Ann. Anim. Sci., Vol. 25, No. 2 (2025) 511–527 *DOI: 10.2478/aoas-2024-0080*

sciendo

DETERMINANTS OF THE EXPRESSION OF SEXUAL BEHAVIOUR IN MAMMALS – REVIEW*

Stanisław Kondracki[1], Krzysztof Górski[1♦], Maria Iwanina[1], Anna Wysokińska[1], Arkadiusz Pietruszka[2], Dariusz Gączarzewicz[3], Karolina Stasiak[4]

[1]Institute of Animal Production and Fisheries, Faculty of Agricultural Sciences, University of Siedlce, Prusa 14, 08-110 Siedlce, Poland
[2]Faculty of Biotechnology and Animal Husbandry, West Pomeranian University of Technology in Szczecin, 71-270 Szczecin, Poland
[3]Department of Animal Reproduction, Biotechnology and Environmental Hygiene, West Pomeranian University of Technology in Szczecin, 71-270 Szczecin, Poland
[4]Department of Biology and Animal Environment, Faculty of Animal Breeding and Biology, Bydgoszcz University of Science and Technology, Mazowiecka 28, 85-084 Bydgoszcz, Poland
♦Corresponding author: krzysztof.gorski@uws.edu.pl

Abstract

The article contains a literature review of facts and views on the strategies of sexual behaviour in mammals, taking into account the role of the animal's species, sex, and position in the herd. The role of the senses, brain, and hormones in the expression of animals' sexual behaviour is discussed, as well as the role of induction of the coitus reflex and social behaviour in the reproduction of present-day wild and domesticated animals. The analysis shows that the predominant strategy of sexual behaviour in females is to attract multiple potential partners to acquire the best male. The predominant strategies in the sexual behaviour of males of most mammalian species are aimed at fertilizing as many females as possible. Expression of sexual behaviour requires the generation of a set of characteristic sexual reflexes that indicate readiness to copulate and are sexually stimulating. Animals differ in expressing their sexual behaviour. Some individuals react quickly and dynamically to sexual stimuli and immediately begin coitus, while others require longer preparation for successful coitus. Sexual behaviour influences the status of individuals in some species. Wild mammals with high expression of the sexual behaviour typical of a given species usually occupy a dominant position, which gives them an advantage in the search for breeding partners, access to food, and the expression of preferred social behaviour. Expression of sexual behaviour is stimulated by stimuli from potential sexual partners, which induce copulatory reflexes. These reflexes have been described in numerous animal species. They should be generated in the proper order and proceed without disruption for successful coitus and fertilization to occur.

Key words: sexual behaviour, copulatory reflexes, social behaviour

Sexual reproduction is an effective strategy, developed by evolution, for prolonging the existence and development of a species (Colegrave, 2012). In gonochoric animals, representatives of both sexes take part in this process; however, they play different roles, which is particularly evident in higher organisms (Molloy and Gage, 2006). Through evolution, animals have developed species-specific behaviours (Wallen and Zehr, 2004).

The most clearly exhibited are sexual behaviours, manifested in a species-specific ritual, separate for males and females (Jennings and De Lecea, 2020). Sexual behaviour is the total set of conscious and unconscious responses aimed at obtaining sexual satisfaction. It consists of several reactions, such as desire, arousal, coitus, relaxation, and parenting. Most of these reactions are reflexes conditioned by the libido and the presence of an object inducing sexual responses (Dewsbury, 1972; Resko et al., 1999; Schulte-Hostedde et al., 2004; Kvarnemo, 2018; Dixson, 2018). Individual animal species have developed very specific sexual behaviours and completely different reproductive strategies. Sexual behaviour also depends on the sex of the individual and its position in the group (Wodzicka-Tomaszewska et al., 1981; Chenoweth, 1981; Price, 1987; Chenoweth and Landaeta-Hernandez, 1998; McDonnell, 2000; Heitor et al., 2006; Evans and Walsh, 2012). The sexual behaviour of present-day animals, both wild and domesticated, is subject to the pressure of changes in their living environment and anthropogenic factors (Górski et al., 2017). This may alter the nature and expression of the sexual behaviour of animals and affect the effectiveness of reproduction.

Strategies of sexual behaviour in animals

The sexual behaviour strategy of an animal may be highly varied. It depends on numerous factors, but primarily on the animal's species, sex and position in the herd.

*This study was financed by statutory research and development activity funds from Ministry of Education and Science assigned to the Faculty of Agricultural Sciences, University of Siedlce.

