Pregledni znanstveni članek / Scientific review paper

REPRODUCTIVE POTENTIAL OF ROE DEER (*Capreolus capreolus* L.): REVIEW OF THE MOST IMPORTANT INFLUENTIAL FACTORS

RAZMNOŽEVALNI POTENCIAL EVROPSKE SRNE (*Capreolus capreolus* L.): PREGLED NAJPOMEMBNEJŠIH VPLIVNIH DEJAVNIKOV

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ABSTRACT

European roe deer (*Capreolus capreolus* L.) is the most important game-management species not only in Slovenia but also in other European countries. For effective game management it is crucial to have an understanding of the ecology and population parameters that shape the population dynamics of the species. Knowledge about the variability of its reproductive potential, i.e. the proportion of fertilized females, litter size and fawn sex ratio, apart from the parameters that are already in use, would be very beneficial for methods of control as it could lead to more efficient adaptive game management, including proper planning of culling measures. Factors affecting the reproductive potential of roe deer include individual (particularly maternal phenotype, i.e. body size, body mass, physical condition), population (e.g. population density, demographic structure, social stress, genetics) and environmental characteristics (habitat quality, weather conditions, interspecific interactions, etc.). The final output of reproductive potential is the sum of all influencing factors and several combinations between them and therefore varies among different populations and environments. Higher densities can lower roe deer fertility rates and furthermore number of fawns per doe. Litter size is influenced by doe's body mass, as heavier females have more fawns in a litter. There are some contradictory findings in studies of sex ratio variation in connection to female body mass. Litter size can also be influenced by age of does, as primiparous females have smaller litters than adults, but also decreases with animal senescence. Roe deer populations from northern environments (Scandinavia) have higher body masses and larger litters than those from the south (e.g. Italy, Spain), which shows the importance of environment for roe deer reproduction. However, in Slovenia this issue has been neglected until now. In the following report we present an overview of the recent European research on factors affecting the fertility and reproductive potential of roe deer. Similar research in Slovenia would also be valuable, as roe deer is exposed to various environmental factors in this area. In addition, it is also involved in unique interspecific interactions that have not been studied in recent foreign research. Furthermore, Slovene distinguishing databases provide an outstanding platform for proficient understanding of different effects on roe deer yield in Central Europe.

Key words: roe deer, reproductive potential, doe fertility, embryo, fawn sex ratio

IZVLEČEK

Evropska srna (*Capreolus capreolus* L.) je v Sloveniji in tudi drugod po Evropi najpomembnejša lovsko-upravljavska vrsta. Učinkovito upravljanje populacije lahko zagotovimo le na podlagi dobrega poznavanja njene ekologije in osnovnih populacijskih parametrov, ki vplivajo na populacijsko dinamiko vrste. Za čim boljše adaptivno upravljanje s srnjadjo, vključno z ustreznim načrtovanjem poseganja v populacije, je poleg kazalnikov, ki se že uporabljajo v kontrolni metodi, zelo želeno tudi poznavanje variabilnosti razmnoževalnega potenciala, tj. stopnje oplojenosti samic, velikosti legel in spolnega razmerja zarodkov. Dejavniki, ki vplivajo na razmnoževalni potencial vrste, so lahko individualni (še zlasti fenotip samic, tj. velikost, telesna masa, fizična kondicija), populacijski (npr. populacijske gostote, demografska struktura, socialni stres, genetske značilnosti) in okoljski (kakovost habitata, vremenske razmere, medvrstne interakcije itn.). Dejanski razmnoževalni potencial je posledica naštetih vplivnih dejavnikov in delovanj med njimi, zato se med različnimi populacijami in okolji močno razlikuje. V prispevku je predstavljen pregled evropskih raziskav o vplivu različnih dejavnikov na oplojenost in razmnoževalni potencial srnjadi. Z naraščanjem gostote populacije se praviloma zmanjšuje stopnja oplojenosti samic, prav tako pa se zmanjšuje tudi število mladičev na posamezno srno. Na velikost legla vpliva tudi telesna masa, in sicer se z večanjem telesne mase samic število mladičev na posamezno samico zvišuje. Pri raziskavah vpliva telesne mase na spolno razmerje mladičev pa so različni avtorji prišli do nasprotujočih se rezultatov. Vpliv starosti se kaže v velikosti legla, saj raziskave kažejo na to, da imajo primiparne samice praviloma manjša legla kot odrasle, upad rodnosti pa je povezan tudi s staranjem osebkov. Srnjad iz severnih območij (Skandinavija) ima praviloma večjo telesno maso in posledično tudi večja legla kot srnjad iz južnih območij (npr. Italija, Španija), kar kaže tudi na pomen življenjskega prostora pri reprodukciji srnjadi. Pri nas srnjad živi v širokem gradientu okoljskih dejavnikov in je udeležena tudi v specifičnih medvrstnih interakcijah, ki jih dosedanje raziskave, opravljene v tujini, ne vključujejo. Domače raziskave bi bile dobrodošle, poleg tega pa imamo v Sloveniji tudi izjemne podatkovne baze o odstrelu, masah, spolni in starostni strukturi srnjadi, ki zagotavljajo odlične predpogoje za še boljše razumevanje vplivnih dejavnikov na variabilnost prirastka srnjadi v srednjeevropskem prostoru.

Ključne besede: evropska srna (srnjad), razmnoževalni potencial, oplojenost srn, zarodek, spolno razmerje mladičev

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1 INTRODUCTION

European roe deer (*Capreolus capreolus* L.) is one of the key species of European terrestrial ecosystems and also represents the most important game-management species not only in Slovenia but also in the vast majority of European countries (Andersen et al., 1998; Apollonio et al., 2010). In the period between 2001 and 2010, more than 428,000 roe deer were taken from hunting sites (total recorded mortality) in Slovenia, which is between 41,150 and 44,736 animals per year (Statistični..., 2012a; 2012b). It is estimated that there are more than 200,000 roe deer living in Slovenia (Jerina et al., 2013). Owing to the great abundance and prevalence of roe deer within the whole country, its important hunting and management role, and its impacts on forest and agricultural ecosystems, it is crucial for a balanced development of terrestrial ecosystems and sustainable use of their potential, including the potential of roe deer as a natural resource, that effective management is in accordance with the ecosystem, economic and socio-political carrying capacity of the environment (Pokorny, 2008; 2009).

Game management in Slovenia, based on sustainable use of game as a renewable natural resource (Hlad and Skoberne, 2001), is relatively well organised, i.e. systematic, well planned and controlled (Pokorny, 2009). Collection of various and quality data and the existence and development of integrated databases rank Slovenia (from this point of view) as one of the top countries in the world (Putman, 2008). Management planning in populations of game species (including roe deer) in Slovenia is based on various expert platforms, which rely on various parameters, such as: (i) previous harvest of individual game species; (ii) trends of damage on agricultural crops, cattle, forests, transport infrastructure and other; (iii) trends of (bio)indicators in populations and their environment; (iv) evaluation of conditions in hunting units, carried out by hunting unit managers; (v) empirical experience and knowledge of animal population managers and planners (Pravilnik o vsebini..., 2005; Kazalci okolja..., 2007; Stergar et al.., 2012).

For effective game management, information is still lacking on the basic population parameters that shape the population dynamics of the species (Pokorny, 2008). In contrast with other European countries (collected in Andersen et al., 1998; Appolonio et al., 2010; Putman et al., 2011), almost no systematic research of roe deer has been carried out in Slovenia, despite the existing complex and extensive databases on every single culled animal (Virjent and Jerina, 2004; Stergar et al., 2012). Consequently, for roe deer, there are no relevant data on the biological parameters that influence

1 UVOD

Evropska srna (*Capreolus capreolus* L.) je ena ključnih vrst kopenskih ekosistemov Evrope in najpomembnejša lovsko-upravljavska vrsta ne le v Sloveniji, marveč tudi v veliki večini evropskih držav (Andersen in sod., 1998; Apollonio in sod., 2010). V Sloveniji je bilo v obdobju 2001–2010 iz lovišč odvzetih (tj. skupna registrirana smrtnost) >428.000 osebkov srnjadi oz. med 41.150 in 44.736 živali letno (Statistični..., 2012a; 2012b), po ocenah pa številčnost vrste pri nas presega 200.000 živali (Jerina in sod., 2013). Zaradi velike številčnosti srnjadi in njene razširjenosti po skoraj celotni državi, poudarjenega lovsko-upravljavskega pomena, vloge in vplivov v gozdnih ter agrarnih ekosistemih je za uravnotežen razvoj kopenskih ekosistemov in trajnostno rabo njihovih potencialov, vključno s samimi potenciali srnjadi kot obnovljivega naravnega vira, zelo pomembno učinkovito upravljanje z vrsto v skladu z ekosistemsko, ekonomsko ter socio-politično nosilno zmogljivostjo okolja (Pokorny, 2008; 2009).

Upravljanje s srnjadjo v Sloveniji, ki temelji na načelu trajnostne rabe divjadi kot obnovljivega naravnega vira (Hlad in Skoberne, 2001), je razmeroma dobro urejeno, tj. je sistematično, dobro načrtovano in kontrolirano (Pokorny, 2009). Slovenija zaradi zbiranja številnih in kakovostnih vhodnih podatkov ter obstoja in razvoja celostnih podatkovnih baz, ki so na voljo v upravljavskem procesu, v tem pogledu sodi med vodilne države na svetu (Putman, 2008). Kot osnova za načrtovanje upravljanja s populacijami divjadi (vključno s srnjadjo) v Sloveniji se danes upoštevajo različna strokovna izhodišča, ki se opirajo na različne parametre (kazalnike), in sicer: (i) dosedanji odvzem posameznih vrst divjadi; (ii) trend ugotovljenih škod na kmetijskih kulturah, živini, objektih v prometu in drugje; (iii) trend kazalnikov (bioindikatorjev) v populacijah in njihovem okolju; (iv) ocene stanja v loviščih, ki ga podajajo upravljavci lovišč; (v) empirične izkušnje in znanje načrtovalcev in upravljavcev s populacijami (Pravilnik o vsebini..., 2005; Kazalci okolja..., 2007; Stergar in sod., 2012).

Za učinkovitejše upravljanje s srnjadjo v Sloveniji vendarle manjkajo nekatere nujne vhodne informacije o populacijskih parametrih, ki vplivajo na populacijsko dinamiko vrste (Pokorny, 2008). V nasprotju s številnimi evropskimi državami (zbrano v Andersen in sod., 1998; Apollonio in sod., 2010; Putman in sod., 2011) pri nas v preteklosti sistematičnih raziskav srnjadi (skoraj) ni bilo, navkljub obstoju kompleksnih in izjemno obsežnih podatkovnih baz o vsaki posamezni izločeni živali (Virjent in Jerina, 2004; Stergar in sod., 2012). Zaradi tega v slovenskem prostoru v nasprotju its population dynamics, i.e. reproductive potential or fertility rate and yield (e.g. Vincent et al., 1995; Hewison, 1997) and/or early fawn mortality (e.g. Linnell et al., 1995; Jarnemo, 2004; Panzacchi et al., 2009). In contrast, there has been some research on the reproduction of chamois (*Rupicapra rupicapra* L.), red deer (*Cervus elaphus* L.) and wild boar (*Sus scrofa* L.) (Valentinčič, 1975; Žele, 2000; Mihelič, 2009; Jelenko et al., 2012). Knowing these parameters is crucial to determine suitable strategies for the sustainable management of the species. Furthermore, these strategies must be suitable from ecological and economic points of view. For the most optimal roe deer management, which includes adjusting population densities to environmental carrying capacities, compliance and conservation of the ecosystem roles of the species, and sustainable use of roe deer as a renewable natural resource in the Slovenian area, it is crucial to gain new knowledge about roe deer population dynamics and its response to the variability of this particular environment, especially information concerning the impacts of individual, population and environmental factors on its reproductive potential.

