 January 1998 and 31 December 2008 were included in the data set. Records for 20963 cows were censored, while records of 21157 cows were complete. For the estimation of the fixed effects, variance components and a prediction of random effects in the training set was formed with 37908 cows. The remaining 4212 cows that were the progeny of 63 bulls formed a validation data set to estimate the correlation between the predicted breeding values of sires and the survival of their second-crop daughters. Median length of productive life was 1192 days for cows in the training data set, and 1131 days for cows in validation data set. Pedigree was traced back for bulls only and consisted of 886 bulls.

Slovenian Black and White cattle records from cows with at least one of their first five calvings occurring between 1 January 1998 and 31 December 2008 were considered. The final data set consisted of 89808 cows, while the records for 39509 cows were censored. Median length of productive life was 987 days, which was shorter when compared to the Slovenian Brown cattle breed. Pedigree was traced back for bulls only and consisted of 1682 individuals. This data was used to predict random effects and variance components estimation.

Survival analysis with a proportional hazard model was used for modelling longevity data. A piecewise Weibull proportional hazard model, with different baseline functions within lactation and stage of lactation, was used for the estimation of parameters in the proportional hazard model. Survival Kit software was used to estimate systematic effects and to predict breeding values. The model included the following systematic effects: change in herd size between different years, region within year of production, and – only in the model for the estimation of functional longevity – the effect of milk yield. The model included the random additive genetic effect of sire and maternal grand sire and the random environment effect of the interaction between herd and year.

Culling risk increased in herds with a decrease in the number of cows, while the relative risk of culling decreased in herds that were increasing in size. The highest relative risk of culling was observed for cows from the eastern and central regions of Slovenia. A cyclic pattern of culling risk existed within years was recognised. Culling risk was lowest between April and June and the highest between October and December. The reason for this change in hazard within years could be due to a feed shortage during winter. Cows with high milk production had a lower risk of culling. The highest risk of culling was observed for cows exhibiting the lowest milk yield.

Estimates for true and functional heritabilities were lower for Black and White cattle when compared to Brown cattle. For Brown cattle, the estimated heritability for true longevity was 0.094, while functional longevity was 0.099. For Black and White cattle, the estimated heritability for true longevity was 0.084, while functional longevity was 0.085. Correlation between the predicted breeding values for functional and true longevity was 0.94 for Brown and 0.87 for Black and White cattle. Additionally, the correlation between predicted breeding values for Brown bulls and their second-crop daughters was estimated to be 0.39 for true longevity and 0.43 for functional longevity.

Data from Brown cattle were further analysed in a comparison of sire-maternal grand sire and animal models. The two models were compared with different restrictions on minimum herd size. Herd size was restricted to a minimum of either: 2, 3, 5, or 10 cows within each year. With this restriction, the original data set of 37908 cows decreased to 37683 (2), 37084 (3), 32907 (5), and 18954 (10) cows. The size of the pedigree in the sire-maternal grand sire models were, from the original 886 bulls, reduced to 885 (2), 885 (3), 864 (5), and 806 (10) bulls. In the animal model, the original pedigree of 57005 animals was reduced to 56738 (2), 55961 (3), 50741 (5), and 31796 (10) animals. In addition, the effect of using either herd or the interaction between herd-year was studied.

Computing time for the evaluation of the sire-maternal grand sire model was approximately 10 minutes for each of the models. Computing time for the animal model ranged from 40 minutes for the model with the highest restriction on a minimum number herd-year class to approximately 2 hours for the model with no restriction on a minimum herd-year class size. Sire-maternal grand sire models used approximately 0.16 GB of

memory, whereas animal models used approximately 25 GB of computer memory. This illustrates the unfeasibility of animal model evaluations for large populations.

Heritability estimates for functional longevity were between 0.096 and 0.119 for the sire-maternal grand sire model with the herd effect included and between 0.098 and 0.110 when the herd-year effect was included. Heritability estimates were between 0.125 and 0.160 for the animal model with the herd effect included and between 0.171 and 0.210 when the herd-year effect was included. Variance components estimates were different when herd or herd-year random effect was included. Estimates of herd variance were stable for both the sire-maternal grand sire and animal models. However, herd-year variance was from 1.5 to 1.9 times higher using the sire-maternal grand sire model compared to the animal model. Additive genetic variance estimates were higher when using the animal model: 1.4 to 1.5 times higher when including herd effect and 1.8 to 2.5 times when including herd-year effect.

Using the animal model, rank correlation between cow breeding values for functional longevity, when estimated with breeding values for sires, maternal grand sires, and cow breeding values, was between 0.83 and 0.86 in the models with random herd effect and between 0.71 and 0.80 in the models with random herd-year effect. When the approximate animal model was used, the correlation between cow breeding values estimated with animal model was higher. This correlation was 0.94 for the model using herd effect, and 0.90 for the model with herd-year effect. Rank correlations between breeding values for bulls estimated using both the sire-maternal grand sire and animal model were 0.93. The highest rank correlation was obtained between breeding values obtained from the animal model using either variance components estimated with the animal or sire-maternal grand sire model. The value of rank correlation in that case was between 0.95 and 0.99 for different restrictions in minimum herd size.