Individual species usually use one of two basic reproductive strategies (Heitor et al., 2006; Evans and Walsh, 2012). One of these, which biologists call the r-strategy, involves bringing a very large number of offspring into the world. In this strategy, the parents do not look after the offspring at all, and the survival rate of the young is very low (Stearns, 1976). Reproductive success is to be guaranteed by the large number of offspring. These strategies are very common in insects, fish and amphibians, but are also found in some species of birds and mammals. The other reproductive strategy, which biologists call the K-strategy, involves producing a small number of offspring which are generally cared for by one or both parents, and this guarantees a high survival rate. This second strategy is often used in birds and mammals. Litter size in mammals is varied and depends on the species. The females of some species (e.g. mares) usually give birth to only one offspring, while the females of other species give birth to larger litters (e.g. dogs are animals with overall mean litter size of 5.4) (Borge et al., 2011). The reproductive strategy determines the behaviours leading to procreation and the production of offspring (Reznick et al., 2002). Reproductive strategies reflect how an individual or population allocates its reproductive effort and energy cost throughout its life cycle. The two main strategies can be presented as follows: the r-strategy, with the maximum allocation of energy to the number of eggs or offspring (productivity), and the K-strategy, in which the maximum amount of energy is allocated to each egg cell or offspring (efficiency) (Pianka, 1970; Price, 1973). Marsupials and placentals spend more energy on reproduction than most other vertebrates and devote more parental care to a small number of young than on a large litter (Angelini and Ghiara, 1984).

The sexual behaviour of males and females serves to transfer their genes to the largest possible number of offspring. In mammals, the biological importance of females is much greater than of males. Females, at great cost to their bodies, build a gene carrier (the offspring) and most often care for the offspring. The development of the mammalian organism in the prenatal period depends on the females, as does its development and safety in the early postnatal period. Hence the bodies of females have been better equipped by nature and are physiologically stronger. Female mammals ensure safety, and owing to the possession of mammary glands, also supply food to neonates. The condition of female bodies determines not only fertilization but also rearing of the offspring, and this is what guarantees continuous transfer of genes.

The reproductive capacity of female mammals is limited by the occurrence of oestrous cycles. This means that fertilization can occur only during the relatively short period of female fertility. Another limiting factor is the relatively small number of gametes produced by females. Females must give birth to and rear the young themselves, so the number of sexual partners is usually not of the greatest importance in the sexual strategy (Weir and Rowlands, 1973; Csermely, 1984; Maccoby, 1991). The quality of the partner is much more important. The sire of the offspring of a given female is usually one male, and therefore it is important. The "best male" may have completely different meanings in different species of mammals. It may be the male that is the largest, the strongest, the fastest, or the loudest, or it may be the male that successfully defeats its rivals in a fight. In every case, however, the preferred partner must have a high level of traits which are important for the functioning of individuals of a given species (Rittschof et al., 2012). Therefore in the sexual behaviour strategy of females, it is important to attract all potential partners, but only in order to acquire the best one, whose genes will guarantee the high quality and survival of the offspring. The involvement of the female in the course of courtship and coitus is much "deeper". The female is usually more particular than the male in choosing a partner, and the male must make an effort to be selected (Garces-Restrepo et al., 2017; Coombes et al., 2018). Dominant males are usually distinguished by greater expression of sexual behaviour and exhibit a high level of aggression, manifested in the fight against rivals and efforts to procreate (Wroblewski et al., 2009). Subordinate individuals also strive to take part in reproduction; however, expression of their behaviours is lower, increasing when there are no dominant individuals (Creel et al., 1997). At the onset of the breeding season, males of the American bison engage in numerous fights (Lott, 1981). As a result, the dominant male has the possibility to mate with most oestrous females. Chimpanzee males compete in an aggressive manner to gain access to cycling females, and dominant males consistently maintain higher copulation rates during the periovulatory period (Muller and Mitani, 2005). Male mammals do not give birth and do not rear the offspring. Their genes can be fixed in the population only through their offspring, born to and reared by females. Males produce a practically unlimited number of gametes, which allows them to fertilize many females. The sexual behaviour strategy of males of most species therefore involves fertilization of as many females as possible (Ben-Ari, 2000). Fertilization of a large number of females guarantees that the genes of the male will spread in the population of a given species (Hoffman et al., 2003). It is also important that the females fertilized should be young, healthy, and strong, as only these traits will guarantee the birth and rearing of healthy offspring. The essence of the sexual behaviour of males is to show their advantages over their rivals, overcome their competition, and strive to mate with a large number of females, preferably young, healthy and strong ones. The genes of males that fertilize few females or choose older and weaker females, incapable of rearing their offspring, have little chance of making a major contribution to the genetic structure of the population (Hurtado-Gonzales and Uy, 2010).

The role of the senses, brain, and hormones in the generation of sexual behaviour in mammals

The animal's brain is involved in the generation of sexual behaviour. Olfactory and visual pathways receive

and analyse signals sent during courtship, while motor pathways allow animals to assume a copulatory posture. However, these pathways have been shown not to be specific to sexual activity alone. Shortly after courtship, or even immediately after coitus, the male may begin to obtain food or build a lair using the same brain pathways (Igbokwe, 2009). The sexual behaviour of mammals is formed at the early stage of development by sex hormones acting on the hypothalamus. When a substantial fragment of the brain of a female rat or cat is removed, but the hypothalamus and brainstem are left, the female continues to exhibit the lordosis reflex, under the influence of hormones and sexual stimuli.