Because of the outstanding landscape and ecological variability of Slovenia, it is very important to determine the impacts of individual, population and environmental factors on roe deer yield, i.e. fertility rate, number of embryos and number of fawns per reproductive doe, among the whole gradient of ecological factors. The latter is also important from a wider European perspective, since elsewhere in Europe roe deer does not experience such a gradient of ecological factors and interspecific interactions. In the following report, we present a review of the most important conclusions of systematic research on roe deer reproductive potential in other European countries. Our goal is to (i) partly contribute to understanding and complying of great variability in roe deer fertility and yield in the management process; (ii) prepare suitable platforms for initiating systematic research of the reproductive potential of roe deer in Slovenia.

2 REPRODUCTIVE POTENTIAL OF ROE DEER: REVIEW OF EXISTING FINDINGS

Almost all cervids of the northern temperate zone give birth in spring (April to June), so the mating season occurs in autumn (October, November). Most female cervids are seasonally polyoestrous (Andersen et al., 1998). Ovulation is controlled by day length and is induced by the shortening of the photoperiod after the autumn equinox. Decreasing day length also impacts testosterone levels and consequently rutting behaviour. The roe deer is an exception to these rules,

z gamsom (*Rupicapra rupicapra* L.), navadnim jelenom (*Cervus elaphus* L.) in divjim prašičem (*Sus scrofa* L.), za katere je v preteklosti potekalo tudi nekaj raziskav s področja reprodukcije (Valentinčič, 1975; Žele, 2000; Mihelič, 2009; Jelenko in sod., 2012), za srnjad nimamo relevantnih podatkov o tistih bioloških značilnostih, ki usmerjajo populacijsko dinamiko vrste, kot so razmnoževalni potencial oz. stopnja oplojenosti in prirastek (npr. Vincent in sod., 1995; Hewison, 1997) in/ali zgodnja smrtnost mladičev (npr. Linnell in sod., 1995; Jarnemo, 2004; Panzacchi in sod., 2009). Poznavanje teh parametrov je odločilno za določanje najprimernejših strategij trajnostnega upravljanja z vrsto, ki bodo ustrezne tako z ekološkega kot tudi gospodarskega vidika. Za optimalno upravljanje s srnjadjo v smislu prilagajanja velikosti populacij nosilnim zmogljivostim okolja, upoštevanja in ohranjanja ekosistemskih vlog vrste ter trajnostne rabe tega obnovljivega naravnega vira je v slovenskem prostoru treba nujno pridobiti novo, iz domačih razmer izhajajoče znanje, ki bo prispevalo k razumevanju populacijske dinamike srnjadi in njenega odziva na variabilnost okolja. Zaradi izjemne krajinsko-ekološke variabilnosti Slovenije je ključnega pomena ovrednotiti vplive na stopnjo rodnosti srnjadi, tj. stopnjo oplojenosti, število zarodkov in število mladičev, ki jih vodi posamezna srna, vzdolž gradienta okoljskih dejavnikov. To je pomembno tudi iz širše evropske perspektive, saj takšnega gradienta okoljskih dejavnikov in medvrstnih odnosov, v katerih je udeležena tudi srnjad, drugod po Evropi ni. V pričujočem prispevku podajamo pregled najpomembnejših ugotovitev, do katerih so s sistematičnimi raziskavami razmnoževalnega potenciala srnjadi prišli raziskovalci v drugih evropskih državah. S preglednim člankom želimo: (i) prispevati k boljšemu razumevanju in upoštevanju velike variabilnosti v oplojenosti in posledično prirastka srnjadi v upravljavskem procesu; (ii) pripraviti ustrezna izhodišča za začetek sistematičnih raziskav razmnoževalnega potenciala srnjadi v našem okolju.

2 RAZMNOŽEVALNI POTENCIAL SRNJADI: PREGLED DOSEDANJIH UGOTOVITEV

Skoraj vse vrste iz družine jelenov (Cervidae) s severnega dela zmernega pasu polegajo mladiče spomladi (med aprilom in junijem), paritveno obdobje pa poteka jeseni (med oktobrom in novembrom). Večina samic je sezonsko poliestričnih (Andersen in sod., 1998). Ovulacijo uravnava dolžina dneva in se praviloma začne s krajšanjem fotoperiode po jesenskem enakonočju. Od skrajševanja dolžine dneva je odvisna tudi količina testosterona v testisih samcev. Izjema je srnjad, pri as mating occurs in late summer (*ibid*.). The rut starts around the 20th of July and ends around the 20th of August. There can be some margins, correlated with altitude and temperature (Krže, 2000).

Female roe deer are monoestrous, i.e. they have only one oestrous cycle per year (Andersen et al., 1998). They undergo embryonic diapause (delayed implantation), when the implantation of the blastocyst is delayed by five months. During this period - from early August (after the rut) to late December - the blastocyst enters a period of diapause at the 20-30-cell stage. The blastocyst undergoes a low level of mitosis during the last six weeks of diapause and reactivates at approximately the 100-cell stage. At this stage it is attached to the placenta. Various factors could be associated with the reactivation of the roe deer blastocyst from diapause including environmental cues, changes in the profile of maternal hormones or secretion of biochemical signals by the endometrium or conceptus (Lambert et al., 2001). Embryonic diapause exists in numerous mammals, such as some mustelids (Mustelidae) and seals (Pinnipedia), but the roe deer is the only artiodactyl known to use embryonic diapause as a reproductive strategy (Andersen et al., 1998).

The distribution of roe deer in Europe ranges from the south of Spain (36°N) to the northern parts of Norway (68°N). It is rather unexpected that small ungulates could live and survive in such northern environments, but it is probable that the delayed implantation, which appears to be a secondary sexual adaptation, allows females to mate during the favourable season (summer) and also to give birth in spring, at the best time for the survival of fawns. The survival of fawns depends on the lactating capacity of the females, and during this period, the food and energy requirement of the females is at a maximum. It has been shown that lactation after a period of lower food availability could affect the reproduction of red deer in the following breeding season and decreases the fertility of polyestrous female red deer (Andersen et al., 1998).

2.1 Factors affecting roe deer reproductive potential

Roe deer reproductive potential – the number of fertilized ovulations (potential litter size), litter size and sex ratio of embryos/fawns – is affected by individual, population and/or environmental factors (Figure 1, Table 1). The number of fertilized ovulations is determined by the identification and counting of the corpora lutea (*corpora lutea* (pl); *corpus luteum*) in roe deer ovaries. Litter size is determined by embryo counts and later by counting newborn fawns. Litter

kateri se paritveno obdobje (prsk) začne že v sredini poletja (*ibid*.). Prsk srnjadi traja nekje od 20. julija do 20. avgusta, zamiki pa so odvisni od nadmorske višine in temperature (Krže, 2000).

Srne so monoestrične, kar pomeni, da imajo samo en ovulacijski cikel letno (Andersen in sod., 1998). Zanje je značilna tudi embrionalna diapavza (odložena implantacija oz. zadržana brejost), ki traja cca. 5 mesecev. Pri embrionalni diapavzi se oplojeno jajčece v steno maternice ne ugnezdi takoj, ampak ostane neaktivno v obliki zarodnega mehurčka (blastociste) pri velikosti približno 20–30 celic. Gre za obdobje od oploditve v prsku (julij/avgust) do zgodnjega januarja. V času diapavze poteka v blastocisti nizka stopnja mitoze. Ob koncu diapavze ima zarodni mehurček velikost okoli 100 celic in se lahko ugnezdi v maternično steno. Predvideva se, da na reaktivacijo blastociste pri srnjadi vplivajo okoljski dejavniki, spremembe v hormonalnem razmerju pri materi ali pa biokemični signali iz maternične ovojnice (Lambert in sod., 2001). Embrionalno diapavzo imajo sicer tudi nekatere druge skupine sesalcev, npr. kune (Mustelidae) in plavutonožci (Pinnipedia), vendar je srnjad edina predstavnica parkljarjev (kopitarjev), pri kateri se je, kot razmnoževalna strategija, razvila embrionalna diapavza (Andersen in sod., 1998).

Razširjenost srnjadi v Evropi sega od Španije na jugu (36° SGŠ) do severnih delov Norveške (68° SGŠ). Kljub manjši telesni velikosti lahko preživi v severnih okoljih. Embrionalna diapavza, ki se je pojavila kot sekundarna spolna prilagoditev, samicam najprej omogoča parjenje v obdobju ugodnih klimatskih razmer (poletje), kasneje pa lahko polegajo mladiče spomladi, ko je najbolj primeren letni čas za preživetje mladičev. Slednje je namreč odvisno od sposobnosti laktacije samic, med katero imajo samice največje energijske (prehranske) zahteve. Pri navadnem jelenu je bilo dokazano, da lahko laktacija v obdobju slabše razpoložljivosti hrane vpliva na reprodukcijo v naslednjem paritvenem obdobju in zmanjša rodnost poliestričnih košut (Andersen in sod., 1998).

2.1 Dejavniki, ki vplivajo na razmnoževalni potencial srnjadi

Na razmnoževalni potencial srnjadi, ki ga opredeljujejo stopnja oplojenosti samic, velikost legla in spolno razmerje zarodkov/mladičev, vplivajo dejavniki, ki so lahko individualni, populacijski in/ali okoljski (slika 1, preglednica 1). Stopnjo oplojenosti določamo z ugotavljanjem prisotnosti in štetjem rumenih telesc (*corpora lutea* (mn.); *corpus luteum*) v jajčnikih srn, velikost legla pa s štetjem živih zarodkov oziroma kasneje z ugotavljanjem števila živorojenih mladičev; velikost size depends on the success of blastocyst implantation, and due to implantation failure, it can significantly differ from potential litter size (number of fertilized ovulations). The sex ratio of embryos (primary sex ratio) or fawns (secondary sex ratio) is the proportion of males or females in a litter.

The most important factors that influence roe deer reproductive potential are: population density (Andersen in Linnell, 2000; Nilsen et al., 2009); weather conditions and habitat quality (Nilsen et al., 2004; Toïgo et al., 2006); demographic structure of population and female roe deer phenotype, i.e. body size, body mass, physical condition (Kjellander et al., 2004a; Hamel et al., 2009a); genetic characteristics of populations and individual does (Hewison, 1997); and other factors, such as population age structure and the age of individuals (Figure 1, Table 1).

Factors affecting roe deer reproductive potential are linked and can influence each other. For example, environmental factors can influence individual factors (e.g. body mass, size and physical condition of does), which consequently have an effect on the number of fertilized ovulations, litter size and fawn sex ratio. Individual factors can be shaped by population parameters (especially population density), and their effect can differ according to the demographic structure of a population. The actual reproductive potential is the sum of many different factors and interactions between them and therefore differs among different environments (Figure 1).

legla je odvisna od uspešnosti ugnezdenja (implantacije) blastociste v maternično sluznico, zato se lahko pomembno razlikuje od stopnje oplojenosti. Spolno razmerje zarodkov (primarno spolno razmerje) oz. mladičev (sekundarno spolno razmerje) nam pove, kakšen delež mladičev je moškega oziroma ženskega spola.

Najpomembnejši dejavniki, ki vplivajo na razmnoževalni potencial srnjadi, so: populacijska gostota (Andersen in Linnell, 2000; Nilsen in sod., 2009); vremenske razmere in kakovost habitata (Nilsen in sod., 2004; Toïgo in sod., 2006); demografska struktura populacije(Andersen and Linnell, 2000; Hewison and Gaillard, 2001) in fenotip samic, tj. njihova velikost, telesna masa, fizična kondicija (Kjellander in sod., 2004a; Hamel in sod., 2009a); genetske značilnosti populacij in posameznih srn (Hewison, 1997); ter nekateri drugi dejavniki, kot so starostna struktura populacij in starost posameznih srn (slika 1, preglednica 1).

