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Editorial

The Evolution of Reproductive Strategies in Animals– Implications for Theriogenology

Razmnoževanje skozi prizmo evolucije – pomen za sodobno veterinarsko medicino

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Reproduction is one of the fundamental biological imperatives shared by all living beings. Organisms must reproduce to pass on their genes to the next generation, ensuring the survival and continuation of their species. In pursuit of this goal, nature has evolved a remarkable diversity of reproductive methods and behaviors, including external fertilization in aquatic species, internal fertilization in terrestrial animals, oviparity, viviparity, complex hormonal regulation, and diverse strategies of parental investment (1, 2). In the Slovenian Veterinary Research journal, we welcome articles addressing various aspects of veterinary and comparative reproductive research and medicine. In this issue, we have placed particular emphasis on this topic. With this editorial, we would also like to bring attention to these articles, including a review of the phenomics evaluation and research on hormone GnRH injection in cattle and sheep breeding (3, 4), the effect of food additives and environmental enrichment on fertility protection against toxicity (5) and egg production (6, 7) and a case report on canine idiopathic oligoasthenoteratozoospermia (8).

We would also like to highlight a recent book published by our former editor, Dr. Gregor Majdič, titled Soul Mate Biology: The Science of Attachment and Love. This book takes us on a journey through the complex world of genes, molecules, and brain cells involved in the emotions of love, attachment, affection, and even sexual reproduction." (9).

Razmnoževanje je temelj življenja. Omogoča prenos genov na naslednje generacije in s tem ohranjanje vrst. Narava je skozi evolucijo razvila osupljivo paleto strategij, od zunanje oploditve pri vodnih organizmih do notranje oploditve pri kopenskih živalih, jajcerodnosti, živorodnosti, kompleksnega hormonskega uravnavanja in različnih oblik starševske skrbi (1, 2). V reviji Slovenian Veterinary Research z veseljem objavljamo prispevke, ki obravnavajo različne vidike veterinarskih in primerjalnih raziskav ter medicine razmnoževanja. V tej številki smo temu področju namenili poseben poudarek. Predstavljamo prispevke, ki osvetljujejo fenomsko evalvacijo in raziskave vpliva hormona GnRH na plodnost goveda in ovc (3, 4), vpliv prehranskih dodatkov in obogatitve okolja na zaščito plodnosti (5), in proizvodnjo jajc (6, 7) ter primer idiopatske oligoasteno-teratozoospermije pri psu (8).

Posebej želimo izpostaviti tudi nedavno knjigo našega nekdanjega urednika, dr. Gregorja Majdiča, z naslovom Soul Mate Biology: The Science of Attachment and Love. Knjiga nas popelje na potovanje skozi zapleten svet genov, molekul in možganskih celic, ki sodelujejo pri čustvih ljubezni, navezanosti, naklonjenosti in celo spolnega razmnoževanja (9). Čeprav nespolno razmnoževanje, kot je binarna delitev pri enoceličnih organizmih, prinaša določene prednosti, zlasti v stabilnih okoljih, ostaja genetska raznolikost ključna za prilagajanje v nenehno spreminjajočem se svetu. Mehanizmi za izmenjavo genov so se pojavili že zelo zgodaj

Although asexual reproduction, such as binary fission in unicellular organisms, offers certain advantages, particularly in stable environments, genetic diversity remains a key factor for adaptation in an ever-changing world. To encourage this diversity, mechanisms for gene exchange emerged early in the history of life. Even bacteria, some of the simplest life forms, developed methods like conjugation, transformation, and transduction to exchange genetic material and increase variability within their populations (10). As life became more complex, so did the mechanisms for generating genetic diversity. The most significant among these, especially in multicellular organisms, is sexual reproduction. By combining genetic material from two individuals, sexual reproduction allows for greater variation among offspring. This variation is a key driver of evolution, enabling species to adapt continuously to changing environmental pressures.