Rank correlations between predicted breeding values from models with herd or herd-year random effect within the same restrictions for minimum herd size was high, and increased with higher restrictions on minimum herd size. Rank correlation between predicted breeding values from models with different restrictions on minimum herd size with predictions from model with at least 10 cows in a herd was between 0.83 and 0.89 for

models including herd effect, and between 0.76 and 0.88 for models including herd-year effect. When herd-year effect was included in the model, the correlation between breeding values from 63 bulls and the survival of 4212 second crop daughters from the validation data set was higher when compared to the models with herd effect only. The survival curve of cows from the validation data set indicated that the daughters of bulls with higher breeding values exhibited a higher rate of survival. After five years from first calving, the survival rate of daughters from bulls with the highest breeding value was 0.14 higher than the daughters from bulls with the lowest breeding value.

In the third part of the thesis, a multivariate linear model was used to estimate the genetic correlation between longevity, which is expressed as length of productive life, lifetime milk production, and milk yield in first lactation. For this study, records from 36663 Slovenian Brown cows with first calving between 1 January 1998 and 31 December 2008 were obtained. Data for the length of productive life and lifetime milk production were collected until 31 August 2014, when 1964 cows remained alive. After filtering, a data set of 14389 cows with known milk yield was obtained. For cows with known first lactation milk yield, there were 12416 cows where the data for length of productive life and lifetime milk production were available. The pedigree consisted of 25468 individuals. On average, cows included in the analysis were producing 5109 kg of milk in the first lactation and 24376 kg total in 1544 days.

The following systematic effects were included in the model: region, year-season of first calving, age at first calving, length of lactation (only for the first lactation milk yield), and correction for within-herd first lactation milk yield (only for the length of productive life). The effect of year-season oscillated between different seasons. Oscillations followed a seasonal pattern for milk yield in first lactation which was not recognized for length of productive life and lifetime milk production. Cows with first calving during winter exhibited higher first lactation milk yield when compared to cows with first calving during summer. A stable trend was observed for the effect of age at first calving on lifetime milk production and length of productive life. For age at first calving, there was a positive effect for milk yield in first lactation. The differences between regions in the length of productive life were congruent with results obtained from the proportional hazard model. In the

eastern region of Slovenia, conditions were favourable for first lactation milk yield, whereas in the western region, conditions were favourable for lifetime milk production and length of productive life.

Estimated heritabilities were: 0.15 for milk yield in first lactation, 0.12 for lifetime milk production, and 0.09 for length of productive life. The variance in first lactation milk yield explained by common herd environment was 2.7 times larger when compared to the variance explained by additive genetic variance. For length of productive life and lifetime milk production, the variances explained by common herd environment and additive genetic variance were similar. The proportion of unexplained variability was 79% for lifetime milk production, 81% for length of productive life, and 46% for milk yield in first lactation. Both phenotypic and genetic correlations between lifetime milk production and length of productive life were very strong (0.95 and 0.96, respectively). This indicates that selection for one trait improves the other trait. The phenotypic correlation between lifetime milk production and first lactation milk yield was much weaker (0.27), and even weaker between length of productive life and first lactation milk yield. The genetic correlation between first lactation milk yield and lifetime milk production was slightly higher (0.48). The genetic correlation between first lactation milk yield and length of productive life was weak and positive (0.23). The correlation between the common herd environment effect for length of productive life and first lactation milk yield was moderately negative (-0.41). This indicates that the improvement in herd environment for first lactation milk yield deteriorated the herd environment for length of productive life.

In the fourth part of this thesis, lifetime milk production was predicted with a multivariate random regression model for milk yield in the first three lactations. Random regression enables variance and covariance to change with time, and it is therefore possible to estimate dispersion parameters and predict breeding values for each day of lactation. Twelve scenarios were used for the prediction of lifetime milk production. They included various combinations of predicted breeding values for milk yield and lactation persistency in the first three lactations for Slovenian Brown cattle.

Slovenian Brown cows with first milk records from first lactation after January 1 1998 were included in the analysis. For this analysis, daily milk records from between January 1

1998 and December 31 2008 were obtained. After filtering, 638688 daily milk records were obtained from 131739 milk recording days on 36604 cows. The predicted breeding values were checked in the validation data set, where 10% of all cows were included. The validation data set was used to test the differences in predicted breeding values for lifetime milk production based on different scenarios.

The systematic effects included in the model for the prediction of lifetime milk production were: region, season of calving, and the interaction between gestation stage and stage of lactation. Additionally, age at first calving was included only for milk yield in first lactation. Random part of the model included the effect of herd and animal. The effect of season and the two random effects were included as a cubic Legendre polynomial. As with the multivariate linear model, older cows at first calving showed a positive effect on the milk yield. The same was true for the effect of region, where milk yield in the east region of Slovenia was higher. These differences increased in the second and third lactation. A negative effect of gestation stage on milk yield was observed. As previously observed in multivariate analysis, cows that calved during the summer also exhibited lower milk production.

The estimated average heritability for milk yield in first, second, and third lactation was 0.19, 0.15, and 0.13, respectively. Only small differences existed between the twelve scenarios for the estimation of lifetime milk production. The correlation between the predicted breeding values for lifetime milk production for bulls and the phenotypic lifetime milk production of their daughters were between 0.07 and 0.09. Inclusion of breeding values for second and third lactation had only a small effect. The same was observed for the effect of lactation persistency and the application of different economic weights. Low correlations between the predicted breeding values for lifetime milk production for bulls and the phenotypic lifetime milk production of their daughters suggests that the application of productive traits only is not the most appropriate method for predicting lifetime milk production breeding values.

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