Dejavniki, ki vplivajo na razmnoževalni potencial srnjadi, se med sabo prepletajo in lahko vplivajo drug na drugega. Okoljski dejavniki, na primer, lahko vplivajo na individualne dejavnike (npr. na telesno maso, velikost in fizično kondicijo), kar posledično vpliva na stopnjo oplojenosti, velikost legel in spolno razmerje mladičev. Na individualne dejavnike lahko vplivajo tudi populacijski parametri (še zlasti gostota populacije), ki pa lahko imajo različen učinek glede na to, kakšna je demografska struktura neke populacije. Dejanski razmnoževalni potencial srnjadi je tako vsota neštetih vplivnih dejavnikov in delovanj med njimi ter se med različnimi populacijami ter okolji močno razlikuje (slika 1).

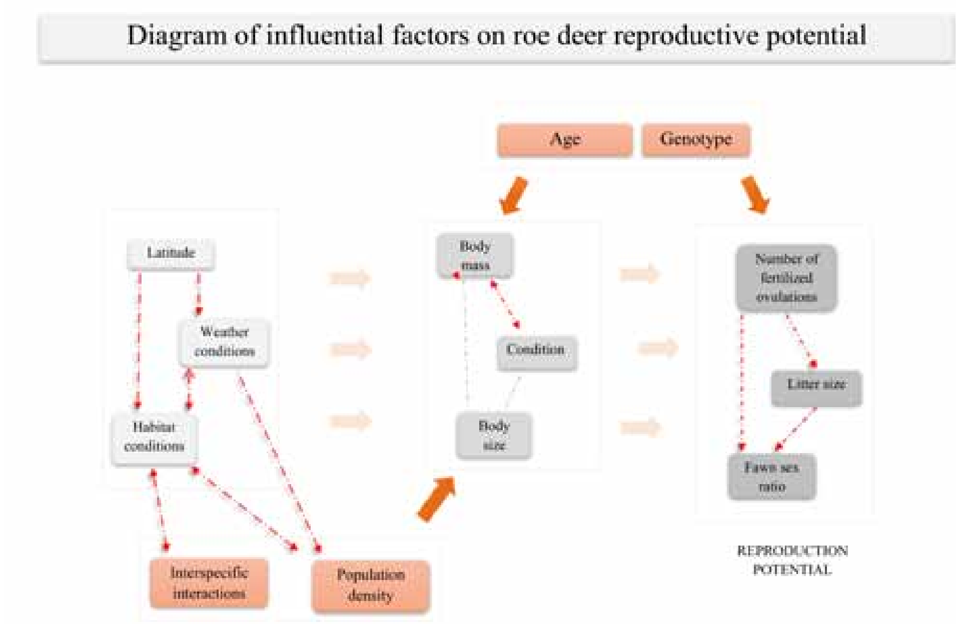

Fig. 1: Overlapping of various factors influencing the reproductive potential of roe deer

Slika 1: Prepletanje vpliva različnih dejavnikov na razmnoževalni potencial srnjadi

Table 1: Review of findings on the main influential factors affecting reproductive potential of roe deer in Europe

Preglednica 1: Pregled ugotovitev o najpomembnejših dejavnikih, ki vplivajo na razmnoževalni potencial srnjadi v Evropi

Target parameter / *Ciljni parameter*	Impact[1] / *Vpliv*[1]	Period / *Obdobje*	Location / *Lokacija*	Reference / *Vir*
Population density / *Gostota populacije*				
potential litter size (fertility rate) / *potencialna velikost legla (stopnja oplojenosti)*	+	1995–1999	Italy / *Italija* (Tredozio - Collinacia and Monti)	Focardi et al., 2002
litter size / *velikost legla*	0 / + *	1991–1994	Norway / *Norveška* (Storfosna)	Andersen and Linnell, 2000
fawn birth body mass / *masa mladičev ob skotitvi*	+	1987–1995	France / *Francija* (Chizé)	Andersen et al., 2000
fawn mortality / *zgodnja smrtnost mladičev*	+	1987–1995	France / *Francija* (Chizé)	Andersen et al., 2000
fawn sex ratio / *spolno razmerje mladičev*	+	1995–1999	Italy / *Italija* (Tredozio - Collinacia and Monti)	Focardi et al., 2002
	0	1987–1993	Belgium (various locations) / *Belgija (več lokacij)*	Wauters et al., 1995
Habitat conditions / *Habitatne značilnosti*				
potential litter size (fertility rate) / *potencialna velikost legla (stopnja oplojenosti)*	0	1989-1994	Sweden / *Švedska* (Bogesund)	Wahlström and Kjellander, 1995
litter size / *velikost legla*	+	1991–1994	Norway / *Norveška* (Storfosna)	Nilsen et al., 2004
sex ratio of embryos / *spolno razmerje zarodkov*	+	1983–1990	Great Britain (various locations) / *Vel. Britanija (več lokacij)*	Macdonald and Johnson, 2008
Weather conditions / *Vremenski vplivi*				
implantation success (average T in the previous winter) / *uspeh pri implantaciji (povprečna T v pretekli zimi)*	0 / + **	1970–1990	Great Britain (various locations) / *Vel. Britanija (več lokacij)*	Hewison and Gaillard, 2001
potential litter size (fertility rate) (average T in the previous winter) / *potencialna velikost legla (stopnja oplojenosti) (povprečna T v pretekli zimi)*	0	1970–1990	Great Britain (7 locations) / *Vel. Britanija (7 lokacij)*	Hewison and Gaillard, 2001
	+	1970–1990	Great Britain / *Vel. Britanija* (Spadedam, Thetford)	Hewison and Gaillard, 2001
potential litter size (fertility rate) (precipitation May-June) / *potencialna velikost legla (stopnja oplojenosti) (količina padavin maj-junij)*	0	1970–1990	Great Britain (8 populations) / *Vel. Britanija (8 populacij)*	Hewison and Gaillard, 2001
	+	1982-1990	Great Britain / *Vel. Britanija* (Pickering)	Hewison and Gaillard, 2001
litter size (effects of hurricane Lothar) / *velikost legla (vpliv orkana Lothar)*	0	1978-2000	France / *Francija* (Chizé & Trois Fontaines)	Gaillard et al., 2003
Maternal body mass / *Masa samic*				
potential litter size (fertility rate) / *potencialna velikost legla (stopnja oplojenosti)*	+	1970–1990	Great Britain (various locations) / *Vel. Britanija (več lokacij)*	Hewison and Gaillard, 2001
	+	1995–1999	Italy / *Italija* (Tredozio - Collinacia & Monti)	Focardi et al., 2002
litter size (number of embryos) / *velikost legla (št. zarodkov)*	+	1994–2005	England and Wales / *Anglija in Wales*	Macdonald and Johnson, 2008
litter size / *velikost legla*	+	1987–1995	France / *Francija* (Chizé)	Andersen et al., 2000
	+	1991–1994	Norway / *Norveška* (Storfosna)	Nilsen et al., 2004; Andersen and Linnell, 2000
	+	1987–1993	Belgium (various locations) / *Belgija (več lokacij)*	Wauters et al., 1995
fawn survival / *preživetje mladičev*	+	1987–2003	France / *Francija* (Chizé)	Toïgo et al., 2006
sex ratio of embryos / *spolno razmerje zarodkov*	0 / +	1994–2005	England and Wales / *Anglija in Wales*	Macdonald and Johnson, 2008
	+	1983–1990	Great Britain (various locations) / *Vel. Britanija (več lokacij)*	Macdonald and Johnson, 2008
fawn sex ratio / *spolno razmerje mladičev*	+	1987–2003	France / *Francija* (Chizé)	Toïgo et al., 2006
	+	1987–1993	Belgium (various locations) / *Belgija (več lokacij)*	Wauters et al., 1995
	+	1995–1999	Italy / *Italija* (Tredozio - Collinacia & Monti)	Focardi et al., 2002
	+	1985–1996	France / *Francija* (Trois Fontaines)	Hewison et al., 1999
Mother's age / *Starost matere*				
implantation success / *uspeh pri implantaciji*	+	1970–1990	Great Britain (various locations) / *Vel. Britanija (več lokacij)*	Hewison and Gaillard, 2001
potential litter size (fertility rate) / *potencialna velikost legla (stopnja oplojenosti)*	0	1970–1990	Great Britain (7 locations) / *Vel. Britanija (7 populacij)*	Hewison and Gaillard, 2001
	+	1970–1990	Great Britain / *Vel. Britanija* (Spadedam & Pickering)	Hewison and Gaillard, 2001
litter size / *velikost legla*	0 / + *	1991–1994	Norway / *Norveška* (Storfosna)	Andersen and Linnell, 2000
	+	1987–1993	Belgium (various locations) / *Belgija (več lokacij)*	Wauters et al., 1995
	+	1978-2000	France / *Francija* (Chizé)	Gaillard et al., 2003
fawn sex ratio / *spolno razmerje mladičev*	+	1987–1993	Belgium (various locations) / *Belgija (več lokacij)*	Wauters et al., 1995
proportion of breeding females / *delež brejih samic*	+	1978-2000	France / *Francija* (Chizé)	Gaillard et al., 2003

1 +...impact detected / *vpliv zaznan*, 0... no impact detected / *vpliv ni zaznan*

*only 2-year old does / *samo 2-letne srne*

**interpopulation level / *medpopulacijska raven*

2.1.1 Population density

Population density is an important population parameter that can affect the fertility of a certain population (Tome, 2006). In this context, density is considered to affect fertility through different indirect parameters, such as stress, food availability, body masses, etc. Roe deer body mass can be density-dependent; as population density increases, there is a reduction in body mass of roe deer (Andersen et al., 2000; Petorelli et al., 2001; Focardi, 2002) and roe deer fawns (Petorelli et al., 2001; Toïgo et al., 2006). Population density effects are also reflected in home-range size and in intraspecific interactions, e.g. food and land competition, parasite transport, etc. (Hewison et al., 1996; Body et al., 2011; Courturier et al., 2012). Impacts of population density on reproductive parameters have been detected in various large herbivore species (red deer: Bonenfant et al., 2002; McLoughlin et al., 2008; other species: Bonenfant et al., 2009; Hamel et al., 2009a). In the case of roe deer, it is reflected in the number of fertilized ovulations and fertility of does (Focardi et al. 2002), litter size and number of fawns per doe (Vincent et al. 1995; Andersen and Linnell, 2000; Focardi et al., 2002), fawn sex ratio (Focardi et al., 2002) and age of primiparity (Vincent et al., 1995).

European roe deer is a species with great population growth potential in an environment without predators and hunting (Vincent et al., 1995; Andersen and Linnell, 2000). It is adapted to utilize early successional stage environments, which are often promoted by human activities. In addition, throughout most of the range of the European roe deer, large predators are absent or occur at low densities, resulting in an often negligible or non-existent effect of predation. Consequently, roe deer populations have increased in density and distribution during the 20th century in Europe (Andersen and Linnell, 2000).

In relation to increasing population density, several changes in reproduction can occur. Increasing population density lowers the number of fawns per doe (Vincent et al., 1995; Gill et al., 1996; Andersen et al., 1998; Andersen and Linnell, 2000). Some Swedish studies have demonstrated that density-dependence affects litter size. Thus the number of fawns born per adult female decreased from 2.3 to 1.4 in Ekenäs (Sweden) and from 2.1 to 1.7 in Bogesund (Sweden) with a threefold and two-fold increase in population density, respectively (Andersen et al., 1998). Similar results have also been shown in Norway, where after an effective halt to legal harvest and poaching, the roe deer population increased from 10.1 animals/km^2 in 1991 to 19.3 animals/km^2 in 1992; in 1994, the density expanded to

2.1.1 Gostota populacije

Gostota populacije je pomemben populacijski parameter, od katerega je lahko odvisna rodnost določene populacije (Tome, 2006). Tukaj govorimo o gostoti, ki na rodnost ne vpliva sama po sebi, temveč prek različnih posrednih dejavnikov, kot na primer: stres, prehranski viri, telesne mase ipd. Vpliv gostote na telesno maso osebkov srnjadi se lahko kaže tako, da se z naraščajočo gostoto populacij telesna masa praviloma zmanjšuje (Andersen in sod., 2000; Petorelli in sod., 2001; Focardi, 2002), praviloma se zmanjšuje tudi povprečna telesna masa mladičev (Petorelli in sod., 2001; Toïgo in sod., 2006). Populacijska gostota pomembno vpliva na velikosti območij aktivnosti živali (Kjellander in sod., 2004a) in na znotrajvrstne interakcije, kot so konkurenca za prostor in hrano in prenos zajedavcev. (Hewison in sod., 1996; Body in sod., 2011; Courturier in sod., 2012). Vpliv gostote populacije na različne reprodukcijske parametre je bil ugotovljen pri različnih vrstah velikih rastlinojedov (pri jelenjadi: Bonenfant in sod., 2002; McLoughlin in sod., 2008; pri različnih vrstah: Bonenfant in sod., 2009; Hamel in sod., 2009a). Pri evropski srni se kaže v stopnji oplojenosti in plodnosti samic (Focardi in sod., 2002), velikosti legla in številu mladičev na posamezno samico (Vincent in sod., 1995; Andersen in Linnell, 2000; Focardi in sod., 2002), spolnem razmerju mladičev (Focardi in sod., 2002) in starosti, pri kateri so samice prvič breje – t. i. primiparnost (Vincent in sod., 1995).