Most vertebrates reproduce sexually, which provides the advantage of increased genetic diversity. However, there are some fascinating exceptions, particularly among fish. For instance, the Amazon molly (Poecilia formosa) is an all-female species that reproduces through parthenogenesis, a form of asexual reproduction. Additionally, in many fish species, biological sex is not fixed at birth and can change in response to social signals. In clownfish, for example, a typical social group consists of one adult female and one adult male. If the female dies, the male will transform into a female, and one of the juveniles will mature into a new male (11). Some fish species are also facultatively asexual, reproducing without a partner if none of the opposite sex is available.

In birds and mammals, by contrast, biological sex is genetically determined and fixed at birth. Nevertheless, these animals exhibit a rich variety of mating systems and parental strategies. In birds, offspring are typically altricial (born immature) and require extensive parental care. The most common parenting strategy is biparental care, found in more than 90% of bird species (12). However, there are variations in parental care. For example, maternal-only care is observed in species like domestic hens, while paternal-only care occurs in species such as the African jacana. Additionally, brood parasitism is another fascinating strategy, where birds like cuckoos and cowbirds lay their eggs in the nests of other species, effectively outsourcing the responsibility of parenting to unsuspecting foster parents. This behavior raises an interesting question: why do these foster parents care for chicks that are not only unrelated to them but often of a different species? One hypothesis suggests that parental care is triggered by instinctive cues, such as begging behavior and chick morphology. More provocatively, some studies have found that parasitic parents may linger near the foster nest and even destroy the host's eggs or chicks if their own offspring is rejected—this is known as the 'mafia hypothesis,' a form of reproductive blackmail (13).

v zgodovini življenja. Tudi bakterije, med najpreprostejšimi oblikami življenja, so razvile mehanizme, kot so konjugacija, transformacija in transdukcija, ki omogočajo izmenjavo genskega materiala in povečujejo raznolikost v populacijah (10). Z naraščajočo kompleksnostjo organizmov so se razvijali tudi mehanizmi za ustvarjanje genetske raznolikosti. Najpomembnejši med njimi pri večceličnih organizmih je spolno razmnoževanje, ki združuje genski material dveh staršev in tako omogoča večjo variabilnost med potomci. Ta raznolikost je gonilna sila evolucije, saj vrstam omogoča stalno prilagajanje na okoljske spremembe.

Večina vretenčarjev se razmnožuje spolno, kar omogoča večjo genetsko raznolikost, vendar obstajajo zanimive izjeme — predvsem med ribami. Amazonka (Poecilia formosa) je na primer vrsta, sestavljena izključno iz samic, ki se razmnožujejo s partenogenezo, obliko nespolnega razmnoževanja. Pri številnih ribah spol ni določen ob rojstvu in se lahko spreminja glede na socialne signale. Pri ribah klovnih na primer socialno skupino sestavljata ena odrasla samica in en odrasli samec. Če samica pogine, se samec spremeni v samico, eden izmed mladičev pa dozori v novega samca (11). Nekatere vrste rib se lahko občasno razmnožujejo tudi brez partnerja, če ta ni na voljo.

Pri pticah in sesalcih je biološki spol genetsko določen in fiksen ob rojstvu, vendar te živali kažejo izjemno raznolikost paritvenih sistemov in starševskih strategij. Pri pticah so mladiči pogosto nebogljeni ob izvalitvi in zahtevajo obsežno starševsko skrb. Pri več kot 90% vrstah ptic oba starša skrbita za zarod (12). Obstajajo pa izjeme: pri domačih kokoših za mladiče skrbi le mati, medtem ko pri afriških jakanah skrb prevzame samo oče. Posebna strategija je gnezditveni parazitizem, pri katerem vrste, kot sta kukavica in kravja pastirica, odlagajo jajca v gnezda drugih vrst, ki nato skrbijo za njihove mladiče. Ena od hipotez, znana kot »mafijska hipoteza«, pravi, da parazitski starši uničijo jajca ali mladiče gostiteljev, če ti zavrnejo njihove mladiče (13).

Čeprav je večina ptic monogamnih, gre pogosto le za socialno monogamijo, ne pa tudi za genetsko. Številne vrste, vključno z labodi, so socialno monogamne, a spolno promiskuitetne — mladiči v istem gnezdu imajo pogosto različne očete, kar povečuje genetsko raznolikost in verjetnost preživetja (14). Moški vlagajo v mladiče, čeprav ti morda niso njihovi, bodisi zaradi negotovosti očetovstva bodisi zaradi nagona po zaščiti celotnega legla.