Srnjad je vrsta, ki ima v okolju brez plenilcev in vpliva lova zelo velik potencial rasti številčnosti (Vincent in sod., 1995; Andersen in Linnell, 2000). Dobro je prilagojena okolju v zgodnjih sukcesijskih fazah, ki so v večini primerov nastajali in še nastajajo pod vplivom človeških dejavnosti (Sinclair, 1997, cit. po Andersen in Linnell, 2000). Kot posledica dejstva, da večine plenilcev srnjadi v velikem delu območij v Evropi danes ni oziroma se pojavlja v majhnih gostotah, je njihov vpliv na srnjad pogosto majhen ali ga sploh ni. Posledično so gostote populacij srnjadi in absolutne številčnosti te vrste v dvajsetem stoletju skoraj povsod v Evropi narasle, povečalo pa se je tudi območje njene razširjenosti (Andersen in Linnell, 2000).

Hkrati z naraščajočimi populacijskimi gostotami se spreminjajo tudi lastnosti v reprodukciji srnjadi. Z naraščanjem gostote se praviloma zmanjšuje število poleženih mladičev na posamezno srno (Vincent in sod., 1995; Gill in sod., 1996; Andersen in sod., 1998; Andersen in Linnell, 2000). Tako se je, na primer, na Švedskem povprečno število mladičev na posamezno srno pri trikratnem povečanju gostote zmanjšalo z 2,3 na 1,4 (Ekenäs) in pri dvakratnem povečanju gosto-

34.5 animals/km^2 (Andersen and Linnell, 2000). Along with increasing density, the average number of fawns per doe decreased from 2.44 fawns in a year with the lowest density (1991) to 2.04 in 1994, when the density was the highest. During this period, the proportion of non-producing does also proportionally increased; on average, however, 82 % of the females gave birth to fawns each year (*ibid*).

In contrast to the extremely high roe deer yield in Norway (as mentioned above) was the average number of fawns per doe in Italy (Tredozio: Province di Forli-Cesena), only 0.75 ± 0.4. In this area, roe deer density was significantly higher, with 53.8 ± 4.8 animals/km^2 (in comparison: in Slovenia, on average, only 2.0 – 2.5 animals/km^2 are culled annually). The study area was divided into two separate subareas, closely located and ecologically comparable, but with different roe deer population densities. The number of fawns per doe was higher in the area with lower density. Effects of density also reflected in fawn sex ratio, as the proportion of male fawns was higher in the area of higher density (Focardi et al., 2002). However, there was no observed link between density and fawn sex ratio in studies done in Belgium (Wauters et al., 1995).

2.1.2 Habitat conditions

Differences in density are also reflected in home-range sizes. Increasing density of roe deer leads to smaller home ranges, while home ranges of roe deer from areas with lower population densities are larger (Kjellander et al. 2004). Impacts of home range can be direct, in connection to mating possibilities (in low density areas, where home-ranges are larger, finding a mating partner is more difficult) and indirect, as resource availability. The pattern of habitat selection within a winter home range may result from a strategy of maximising net energy gain - high food intakes and low energy expenditures (Andresen et al., 1998). Females with the greatest availability of preferred habitat during winter produce larger litters in the subsequent spring (Nilsen et al. 2004). Nevertheless, habitat quality does not necessarily always affect roe deer reproductive potential. In Sweden (Wahlström and Kjellander, 1995), roe deer reproductive potential was compared between low and high quality areas. No significant differences were found in any of the reproductive parameters, as the number of *corpora lutea* was the same in both areas (1.8). The authors concluded that these results are connected with the dispersal of animals in the area. Female dispersal in roe deer is "voluntary" and not socially stimulated, with the underlying cause being the maximization of resource gain.

te z 2,1 na 1,7 (Bogesund) (Andersen in sod., 1998). Podobno je bilo opaziti tudi na Norveškem, kjer se je populacija srnjadi v dobrem letu po prenehanju lova v okolju brez plenilcev podvojila, in sicer z 10,1 živali/km^2 v letu 1991 na 19,3 živali/km^2 v letu 1992; leta 1994 je gostota narasla že na 34,5 živali/km^2 (Andersen in Linnell, 2000). Hkrati z naraščajočo gostoto se je zmanjševalo povprečno število poleženih mladičev na samico, in sicer z 2,44 mladiča v letu najmanjše gostote (1991) na 2,04 mladiča v letu z največjo gostoto osebkov (1994); v tem obdobju je proporcionalno narasel tudi delež odraslih samic brez mladičev, v povprečju pa je vsako leto imelo mladiče 82 % odraslih srn (*ibid.*).

V primerjavi z zgoraj omenjenim izjemno velikim prirastkom srnjadi na Norveškem je bilo v Italiji (Tredozio: Province di Forli-Cesena) v območju, kjer je bila gostota te vrste bistveno večja in je znašala kar 53,8 ± 4,8 osebkov/km^2 (samo za primerjavo: v Sloveniji znaša odvzem srnjadi v povprečju le 2,0 – 2,5 osebkov/km^2), povprečno število poleženih mladičev na posamezno srno manjše, tj. le 0,75 ± 0,4 mladiča/srno. V dveh raziskovanih podobmočjih, ki sta bili relativno blizu in sta imeli podobne ekološke značilnosti, razlikovali pa sta se po gostoti populacij srnjadi, je bilo število poleženih mladičev na posamezno samico večje na podobmočju z manjšo gostoto srnjadi. Poleg velikosti legla je večja populacijska gostota vplivala tudi na večji delež samčkov (srnjačkov) v spolnem razmerju mladičev (Focardi in sod., 2002). V raziskavah, ki so potekale v Belgiji, povezave med gostoto in spolnim razmerjem mladičev ni bilo (Wauters in sod., 1995).

2.1.2 Habitatne značilnosti

Razlike v gostoti populacij se kažejo tudi v velikosti območij aktivnosti živali. Območja aktivnosti osebkov srnjadi so v območjih z majhnimi gostotami večja kot v območjih z velikimi gostotami (Kjellander in sod., 2004a). Območje aktivnosti na reprodukcijsko sposobnost srnjadi lahko vpliva neposredno, prek možnosti za paritev (v območjih z nizko gostoto in velikimi območji aktivnosti je iskanje partnerjev težje) in pa posredno, prek razpoložljivosti virov. Pozimi srnjad izbira takšna območja aktivnosti, v katerih so na voljo večje količine hrane in kjer za iskanje hrane porabi najmanj energije (Andersen in sod., 1998). Samice, ki imajo med zimo na voljo boljše habitatne razmere, imajo praviloma spomladi večja legla (Nilsen in sod., 2004). Ugodne habitatne razmere so zelo pomembne tudi z vidika poleganja mladičev in njihove zgodnje smrtnosti oz. možnosti preživetja v prvih tednih življenja. Srne izbirajo za poleganje praviloma območja z visoko vegetacijo na suhih tleh, ki so občasno lahko delno izpostavljena sončni

Favourable habitat conditions are also important for the birth of fawns, early fawn mortality or fawn survival in the first weeks after birth. When giving birth, roe deer does select areas with high vegetation on dry soil, partly exposed to sunlight (Nikolandić and Degmečić, 2007). In Croatia (area of Baranja), studies showed (total of 49 monitored fawns) that most of the fawns were born in oak stands (*Quercus robur* L.) and shrub vegetation (44 %), followed by areas of regenerating oak (19%), stands of eastern black walnut (*Juglans nigra* L.) (17%) and finally other types of vegetation (black locusts stands, mixed deciduous trees stands, clover). In favourable habitat conditions, fawns are less vulnerable to predators, consequently lowering the high fawn mortality in the days after birth.

European roe deer inhabit a variety of environments ranging from dry, hot habitat in the Mediterranean region to humid, cold habitat north of the Polar Circle. Roe deer therefore face a wide range of environmental variation across the species range, which can cause a change in the optimal life-history (Andersen et al., 1998). Distribution of roe deer in Europe ranges from Spain in the south to the northern parts of Norway, and according to latitude, there are differences in time of birth and number of fawns in a litter. Southern and Atlantic coast populations give birth before inland, continental populations. In Spain, 80% of fawns are born in April, hence in Denmark, Norway and Sweden the time of birth is moved to a later period between the second half of May and the beginning of June (*ibid*.). On average, northern populations have larger litters than southern populations (Andersen et al. 1998; Andersen and Linnell, 2000). While triplets are more common than single fawns in Scandinavian populations, average number of embryos per adult reproductive female in populations in Central Europe varies between 1.55 (Hungary) and 1.9 (Poland) (Andersen et al. 1998). In 15 populations in the UK, the average number of embryos produced was 1.7. However, there was large inter-population variation: in "low performance" populations, average production of embryos was only 1.1, whereas in other populations 1.95 embryos on average were produced per adult reproductive doe (*ibid.).*

2.1.3 Weather conditions

Weather conditions are closely associated with vegetation characteristics. Females with the greatest availability of preferred habitat during winter are also less exposed to harsh weather conditions (Nilsen et al. 2004). One major determinant of juvenile phenotypic quality is the quantity and quality of food resources available to the mother during the last third of gesta-

svetlobi (Nikolandić in Degmečić, 2007). Na Hrvaškem (območje Baranje) so na podlagi opazovane populacije srnjadi ugotovili, da je bilo (od skupaj 49 spremljanih mladičev) največ poleženih mladičev v sestojih hrasta doba (*Quercus robur* L.) in grmovne vegetacije (44 %), temu so sledila območja z dobovim pomladkom (19 %) in kulture črnega oreha (*Juglans nigra* L.) (17 %). Preostali delež (20 %) je pripadal drugim tipom vegetacije (sestoji robinije, mešani sestoji listavcev, detelja). V ugodnejših habitatnih razmerah so novorojeni mladiči bolj varni pred plenilci, kar posledično vpliva na zmanjšano smrtnost mladičev v prvih tednih življenja (*ibid*.).

Evropska srna naseljuje širok spekter habitatov, od suhih in vročih območij v Mediteranu do vlažnih in hladnih predelov severno od polarnega kroga, zato se v celotnem območju razširjenosti spopada z velikimi okoljskimi razlikami, ki močno vplivajo na življenjsko strategijo vrste (Andersen in sod., 1998). Razširjenost srnjadi v Evropi sega od Španije na jugu do severih delov Norveške, glede na zemljepisno širino pa se spreminja tudi število mladičev v leglu. Severne populacije imajo v povprečju večja legla kot južne (Andersen in sod., 1998; Andersen in Linnell, 2000). V Skandinaviji imajo samice bolj pogosto kot drugje v leglu tri mladiče (takšna legla so v Sloveniji izjema; lastni podatki). Povprečno število zarodkov na odraslo reproduktivno samico je pri populacijah srnjadi iz srednje Evrope med 1,55 (Madžarska) in 1,9 (Poljska) (Andersen in sod., 1998). V 15-ih populacijah iz Velike Britanije je povprečno število zarodkov znašalo 1,7. Kljub vsemu pa se tukaj pojavljajo tudi velike med-populacijske razlike: pri slabše produktivnih populacijah je povprečno število zarodkov na odraslo reproduktivno samico znašalo 1,1 zarodek, medtem ko je pri drugih populacijah znašalo 1,95 zarodka. (Andersen in sod., 1998).