Pri sesalcih je resnična monogamija redka, manj kot 5% vrst velja za monogamne (15). Večina sesalcev je promiskuitetnih, a z zelo raznolikimi vzorci vedenja. Med velikimi opicami najdemo različne strategije: orangutani in gorile imajo dominantne samce, ki monopolizirajo parjenje (gorile – srebrnkasti hrbet; orangutani – velike lične blazinice). Podrejeni samci so pogosto nasilno kaznovani, če se poskušajo pariti. V nasprotju z orangutani in gorilami šimpanzi živijo v velikih, bolj dinamičnih skupinah z bolj sproščeno hierarhijo; samice se parijo z več samci, kar zmanjšuje tveganje za

While most birds form monogamous pairs to raise their offspring, this monogamy is often social rather than sexual. In other words, although the pair works together to care for the chicks, the male is not always the genetic father of all the offspring. Many socially monogamous bird species, including swans, engage in sexual promiscuity, meaning that chicks in the same nest may have different fathers. This strategy enhances genetic diversity and may contribute to better survival rates for the offspring (14). Why, then, do males invest in raising offspring that may not be genetically theirs? One explanation is uncertainty: since males cannot always identify their own offspring, they invest in the entire brood. Another possibility is that the instinct to ensure the survival of the group or species may take precedence over individual genetic interests.

In mammals, true monogamy is rare—less than 5% of species are considered monogamous (15). Most mammals are promiscuous, although their mating behaviors vary widely. Among our closest relatives, the great apes, we observe distinct patterns. Orangutans and gorillas live in systems with dominant males, who monopolize mating opportunities and are often visually marked, silverbacks in gorillas and large cheek pads in orangutans. Subordinate males that attempt to mate are often violently punished, sometimes fatally. Chimpanzees, in contrast, live in large fission-fusion societies with looser hierarchies. Although alpha males maintain social dominance—often with support from brothers or allies, females may mate with multiple males during estrus. This promiscuity makes paternity uncertain and reduces the risk of infanticide by spreading potential paternity across multiple males (16). The only apes that display long-term monogamous behavior are gibbons, native to Southeast Asia. Once considered paragons of fidelity, recent long-term studies reveal that gibbons also experience breakups, infidelity, and partner changes—highlighting social complexity (17).

Among monogamous mammals, interesting cases include dik-diks (a small African antelope) and North American prairie voles. Prairie voles are especially notable due to their neurobiology. Studies have shown that mating in prairie voles triggers the release of oxytocin and vasopressin, which activate the brain's dopamine reward system and reinforce pair bonding. In contrast, promiscuous meadow voles show similar hormonal surges during mating but lack vasopressin receptors in key brain regions like the ventral pallidum. As a result, they do not experience the same rewarding effects and do not form pair bonds (18). In a landmark experiment, researchers genetically modified meadow voles to express vasopressin receptors in the ventral pallidum. These voles, previously promiscuous, began to form pair bonds and remained with their mates after mating, suggesting a direct causal link between neurobiology and social behavior (19). So why does monogamy evolve at all, given that it limits reproductive opportunities? One explanation involves ecological constraints. In dik-diks, for example, the cost of searching for mates—due to predation

infanticid, saj je očetovstvo nejasno (16). Le giboni kažejo dolgotrajno monogamijo, čeprav tudi pri njih opazujemo nezvestobo in menjave partnerjev (17).

Med sesalci, ki so resnično monogamni, so zanimivi primeri dik-diki (majhne afriške antilope) in prerijske voluharice, ki predstavljajo tudi pomemben model za nevrobiološke študije. Pri voluharicah sproži parjenje sproščanje oksitocina in vazopresina, ki aktivirata dopaminski nagradni sistem v možganih in krepita partnersko vez. Travniške voluharice, ki so promiskuitetne, imajo podobne hormonske odzive, a nimajo vazopresinskih receptorjev v ključnih možganskih regijah, zato ne oblikujejo trajnih vezi (18). V znamenitem poskusu so raziskovalci vazopresinske receptorje vstavili v možgane travniških voluharic, nakar so prej promiskuitetne živali začele oblikovati parne vezi (19). Monogamija se lahko razvije tudi zaradi ekoloških omejitev, na primer pri dikdikih, kjer tveganje plenilstva in teritorialnosti odtehta prednosti iskanja več partnerjev.