2.1.3 Vremenski vplivi

Značilnosti vegetacije se povezujejo tudi z vremenskimi vplivi. Samice, ki imajo v zimskem času boljše habitatne razmere, so manj izpostavljene ostrim vremenskim vplivom (Nilsen in sod, 2004). Eden izmed pomembnih faktorjev, ki vplivajo na fenotip mladičev, je količina in kakovost hrane, ki je na voljo samicam v zadnji triadi brejosti in v času laktacije. V zmerno klimatskem pasu vplivajo na količino razpoložljive hrane zlasti vremenske razmere spomladi in poleti, ki določajo primarno produkcijo. Na fenotip mladičev pomembno vplivajo razmere v okolju, katerih vpliv se razlikuje glede na populacijsko gostoto in spol osebkov (Toïgo in sod., 2006). Pri srnjadi iz rezervata Chizé v Franciji so se razlike med spoloma pokazale pri manjšanju velikotion and during lactation. In temperate environments, forage availability depends on the climatic conditions in both spring and summer, which determine primary production. Fawn phenotype is remarkably affected by environmental conditions that can be both density- and sex- dependent (Toïgo et al., 2006). The response of fawn body size to the environmental factors was sex specific in the Chizé reserve in France. Male fawn body size decreased linearly with density irrespective of climatic conditions, whereas female body size in winter was negatively affected by density only after dry summers (*ibid.*). Summer drought is the critical factor, which induces early fawn mortality and survival rate during summer months (Gaillard et al. 2003), and it also reduces fawn winter mass (Toïgo et al., 2006). In the long term, summer drought also decreases the individual quality of adult roe deer (Hamel et al., 2009a).

As roe deer do not rely on body reserves for reproduction, but more on food availability, environmental conditions in the year of primiparity should affect the success of the first reproduction. In species in which age at first reproduction varies, unfavourable environmental conditions in early life can delay primiparity (Hamel et al. 2009a).

Poor weather conditions, especially in the period of embryonic diapause, are likely to affect the implantation of the blastocyst and consequently litter size (Putman et al., 1996; Hewison and Gaillard, 2001; Nilsen et al., 2004). Low winter temperatures (during the gestation period), when only the strong does can survive, as well as good conditions before the rutting season (high temperatures and low rainfall quantity), affect the sex ratio of newborn fawns. In both cases more female fawns are born (Muri et al., 1999). However, the effects of poor weather conditions on reproductive performance of roe deer are not always detected. In studies carried out by Hewison and Gaillard (2001), climatic factors were not consistently correlated with individual female fecundity within populations, but between populations implantation failure increased with climatic severity. They observed a significant influence of temperature in the previous winter on potential litter size in two out of nine populations. Potential litter size increased with increasing temperature in the previous winter (at Spadedam), but decreased with increasing temperature in the previous winter (at Thetford) (*ibid.*).

Studies of the effect of extreme-weather conditions on the reproductive performance of roe deer carried out in France a few years after Hurricane Lothar have shown that extreme weather situations do not necessarily have a negative effect on the proportion of preg-

sti telesa, in sicer se je velikost mladičev moškega spola z naraščanjem gostote manjšala neodvisno od klimatskih razmer, medtem ko se je velikost srnic zmanjšala le, če je bilo preteklo poletje sušno (*ibid.*). Poletna suša je pri srnjadi kritičen dejavnik, ki vpliva na zgodnjo smrtnost mladičev, tj. na stopnjo njihovega preživetja prek poletja (Gaillard in sod., 2003), in na njihovo zimsko telesno maso (Toïgo in sod., 2006), dolgoročno pa tudi na individualno kondicijo odraslih živali (Hamel in sod., 2009a).

Srne pri razmnoževanju niso pomembno odvisne od telesnih zalog, temveč predvsem od razpoložljivosti hrane, zato lahko okoljske razmere v letu, ko samica prvič polega mladiče (primiparnost), pomembno vplivajo na uspeh prve reprodukcije. Pri vrstah, kjer je starost ob prvi reprodukciji spremenljiva (velja tudi za srnjad), lahko neugodne okoljske razmere zamaknejo čas prve reprodukcije v višjo starost (Hamel in sod., 2009a).

Slabše vremenske razmere v času embrionalne diapavze lahko vplivajo na proces implantacije oz. ugnezdenja blastociste v steno maternice in na nastanek zarodka ter s tem zmanjšajo končno velikost legla oz. število poleženih mladičev (Putman in sod., 1996; Hewison in Gaillard, 2001; Nilsen in sod., 2004). Nizke zimske temperature (v času brejosti), v katerih lahko preživijo le močnejše samice, in tudi neugodne razmere pred prskom (visoke temperature in majhna količina padavin) določajo tudi spolno razmerje poleženih mladičev, in sicer se v obeh primerih praviloma poveča delež srnic (Muri in sod., 1999). Vendar vpliv neugodnih vremenskih razmer na uspešnost implantacije zarodka srnjadi ni vedno zaznan. Tako, na primer, Hewison in Gaillard (2001) nista ugotovila nobenih soodvisnosti med verjetnostjo neuspešne implantacije blastociste pri srnah iz različnih populacij v Angliji in vremenskimi vplivi na inter-populacijski ravni (med populacijami). Plodnost samic med populacijami se glede na vremenske razmere ni razlikovala. Drugačno stanje se je pokazalo na intra-populacijski ravni (tj. znotraj populacij), kjer je neuspešnost implantacije sovpadala z zaostritvijo vremenskih razmer. Vpliv temperature v pretekli zimi na velikost legla je bil zaznan v dveh od devetih preučevanih populacij. Velikost legla je narasla z višanjem zimske temperature (območje Spadeadam) in se zmanjšala z nižanjem temperature (območje Thretford) (*ibid.*).

Raziskave vpliva ostrih vremenskih razmer, ki so jih naredili v Franciji nekaj let po silovitem orkanu Lothar, so pokazale, da slabe vremenske razmere nimajo nujno negativnega vpliva na delež brejih samic in na velikost legla. Orkan Lothar, ki je konec decembra 1999 nant does and on litter size. In late December 1999, Hurricane Lothar struck France, Switzerland and Germany and damaged large areas of forest, i.e. roe deer habitats. As the hurricane occurred during the roe deer reproductive cycle when embryos are implanted, it was expected to have a negative effect on roe deer. However, there was no evidence of a decrease in either pregnancy rate or litter size (Gaillard et al., 2003).

2.1.4 Body mass and other phenotypic characteristics

Although body mass is not the only determinant of life-history variation, it is certainly the most important (Andersen et al., 1998). Roe deer fecundity, similar to that of some other ungulate species, depends on body mass (Gaillard et.al., 1992; Gerhart et al., 1997; Andersen and Linnell, 2000; Hewison and Gaillard, 2001; Focardi et al., 2002; Macdonald and Johnson, 2008; also see Table 2). Hewison and Gaillard (2001) investigated the number of fertilized ovulations per reproductive roe deer doe (by counting the number of corpora lutea in ovaries) from nine different populations in Great Britain. They came to the conclusion that does carrying more than one corpora lutea were significantly heavier that does with a potential litter size of one in all but one of the populations in their study. In six of seven studied populations, potential litter size (number of fertilized ovulations) increased proportionally with increasing doe body mass. In some cases, this feature was related to the doe's age. In highly productive populations with better phenotypic quality (higher body masses, better condition) (Alice Holt, n = 74), all females produced at least two corpora lutea, with six producing three. In the poorest of populations (Queens, n=15), all does produced only one corpora lutea (*ibid*.).

Also, in Scandinavia the number of roe deer fawns depends on the mother's body mass. Does with above average body mass appeared to have 40% higher productivity (expressed as a number of fawns per doe) than those with a below average body mass. Heavier females (body mass of live animals: 30.5 ± 1.7 kg) produced on average 2.7 ± 0.5 fawns, whereas the same figure for light females (27.3 ± 1.3 kg) was 1.6 ± 0.5 fawns (Andersen and Linnell, 2000). In a roe deer population from the central part of Italy, the potential litter size depended on female body mass, and a threshold of 20.9 ± 1.4 kg separated adult females carrying one or two embryos (Focardi et al. 2002). Almost no adult female had two embryos if its body mass was lower than 20 kg, and almost every female carried two embryos if their mass exceeded 23 kg (*ibid*.). In England and Wales, the majority (72%) of pregnancies were twins, with 26.6% singletons and 1.4 % triplets. The

pustošil po delih Francije, Švice in Nemčije, je poškodoval velike površine gozda, tj. ugodnih habitatov srnjadi. Glede na čas orkana (konec decembra), ki se je dogajal hkrati s procesom ugnezdenja zarodkov v maternično steno pri srnah, bi pričakovali negativen vpliv na ta proces in posledično manjša legla v sledeči pomladi, a takega vpliva ni bilo (Gaillard in sod., 2003).

2.1.4 Telesna masa in ostale značilnosti fenotipa

Kljub temu da telesna masa živali ni edini dejavnik, ki določa razlike v življenjskih strategijah, je prav gotovo eden pomembnejših (Andersen in sod., 1998). Plodnost samic srnjadi je podobno kot pri nekaterih drugih vrstah parkljarjev odvisna tudi/zlasti od njihove telesne mase (Gaillard in sod., 1992; Gerhart in sod., 1997; Andersen in Linnell, 2000; Hewison in Gaillard, 2001; Focardi in sod., 2002; Macdonald in Johnson, 2008; glej tudi preglednico 2). Hewison in Gaillard (2001) sta na podlagi štetja rumenih telesc v jajčnikih srn iz devetih populacij v Veliki Britaniji ugotovila, da so težje samice bolj plodne in imajo v jajčnikih večinoma več kot eno rumeno telesce, medtem ko imajo lažje praviloma samo eno. V šestih od sedmih analiziranih populacij je potencialna velikost legla (stopnja oplojenosti) narasla z naraščajočo telesno maso srn. V nekaterih primerih je bila ta značilnost povezana tudi s starostjo srne. V populaciji z bolj kakovostnim fenotipom (z večjimi telesnimi masami) in večjo produktivnostjo (Alice Holt, n = 74) so imele vse srne v jajčnikih vsaj dve rumeni telesci, pri šestih srnah pa so odkrili tudi po tri rumena telesca. V populaciji Queens (n = 15), ki je bila v slabši kondiciji (manjše telesne mase) in tudi nizko produktivna, so imele vse srne le po eno rumeno telesce (*ibid.*).

Tudi v Skandinaviji telesna masa srn pomembno vpliva na število poleženih mladičev. Srne z nadpovprečno telesno maso so imele 40 % večjo produktivnost (izraženo s številom poleženih mladičev) kot srne, katerih telesna masa je bila manjša od povprečja. Težje odrasle samice (bruto telesna masa neiztrebljenih živali: 30,5 ± 1,7 kg) so polegle povprečno 2,7 ± 0,5 mladiča, lažje samice (27,3 ± 1,3 kg) pa le 1,6 ± 0,5 mladiča (Andersen in Linnell, 2000). Pri populaciji srnjadi iz centralnega dela Italije so raziskovalci ugotovili prag v telesni masi srn (20,9 ± 1,4 kg), pri katerem je prišlo do spremembe v številu poleženih mladičev (Focardi in sod., 2002). Skoraj nobena odrasla srna ni imela dveh zarodkov, če je bila njena celokupna telesna masa manjša od 20 kg; nasprotno so težje samice (>23 kg) v veliki večini primerov imele po dva zarodka (*ibid.*). V Angliji in Walesu je imela večina (72 %) brejih srn po 2 zarodka, 26,6 % je imelo le en zarodek, 1,4 % pa tri zarodke; verjetnost, da bodo srne imele dva ali več zarodka, se je

Table 2: Effect of roe deer doe body mass on litter size (review of some European studies)

Preglednica 2: Vpliv telesne mase srn na velikost legla (pregled nekaterih tujih raziskav)

Location / *Lokacija*	Period / *Obdobje*	Doe body mass(kg) / *Telesna masa srn (kg)**	Litter size (number of fawns) / *Velikost legla (št. poleženih mladičev)*	Potential litter size (number of embryos/corpora lutea) / *Potencialna velikost legla (št. zarodkov/rumenih telesc)*	Reference / *Vir*
Belgium / *Belgija*	1987–1993	together all does / *skupaj vse srne (?)*	/	1,92 ± 0,61	Wauters et al., 1995
		2-year olds / *2-letne* (15,5)		1,56	
		Adult / *odrasle* (16,7)		2,04	
Norway (Storfosna island) / ***Norveška*** *(otok Storfosna)*	1991	2-year olds / *2-letne* (?)	2,50	/	Andersen and Linnell, 2000
		adult / *odrasle* (29,3)	2,64		
	1992	2-year olds / *2-letne* (27,8)	2,20		
		adult / *odrasle* (28,7)	2,23		
	1993	2-year olds / *2-letne* (26,9)	2,14		
		adult / *odrasle* (29,9)	2,18		
	1994	2-year olds / *2-letne* (26,5)	1,67		
		adult / *odrasle* (27,2)	2,20		
Italy / ***Italija*** (Tredozio)	1995–1999	(22,0 ± 1,0)	0,75 ± 0,40	1,44 ± 0,10	Focardi et al., 2002
England and Wales / ***Anglija in Wales***	1994–2005	(13,4 – 17,9)	/	1,73 (between 1,45 and 1,91 / *med 1,45 in 1,91)*	Macdonald and Johnson, 2008

*Body masses of does are presented either as post-mortem body masses without inner organs, but with head included (Belgium, England and Wales), or as the total body masses of alive does (Norway, Italy), respectively. / *Telesne mase so podane bodisi kot mase iztrebljenih živali brez notranjih organov, a z glavo (Belgija, Anglija in Wales), bodisi kot celotne mase živih živali (Norveška, Italija).*

tendency for a roe deer doe to produce twins increased proportionally with body mass (Macdonald and Johnson, 2008) (see also Table 2).

Patterns of reproductive output are, according to Hewison and Gaillard (2001), a result of a two-stage process. At the beginning, body mass sets an upper limit of potential litter size at a conception, as it impacts the number of fertilized ovulations. However, body mass has no effect on the proportion of fertilized ovulations that are actually implanted. The implantation process and definition of embryos is limited mainly by senescence and climatic severity (*ibid.*)

Body mass does not only affect the number of fertilized ovulations, but also the level of maternal care that females invest in offspring. Prenatal care is all the energy a mother invests in the total body mass of a litter (the average mass of an offspring multiplied by the number of offspring), and postnatal care is the energy investment of lactating does, measured as the sum of the average daily growth of fawns during the first four weeks after parturition (Andersen et al. 2000). Reported average birth masses of fawns, which are closely related to the mother's body mass, are between 1,310 g and 1,880 g and vary among different regions (Andersen et al. 1998).

večala z večanjem telesne mase matere (Macdonald in Johnson, 2008) (glej tudi preglednico 2).

Razlike v razmnoževalnem potencialu med posameznimi srnami Hewison in Gaillard (2001) opisujeta kot posledico procesa, ki ga lahko razdelimo na dve neodvisni stopnji. Na začetku ima glavni pomen telesna masa matere, ki določa potencialno velikost legla, saj vpliva na oplojenost (število rumenih telesc v jajčnikih). Kasneje je uspešnost ugnezditve blastocist neodvisna od telesne mase samice, na proces implantacije, oblikovanje zarodkov in končno število poleženih mladičev pa lahko pomembno vplivajo starost srne in klimatske razmere (*ibid.*).

Telesna masa srn pa ne vpliva le na stopnjo oplojenosti, temveč tudi na predporodno (*prenatalno*) in poporodno (*postnatalno*) nego, ki jo samice namenjajo mladičem. Kot prenatalna nega je mišljena investirana energija matere v skupno maso legla (merjena je kot vsota individualnih telesnih mas mladičev ob skotitvi), kot postnatalna nega pa energetska investicija srn v obdobju laktacije in je merjena kot vsota povprečne dnevne rasti mladičev v obdobju štirih tednov po skotitvi (Andersen in sod., 2000). Povprečne mase skotenih mladičev srnjadi, ki so v značilni soodvisnosti s telesno maso matere, so med 1.310 g in 1.880 g ter variirajo med posameznimi regijami (Andersen in sod., 1998).

Prenatal care is related to litter size, and as litter size depends on female roe deer body mass (Hewison and Gaillard, 2001), important changes in prenatal care between does with different body mass can be observed. Heavier does show a higher level of prenatal care, i.e. higher input into mass growth of all embryos. In a roe deer population from the Norwegian island of Storfosna, by increasing litter size from one to two fawns, doe increased their prenatal care by 1,490 g (95% confidence interval: 1,254-1,745 g), and when comparing does with single fawns and does with triplets, prenatal care increased by 2,690 g (1,371-4,540 g) (Andersen et al. 2000).

Also, the age of maturity and primiparity is correlated with maternal body mass. In most populations of roe deer, it is generally found that nearly all females older than two years ovulate and produce fawns; however, in populations where body masses are lower (<20 kg, Gaillard et al., 1992), the age of the first reproduction can be prolonged to three or four years (Andersen et al. 1998).

Phenotype (especially body mass) influences the sex ratio of the offspring (Wauters et al., 1995; Hewison and Gaillard, 1996, 1999; Hewison et al., 1999; Macdonald and Johnson, 2008). According to the hypothesis of Trivers and Willard (1973), females should vary the sex ratio of offspring in relation to their body condition. Females with better body condition should invest more into male offspring and females with poorer body condition more in female offspring (Wauters et al. 1995). Recent studies suggest two alternatives or modifications to the hypothesis: (i) mothers do not allocate differently, but there is differential mortality of offspring, especially in mothers with poor condition (Clutton-Brock 1991), and (ii) there is a minimum body size (body mass) required for producing good quality sons because they are more demanding in growth (Arnbom et al. 1994).

On the basis of three Belgian populations, Wauters et al. (1995) concluded that heavier adult females produced larger embryos than lighter or primiparous females. Male embryos grew faster than female siblings. They were also bigger in size and weighed more than female embryos. A female's body mass and age significantly affected the proportion of male embryos in a litter. Absolute differences in body mass between siblings (twins and triplets) were larger when embryos were of different sex (x ± SD = 5.33 g ± 6.93 g) than when they were of the same sex (x ± SD = 0.95 g ± 1.12 g). During embryonic development, males grew faster than female siblings. Also, at nine months of age, male fawns were significantly heavier than female fawns

Predporodna nega je odvisna zlasti od velikosti legla; ker je le-ta odvisna od telesne mase srn (npr. Hewison in Gaillard, 2001), prihaja tudi do pomembnih razlik v predporodni negi med različno težkimi srnami, saj težje srne izkazujejo večjo predporodno nego, tj. večji vložek v masni prirast vseh zarodkov. Tako so, na primer, v populaciji srnjadi z norveškega otoka Storfosna z večanjem velikosti legla z enega na dva mladiča srne v povprečju povečale predporodno nego za 1.490 g (95 % interval zaupanja: 1.254–1.745 g), z večanjem velikosti legla z enega na tri mladiče pa za 2.690 g (1.371–4.540 g) (Andersen in sod., 2000).

Tudi starost, pri kateri srne prvič polegajo mladiče, je lahko odvisna od telesne mase. Večina samic je prvič polegala mladiče pri starosti dveh let, toda v večini populacij se je pri tistih z nižjo telesno maso (<20 kg, Gaillard in sod., 1992) starost ob prvi reprodukciji zamaknila na tri ali štiri leta (Andersen in sod., 1998).

Fenotip (zlasti telesna masa) samic vpliva tudi na spolno razmerje potomcev (Wauters in sod., 1995; Hewison in Gaillard, 1996, 1999; Hewison in sod., 1999; Macdonald in Johnson, 2008). Rezultati raziskav povezave med telesno maso samic in spolnim razmerjem potomcev pa so med sabo nasprotujoči. Hipoteza, ki sta jo postavila Trivers in Willard (1973), predvideva, da lahko samice same uravnavajo spolno razmerje mladičev glede na svojo telesno pripravljenost. Bolje telesno pripravljene samice naj bi tako več vlagale v razvoj moških potomcev, slabše pripravljene pa v razvoj ženskih (Wauters in sod., 1995). Novejše raziskave delijo to hipotezo na dve alternativi: (i) samice same ne uravnavajo spolnega razmerja, temveč je vzrok za to različna smrtnost zarodkov glede na spol, še posebej pri samicah (materah), ki so v slabšem fizičnem stanju (Trivers in Willard, 1973; Clutton-Brock, 1991); (ii) obstaja minimalna telesna masa, ki je potrebna za produkcijo zdravih osebkov moškega spola, saj so ti bolj zahtevni v rasti (Arnbom, 1994).

Wauters in sod. (1995) so na podlagi raziskav treh populacij srnjadi iz Belgije ugotovili, da težje odrasle samice proizvajajo večje zarodke kot srne, ki so imele mladiče prvič in so bile tudi lažje. Sam embrionalni razvoj se je razlikoval glede na spol. Moški zarodki so rasli hitreje, bili so večji in so tehtali več kot ženski. Na delež moških osebkov (srnjačkov) v leglu sta vplivali telesna masa in starost mater. Težje srne so imele več moških mladičev kot lažje; starejše samice so imele večji delež moških mladičev kot mlade srne, ki so bile breje prvič. Absolutne razlike v telesni masi mladičev v leglu so bile večje, kadar je šlo za mešano leglo (x ± SD = 5,33 g ± 6,93 g), kot kadar so bili mladiči v leglu istega spola (x ± SD = 0,95 g ± 1,12 g). Med embrionalnim razvojem so mo-

(males: x ± SD = 12.5 kg ± 1.8 kg; females: 11.4 kg ± 2.0 kg) (*ibid.*). Similarly, in Slovenia male fawns are heavier than females during the whole hunting period season (September – December). Studies that produced such results were done by body mass analysis of all culled roe deer fawns (n = 67.453) in the 2007-2012 period (Pokorny and Jelenko, 2013), not by comparisons within the same litters. At this point, it is important to mention that culling of fawns in Slovenia takes place at the time when average age of fawns is 90 or more days. The reason for higher body masses of male fawns could in this case be faster growth during the 90-day period after birth and not the embryonic growth. On the other hand, on Storfosna Island (Norway) and in Trois Fontaines (France), female fawns were significantly heavier than males after 20 and 30 days (Hewison et al., 1999).

Findings in studies of correlations between female roe deer body mass and offspring sex ratio are contradictory. Investigations of variation in the primary sex ratio within and between 14 populations of roe deer from Great Britain (Hewison in Gaillard, 1996) in relation to maternal body condition have shown that the sex ratio was increasingly male biased as average maternal body masses decreased. Neither was this relation affected by the litter size produced. Within populations, this relation has not been reported, so the individual effect of a roe deer doe on offspring sex ratio is less expressed. This effect is more expressed at the population level. The results indicate that where environmental conditions are limiting, roe deer does tend to produce male-biased litters (*ibid.*). The authors suggest that where females experience environmental stress, they tend to produce male kids to avoid potential future local resource competition posed by female offspring.

Results from Hewison et al. (1999) indicate that roe females, which have additional investment potential available, do not invest it in sons, as predicted by Trivers and Willard hypothesis (1973); higher maternal body mass was associated with female-biased litters. These inconsistent results on the effects of body mass on fawn sex ratio may be accounted for by heterogeneity within and among ungulate species but, alternatively, may be due to testing of models for which the assumptions are not fulfilled (Hewison et al., 1999).