Z evolucijskega vidika je razmnoževanje osrednja funkcija življenja. Osupljiva raznolikost paritvenih sistemov in starševskih vedenj odraža številne strategije, ki jih je oblikovala evolucija za ohranjanje genov. Pri ljudeh del te strategije vključuje tudi ljubezen: privlačnost poveča verjetnost razmnoževanja, čustvene vezi in dolgoročna partnerstva pa izboljšujejo preživetje potomcev. Podobno kot pri voluharicah tudi pri ljudeh oksitocin, vazopresin in dopamin sodelujejo pri oblikovanju partnerskih vezi (20). Vendar ljubezen pri ljudeh prežema še plast kognitivne in kulturne kompleksnosti, ki je verjetno edinstvena naši vrsti. Čeprav znanost razkriva biološke temelje navezanosti, nekatere razsežnosti ljubezni ostajajo skrivnostne (Slika 1) (9).

Razumevanje raznolikih reproduktivnih procesov je ključno tudi za razvoj veterinarske reproduktivne medicine, ki zajema vse faze razmnoževanja in upravljanja razmnoževanja. Na primer, spoznanja o metabolni, okoljski in hormonski regulaciji reproduktivne dovzetnosti samic ter sinhronizacije estrusa pri različnih vrstah, vključno pri manj raziskanih vrstah, kot so prepelice, koze in ovce, lahko izboljšajo uspešnost umetnega osemenjevanja (4, 6, 7, 21, 22). Ta znanja lahko prispevajo tudi k optimizaciji hormonske kastracije pri psih in mačkah (23, 24) ter k zaščiti moških zarodnih celic pred toksičnimi vplivi, kar odpira možnosti za ohranjanje plodnosti in zdravljenje neplodnosti (25).

Temeljne in klinične/aplikativne raziskave reprodukcije in fiziologije razmnoževanja so zato ključne za napredek veterinarske reproduktivne medicine ter za izboljšanje dobrobiti in zdravja živali.

risk and territoriality—may outweigh the benefits of promiscuity. Staying with a single partner may increase the likelihood of successful reproduction in such environments.

From an evolutionary perspective, reproduction is the central function of life. The astonishing diversity of mating systems and parenting behaviors observed across species reflects the myriad strategies evolution has produced to ensure gene propagation. In humans, part of this strategy appears to involve love. Attraction between individuals enhances reproductive success, while emotional bonds and long-term partnerships improve offspring survival.

Several studies suggest that similar neurochemical mechanisms to those seen in voles operate in the human brain during romantic attachment, particularly the roles of oxytocin, vasopressin, and dopamine (20). However, human love is shaped by an additional layer, our cognitive and cultural complexity. Romantic love may well be unique to our species, and while science can help illuminate the biological underpinnings of attachment, some dimensions of love may forever remain mysterious (Figure 1) (9).

Understanding diverse reproductive processes is also essential for advancing reproductive veterinary medicine, or theriogenology, which encompasses all phases of reproduction and breeding management. For example, insights into the metabolic, environmental, and hormonal regulation of female reproductive receptivity and synchronization of estrous cycles across species—including less well-studied animals such as quails and goats, and sheep can improve outcomes in assisted reproduction (4, 6, 7, 21, 22). Such knowledge may also enhance the effectiveness of artificial insemination protocols or inform the evaluation of hormonal castration in companion animals such as dogs and cats (23, 24). Equally important is the understanding of male germ cell development and strategies to protect the germline under suboptimal or toxic conditions, which may ultimately lead to advances in fertility preservation and the treatment of infertility (25), including in veterinary patients and laboratory animals (5, 8). Together, fundamental and clinical/applicative research into the molecular underpinnings of reproduction and reproductive physiology is critical for advancing veterinary reproductive medicine and, ultimately, for improving animal welfare and health.

Figure 1: Camels in Amarillo, TX ZOO (Photo: Klementina Fon Tacer)

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