Recent studies of primary and secondary sex ratio suggest that mixed litters are the most optimal life strategy of an "income breeder", the roe deer (Macdonald and Johnson, 2008). Roe deer does not carry fat reserves, and conditions during lactation are unpredictable since they will be a function of the environment at that time. A tendency for mixed pairs might

ški zarodki v istem leglu rasli hitreje kot ženski, tudi pri starosti devet mesecev so bili srnjački značilno težji od srnic (srnjački: x ± SD = 12,5 kg ± 1,8 kg; srnice: 11,4 kg ± 2,0 kg) (*ibid.*). Podobno so tudi v Sloveniji srnjački v lovni sezoni (september – december) v vseh mesecih težji kot srnice, kar je bilo ugotovljeno na podlagi analize telesnih mas vseh uplenjenih mladičev srnjadi (n = 67.453) v obdobju 2007–2012 (Pokorny in Jelenko, 2013), ne pa s primerjavami znotraj istih legel. Pri tem je pomembno omeniti, da se odstrel mladičev srnjadi v Sloveniji začne pri njihovi povprečni starosti 90 dni in več. Vzrok za težje mase samčkov v tem primeru bi posledično lahko bila tudi hitrejša rast v obdobju 90 dni po skotitvi in ne sama embrionalna rast. Nasprotno s prej omenjenimi raziskavami so bile na otoku Storfosna (Norveška) in v Trois Fontaines (Francija) srnice po 20 do 30 dneh značilno težje kakor srnjački (Hewison in sod., 1999).

Podatki, pridobljeni iz 14-ih populacij srnjadi v Veliki Britaniji (Hewison in Gaillard, 1996), so pokazali, da se spolno razmerje v leglih mladičev z upadanjem povprečnih telesnih mas mater med populacijami nagiba v prid moškemu spolu in je tudi neodvisno od števila poleženih mladičev. Znotraj populacije takšne povezave niso bile ugotovljene, torej je individualni vpliv posameznih srn na spolno razmerje potomcev manj izrazit, izražen pa je vpliv telesnega stanja samic na nivoju populacij. Rezultati so pokazali, da kjer so okoljski vplivi omejujoči, srne proizvajajo več moških potomcev (*ibid.*). Avtorja menita, da srne, ki so izpostavljene okoljskemu stresu zaradi slabših okoljskih razmer, proizvajajo večji delež moških potomcev zato, da bi se izognile kasnejši kompeticiji za iste vire z mladimi srnami, tj. s svojimi potomkami.

Tudi Hewison in sod. (1999) so v nasprotju s Trivers in Willard-ovo hipotezo (1973) ugotovili, da vitalnejše srne ne vlagajo svojih razpoložljivih virov v produkcijo moških potomcev; spolno razmerje v leglih težjih samic se je namreč nagibalo na stran srnic. Do neskladij ugotovitev o vplivu telesnih mas samic na spolno razmerje mladičev lahko prihaja zaradi intra- in interspecifičnih razlik v socialnih sistemih, ali pa so le-te posledica neustrezne metodologije (Hewison in sod., 1999).

Novejše raziskave primarnega in sekundarnega spolnega razmerja srnjadi nakazujejo, da so pri takšni življenjski strategiji, kot jo ima srnjad, najbolj optimalna mešana legla (Macdonald in Johnson, 2008). Srnjad namreč ne hrani telesnih rezerv v obliki maščob, razmere med laktacijo pa so nepredvidljive in odvisne od okoljskih dejavnikov. Z oblikovanjem mešanih legel ima samica najboljše možnosti, da optimizira energijo, ki jo vlaga v laktacijo, in energijo, ki jo mladiči porabijo za svojo rast. Tako je bilo v novejših raziskavah v Angliji in Walesu pri leglih z dveallow greater flexibility to optimise investment during lactation and energy that is needed for the growth of fawns. Recent studies from England and Wales have shown the distribution of pregnancy types among does. In twin pregnancies, there were 14.4% of female, 16.1% of male and 42.4% mixed litters. The remaining share belonged to singleton pregnancies. The sex ratio in two-fawn litters was in most cases mixed, so sex ratios of male and female fawns in litter were almost equal (51% males). Singleton litters were male-biased (60%) and, for most populations, more so when an individual female was in better condition. No correlation between the mother's body mass and fawn sex ratio in twin pregnancies and weak tendency towards male offspring in singleton litters by females in better condition contradict the findings of previous studies (Wauters, 1995; Hewison and Gaillard, 1996; Hewison et al., 1999).

Despite the contrary findings, it is clear that roe deer female body mass is an important influencing factor in roe deer reproductive potential. Body mass is affected especially by the sex and age structure of populations; suitable demographic structure of populations therefore has a great impact on body condition of individual animals and female roe deer reproduction (Fruzinski and Labudzki, 1982; Kjellander et al., 2004b; Hamel et al., 2009b; Degmečić et al., 2010).

2.1.5 Mother's age

Roe deer body mass may decline through senescence. Average body mass in roe deer increases until four years of age, and then remains stable for a period and starts to decrease along with senescence (Nussey et al. 2011). The effect of senescence can be detected in roe deer reproduction.

Once roe deer have reached sexual maturity at 15 months, they ovulate in cycles and are fertilized with potential litter size being determined by body mass irrespective of age. The probability that a given roe deer implanted all fertilized blastocyst was strongly related to her age. Across nine populations in England, implantation failure was not related to body mass, but varied in relation to maternal age, being lowest among prime-aged does (2 to 7 years), rather higher among yearlings (12 to 24 months), but markedly higher among senescent females (more than 8 years) (Hewison and Gaillard, 2001). Implantation failure varied widely between populations with observed averages around 30% and ranging from 16.7 (Spadeadam) to 54.5% (Queens) for prime aged does. According to these data, the authors suggest that senescence in fecundity occurs some time after 7 years for roe deer.

ma mladičema 14,4 % samo ženskih legel, 16,1 % samo moških in 42,4 % mešanih legel (*ibid.*). Preostali delež je pripadal leglom z enim mladičem. Spolno razmerje v leglih z dvema mladičema je bilo največkrat mešano, zato sta deleža srnjačkov in srnic v leglih z dvema mladičema skoraj enaka (51 % srnjačkov). V leglih s samo enim mladičem je bil delež srnjačkov večji (60 %). Avtorja sta za večino preučevanih populacij tudi ugotovila, da je večji delež samčkov v leglih s samo enim mladičem povezan z boljšo fizično kondicijo oz. večjo telesno maso njihovih mater (*ibid.*). Izostanek vpliva telesne mase mater na spolno razmerje pri leglih z dvema mladičema in šibka tendenca k moškemu podmladku pri srnah, ki imajo v leglu le enega mladiča in so v fizično boljši kondiciji, so v nasprotju z ugotovitvami predhodnih raziskav (Wauters, 1995; Hewison in Gaillard, 1996; Hewison in sod., 1999).

Ne glede na protislovne ugotovitve je očitno, da imajo telesne mase srn pomemben vpliv na razmnoževalni potencial srnjadi. Telesne mase so odvisne tudi (zlasti) od spolne in starostne strukture populacij; ustrezna demografska struktura populacij ima torej velik vpliv na vitalnost posameznih osebkov in reprodukcijsko sposobnost srn (Fruzinski in Labudzki, 1982; Kjellander in sod., 2004b; Hamel in sod., 2009b; Degmečić in sod., 2010) in je (ne)posredno pomembna za populacijsko dinamiko srnjadi.

2.1.5 Starost matere

S staranjem osebkov pri srnjadi praviloma upada telesna masa. Povprečna telesna masa srn do četrtega leta starosti narašča, kasneje se delno ustali in se nato začne s staranjem osebkov zmanjševati (Nussey in sod., 2011). Vpliv starosti se tako kaže tudi v reprodukciji.

Ko srnjad doseže spolno zrelost (starost okoli 15 mesecev), začne ciklično vsako leto potekati ovulacija. Pri oplojenih samicah velikost legla (tj. število oplojenih jajčnih celic) praviloma določa telesna masa neodvisno od starosti živali. Vendar je verjetnost, da bo pri samici prišlo do ugnezdenja vseh oplojenih blastul v maternično steno, tesno povezana s starostjo srne; tako, na primer, v devetih preučevanih populacijah srnjadi v Angliji stopnja uspešnosti implantacije zarodka ni bila povezana s telesno maso, razlikovala pa se je glede na starost samic (Hewison in Gaillard, 2001). Neuspeh pri implantaciji je bil v primerjavi z mladimi in srednje starimi srnami (med dve in sedem let) večji pri primiparnih samicah, tj. mladicah (od 12 do 24 mesecev), in še večji pri ostarelih srnah (več kot osem let). Neuspeh pri implantaciji zarodkov se je tudi med posameznimi populacijami močno razlikoval. V povprečju je znašal pri srnah, starih med dve in sedem let, 30 % (od 16,7 % v Sapdeadamu do 54,5 % v Queensu). Gle-

Primiparous does (usually yearlings) have on average lower body mass than adult multiparous does (data on average female roe deer body mass from Belgium: primiparous: 15.5 kg; adults: 16.7 kg; Wauters et al., 1995). Litter size also tended to increase with maternal body mass (primiparous: 1.56; adults: 2.04; *ibid.*). On the island of Storfosna (Norway), litter size of 2-year-old does was between 1.67 and 2.20 fawns, and adults between 2.17 and 2.50 fawns. Even in 2-year-old does, more triplets than singletons were produced. These figures are typical for northern populations (Andersen and Linnell, 2000).

In France (Gaillard et al., 2003), litter sizes were highest for primiparous females (1.842 ± 0.060), slightly lower for prime age (1.797 ± 0.023), and lowest for senescent does (>12 years) (1.400 ± 0.112).

2.1.6 Interspecific interactions

Stress and a consequent decrease in reproduction could also be caused by interactions with animal species with overlapping ecological niches. Species with similar life strategies that normally live in the same biotopes, exploit same resources, etc., are called sympatric species (Tome, 2006). When resources are limited, there is more interspecies competition among sympatric species with overlapping ecological niches (*ibid*.). In France (Le Petite Pierre reserve), influences of interspecific competition between red deer and roe deer were studied (Richard et al., 2010). Red deer density in a given year had a marked negative influence on body mass of roe deer fawns. Higher red deer densities caused a decrease in body mass of roe deer fawn. When red deer density changed from high (0.8 deer/km – line transect method) to low (0.4 deer/km), the body mass of roe deer fawns increased from 8.25 to 8.95 kg and from 7.89 to 8.59 kg for males and females, respectively (*ibid*.).

The ecological niche of fallow deer (*Dama dama*) overlaps with roe deer, and fallow deer is usually dominant over roe deer (Focardi et al., 2006; Feretti et al., 2008, 2010). In central Italy (Merema Regional Park), interactions between roe deer and fallow deer have been studied. Roe deer were displaced by fallow deer in feeding grounds. In 83% of cases, roe deer moved away from fallow deer at a distance of >50 m. Most (94%) displacement events occurred while roe deer were feeding; in 50 % of these cases, roe stopped grazing and left the feeding ground. Even when fallow deer did not show any sign of direct aggression to roe, roe moved away from fallow in 72% of the cases. Roe deer in a group were significantly more tolerant of the presence of fallow deer (even in group) than when solitary (Feretti et al., 2008).

de na dobljene rezultate avtorja ugotavljata, da se vpliv starosti na zmanjšano plodnost srn najbolj izraža nekje po sedmem letu starosti, ko se živali začnejo starati.

Primiparne samice (praviloma mladice oz. enoletne živali) so večinoma lažje od multiparnih (podatki o povprečnih masah iz Belgije: primiparne: 15,5 kg; odrasle: 16,7 kg; Wauters in sod., 1995) in polegajo v povprečju manj mladičev (primiparne: 1,56; odrasle: 2,04; *ibid*). Na otoku Storfosna (Norveška) so bile velikosti legla pri dveletnih samicah med 1,67 in 2,20 mladiča, pri odraslih srnah pa med 2,17 in 2,50 mladiča. Tudi pri dveletnih srnah so bili v več primerih v leglu trije kot pa le en mladič, kar je značilno za populacije iz višjih zemljepisnih širin (Andersen in Linnell, 2000).

2.1.6 Medvrstne interakcije

K stresu in posledičnemu zmanjšanju reprodukcije srnjadi lahko prispevajo tudi interakcije z živalskimi vrstami, s katerimi imajo podobne ekološke niše. Vrste, ki imajo podobne življenjske strategije in običajno živijo tudi v istih biotopih, izkoriščajo podobne dobrine, imenujemo simpatrične vrste (Tome, 2006). Ko so viri omejeni, je medvrstno tekmovanje med simpatričnimi vrstami, katerih ekološke niše se prekrivajo, večje (*ibid*.). V Franciji (rezervat Le Petite Pierre) so spremljali učinke medvrstne kompeticije med srnjadjo in jelenjadjo (Richard in sod., 2010). Izkazalo se je, da je na telesno maso mladičev srnjadi značilno vplivala gostota jelenjadi. V letih velike gostote jelenjadi je bila telesna masa mladičev srnjadi manjša kot v letih z manjšimi gostotami. Ko se je gostota jelenjadi spremenila iz visoke (0,8 osebka/km – po metodi transektov) na nizko (0,4 osebka/km), se je telesna masa mladičev povečala z 8,25 kg na 8,99 kg pri samčkih (srnjačkih) in s 7,89 kg na 8,59 kg pri samičkah (srnicah) (*ibid*.).

Vrsta, katere ekološka niša se relativno močno prekriva z nišo srnjadi, je damjak (*Dama dama* L.). Damjak ima nad srnjadjo praviloma dominanten vpliv (Focardi in sod., 2006; Ferretti in sod., 2008, 2010). V raziskavah populacij damjaka in srnjadi iz centralne Italije (Merema Regional Park) se je pokazalo, da damjak največkrat izključuje srnjad iz območij prehranjevanja (Ferretti in sod., 2008). Srnjad se je pred damjaki umaknila več kot 50 m stran v 83 % primerov opazovanj. 94 % premikov se je zgodilo med prehranjevanjem srnjadi in v 50 % teh primerov se je srnjad prenehala prehranjevati ter je celo zapustila prostor hranjenja. Tudi v primeru, ko damjaki niso kazali nobenih neposrednih znakov agresije do srnjadi, se je ta v 72 % primerov umaknila. Pokazalo se je tudi, da srnjad, ki se zadržuje v skupini oz. manjših tropih, izkazuje dosti večjo toleranco do damjakov kot posamezni osebki srnjadi (*ibid*.).

Large herbivores can change the vegetative structure in the long term, and thus grazing has the potential to modify the habitat structure in favour of one or the other of the ungulate species. Studies from southern Italy have shown that population density of fallow deer has negative influence on the reproduction of an Italian subspecies of roe deer (*Capreolus capreolus italicus*). High densities and grazing of fallow deer resulted in a reduced habitat quality for roe deer, which led to poorer condition and lower body mass. In roe deer, litter size depends on the mother's body mass, such that poor conditions may lead to reduced population growth rate (Focardi et al., 2006; see also chapter 2.1.4).

Compared to fallow deer, interspecific interactions between roe deer and wild boar are different. Findings from Italy have shown that wild boar has much less influence on roe deer than fallow deer, as roe deer were displaced from the feeding grounds by fallow deer more frequently than by wild boar. Roe deer moved away or avoided "contact" with wild boar only in 22% of cases (Ferretti et al. 2010). In contrast, some observations from Slovenian hunting units show that roe deer moves away from open grounds in a panic when meeting wild boar (Jelenko, 2013). There is also some photo-documentation of wild boars systematically searching for roe deer fawns (Attack of wild boar..., 2013).

3 CONCLUSIONS

Reproductive potential is one of the most important parameters that influence on population dynamics of species. It includes fertility level (number of fertilized ovulations), litter size and sex ratio of fawns. Previous studies of roe deer reproductive potential suggest that it can be affected by various factors and therefore differs among different environments. Factors affecting roe deer reproduction are population density, habitat and weather conditions, female roe deer characteristics (phenotype; body mass, body size, physical condition), age, interspecific interactions and even genotype. Roughly, we can classify this factors into individual, population and environmental.

Specimen for the research, the cull animals and their reproductive organs can be obtained only during the hunting season period. In Slovenia, the hunting season lasts from the beginning of September till the end of December. Therefore, the only possibility to make studies of the roe deer reproductive potential is by counting corpora lutea in roe deer ovaries. Because of the delayed implantation in roe deer, embryos are not yet developed at that time. Analyses of corpora

Veliki rastlinojedi lahko močno spremenijo vegetacijsko strukturo, dolgoročen vpliv objedanja pa lahko vpliva tudi na spremembo habitatne strukture, ki se razvija v prid ene ali druge vrste parkljarjev (Rocardi in Tinelli, 2005 cit. po Focardi in sod., 2006). Raziskave iz južnih delov Italije so pokazale, da na zmanjšano reprodukcijo ogrožene podvrste italijanske srnjadi (*Capreolus capreolus italicus*) vpliva tudi populacijska gostota damjaka. Z gostoto damjakov se je zaradi objedanja zmanjševala kvaliteta habitata srnjadi; posledično sta se zmanjševala fitnes in telesna masa srn, ki imata ključen pomen na velikost legla srnjadi (Focardi in sod., 2006; glej tudi poglavje 2.1.4).

V primerjavi z damjakom so medvrstne interakcije med srnjadjo in divjim prašičem drugačne. Po nekaterih dognanjih iz Italije ima divji prašič na srnjad dosti manjši vpliv kot damjak; tako se je po neagresivnem medvrstnem kontaktu (srečanju) med divjim prašičem in srnjadjo slednja umaknila samo v <25 % primerov (Ferretti in sod., 2010). Vendar v nasprotju s tem nekatera opažanja iz slovenskih lovišč kažejo, da se srnjad pred divjimi prašiči z odprtih površin vsaj občasno tudi prav panično umika (Jelenko, 2013), znani pa so tudi fotodokumentirani primeri, ko divji prašiči sistematično iščejo mladiče srnjadi (Attack of wild boar..., 2013).

3 ZAKLJUČEK

Razmnoževalni potencial je eden izmed pomembnih parametrov, ki vplivajo na populacijsko dinamiko vrst. Opredeljujejo ga zlasti stopnja oplojenosti, povprečna velikost legla in spolno razmerje zarodkov oz. mladičev. Raziskave razmnoževalnega potenciala srnjadi so pokazale, da nanj vplivajo najrazličnejši dejavniki, zaradi katerih se med različnimi populacijami in okolji močno razlikuje. Znano je, da nanj vplivajo gostota populacije, habitatne značilnosti, vremenski vplivi, značilnosti srn (fenotip; telesna masa, velikost, fizična kondicija), starost samic, medvrstne interakcije in genotip. V grobem lahko te dejavnike razdelimo na individualne, populacijske in okoljske.

Pridobivanje ustreznih vzorcev rodil srn za raziskave razmnoževalnega potenciala je vezano zlasti na odstrel in je časovno omejeno predvsem na čas lovne dobe na srne. V Sloveniji, kjer lovna doba srn, starejših od dveh let, traja od začetka septembra do konca decembra, je ugotavljanje razmnoževalnega potenciala na podlagi odstreljenih srn vezano le na štetje rumenih telesc v jajčnikih, saj zaradi pojava odložene implantacije zarodki v tem obdobju še niso razviti. S štetjem rumenih telesc pridobimo informacijo o stopnji oplojenosti, ne pa tudi informacije o spolnem razmerju mladičev in dejanski velikosti legla. Velikost legla se lutea give information merely on the number of ova released and fertilized, and not about the fawn sex ratio and the actual litter size.

Litter size can be determined by counting embryos from a sample of animals, killed in road traffic accidents in winter and especially in spring time. When embryos are more developed, sex ratio can also be determined. Useful data can be obtained by systematic observations in the field after the parturition, counting fawns per doe and determination of gender in late autumn and winter time.

For the whole insight into roe deer reproductive potential it is important to use different laboratory and field research methods. In the past, no systematic research into roe deer reproductive potential and its influencing factors has been carried out. In order to provide more efficient adaptive management with roe deer populations, systematic studies and collection of data will start in 2013 in the selected areas of Slovenia. All listed methods will be used in the research. This paper is the first but necessary step in understanding the issue and implementation of indigenous research in the near future.

lahko ugotavlja iz vzorcev povoženih srn v zimskem in še zlasti pomladanskem času, in sicer na podlagi štetja zarodkov v maternicah. V primeru, da so zarodki že dovolj razviti, se tako lahko ugotavlja tudi spolno razmerje mladičev. Ustrezne podatke lahko dobimo tudi s sistematičnim terenskim spremljanjem in ugotavljanjem števila mladičev na posamezno (vodečo) srno, v jesenskem in zimskem času pa tudi njihovega spola.

Za celosten vpogled v razmnoževalni potencial srnjadi, ki na najbolj natančen način odslikava realno stanje, je pomembno kombinirati različne raziskovalne, laboratorijske in terenske metode. Do sedaj v Sloveniji sistematičnih raziskav razmnoževalnega potenciala srnjadi in dejavnikov, ki vplivajo nanj, še ni bilo. Ker bi bile tovrstne raziskave in pridobljene informacije dobrodošle oziroma celo nujno potrebne za čim boljše upravljanje s srnjadjo, smo v letu 2013 pričeli s sistematičnim ugotavljanjem razmnoževalnega potenciala srnjadi v izbranih območjih Slovenije, in sicer z uporabo vseh zgoraj navedenih metod. Pričujoči prispevek je tako prvi, a nujno potreben korak za boljše razumevanje te tematike in smiselno zasnovo in izvedbo domačih raziskav v bližnji prihodnosti.

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4 ZAHVALA

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5 SUMMARY

European roe deer (*Capreolus capreolus* L.) is the most important game-management species not only in Slovenia but also in other European countries. In the period between 2001 and 2010, more than 428,000 were taken in Slovenia, and the total number of animals in Slovenia is estimated at 200,000. Because of the high animal density in the country, suitable game management is of great importance. For effective game management it is crucial from economic and ecological points of view to have information on the ecology and population parameters that shape the population dynamics of the species. One of the most important parameters is reproductive potential, which varies in addition to different influential factors. It is determined by the level of fertilized females, litter size and fawn sex ratio. In addition to the parameters that are already in use for control methods, knowledge about reproductive potential provides more efficient adaptive game management, including proper culling planning of populations. Methods required to research reproductive potential include examination of female roe deer reproductive organs. Because of embryonic diapause in roe deer, the level of fertilized females culled during this period is examined by counting corpora lutea in roe deer ovaries, which gives the information on the potential litter size. The actual litter size and fawn sex ratio are researched by counting fetuses and tracking females with newborn fawns. Factors affecting reproductive potential of roe deer are individual (particularly maternal phenotype, i.e. body size, body mass, body condition), population (e.g. population density, demographic structure, social

stress, genetics) and environmental (habitat quality, weather conditions, interspecific interactions etc.). The final output of reproductive potential is the sum of all influencing factors and several combinations between them and therefore varies among different populations and environments. How these factors affect reproductive potential in roe deer has been a subject of several European studies. However, in Slovenia this issue has been neglected until now. This information could also improve the adaptive management of roe deer in Slovenia. Therefore, we will start with systematic research of reproductive potential in selected areas of Slovenia in the year 2013. Roe deer in Slovenia is exposed to various environmental factors and also involved in unique interspecific interactions, such as concurrence with chamois and predation by lynx and wolf, which have not been studied in recent foreign research. Furthermore, Slovene distinguishing databases provide an outstanding prerequisite for the proficient understanding of influential factors on roe deer yield in the area of Central Europe. In the following report we present an overview of the recent European research on factors affecting fertility and reproductive potential of roe deer.

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