An important role as a key regulator of the hypothalamic-pituitary-gonadal axis has recently been ascribed to kisspeptin (Yang et al., 2018). Kisspeptin is a peptide hormone secreted by kisspeptin neurons in the hypothalamus. Kisspeptin stimulates the release of gonadotropin-releasing hormone and is a strong activator of the hypothalamic-pituitary-gonadal axis (Topaloglu et al., 2012). Studies in numerous animal species and in humans have identified the role of kisspeptin in behavioural responses associated with reproduction. Extra hypothalamic kisspeptin signalling is conducive to positive aspects of emotional and sexual brain processing with the goal of reproduction (Comninosa and Dhillo, 2018). Males probably need a larger part of the brain than females to maintain copulatory activity. This may be due to the greater complexity of the sexual behaviour of males. Removal of the part of the brain associated with movement may cut off the flow of visual, olfactory and tactile stimuli, and thus significantly reduce the copulatory capacity of males (Fewell and Meredith, 2002).

Hormones and active peptides play an important role in the generation and reception of sexual stimuli. Hormones are an integral part of all stages of the reproduction process. They act as neuromodulators within the limbic system, facilitating the expression of innate emotions and behaviours essential for reproduction (Yang et al., 2018). Sexual behaviours in males and females are strictly regulated by steroid hormones present in the gonads, including androgens (mainly testosterone), oestrogens (mainly oestradiol) and progesterone (Jennings and De Lecea, 2020).

Oestrous behaviour in females is initiated by oestradiol, which is secreted in large quantities during oestrus by mature ovarian follicles. The hormonal agent inhibiting oestrous behaviour is progesterone, copiously secreted by the corpus luteum in the diestrous phase (Crowell-Davis, 2007). Endocrine regulation of reproduction in female mammals relies on the action of the hypothalamic-pituitary-ovarian axis. Hormonal regulation of the oestrous cycle is controlled by a hierarchical system with the hypothalamus at the top, the pituitary gland below it, and the ovaries at the bottom (Christensen et al., 2012). All three levels influence one another. The most important communication pathway has been shown to be feedback mechanisms in which a substance released into the blood inhibits or, less often, stimulates its own secretion (Colledge, 2013; Herbison, 2020). The most important neurohormone of the hypothalamus for reproductive processes is gonadotropin-releasing hormone (GnRH). The release of GnRH is known to be controlled by two neuropeptides: kisspeptin, which exerts a stimulating effect on GnRH (Seminara and Crowley, 2008), and gonadotropin-inhibitory hormone (GnIH), which exerts a negative effect on GnRH signalling (Tsutsui et al., 2000). GnRH acts on the pituitary gland, stimulating it to produce pituitary gonadotropins. The pituitary gonadotropins – luteinizing hormone (LH) and follicle-stimulating hormone (FSH) – are produced in the anterior pituitary (Lee et al., 2008; Hollander-Cohen et al., 2021). The pituitary gonadotropins stimulate the production and development of ovarian follicles, which produce increasing amounts of oestradiol and progesterone during their development. The production and level of these hormones is modulated by specific feedback systems between the ovaries, pituitary gland, and hypothalamus. These systems play a key role in the regulation of both physiological and behavioural aspects of the oestrous cycle (Curry et al., 2007).

Full expression of sexual behaviour in females requires gonadal steroids – oestrogen and progesterone. Steroid hormones are believed to regulate the sexual behaviour of females by binding to intracellular receptors in structures of the hypothalamus and limbic system and inducing changes in synthetic proteins, which lead to long-term changes in nerve excitability (Pfaff and McEwen, 1983). Ovarian steroids have been shown to play the main role in controlling sexual behaviour in female domesticated ruminants. Females whose ovaries have been removed exhibit no sexual behaviour (Thimonier and Mauléon, 1969). In the females of most mammalian species, including rodents, dogs, and sheep, removal of the ovaries has been shown to reduce or completely eliminate signs of sexual behaviour (Blaustein, 2008). Developing ovarian follicles produce oestradiol, which has a dominant role in the preovulatory phase of the oestrous cycle. The dominant hormone in the post-ovulatory phase of the oestrous cycle, i.e. the diestrous phase, is progesterone, produced by the corpus luteum, which is formed at the site of the ruptured ovarian follicle (Ginther, 1992). Observations of hormonal changes taking place during oestrus in domestic ruminants and rodents have shown that the oestradiol concentration increases 1–2 days before expression of sexual behaviour. This means that the oestradiol level can be a marker used to control sexual behaviour (Morali and Beyer, 1979). The progesterone level may begin to increase during oestrus, but the main period when its concentration increases is varied in different mammalian species. In sheep, goats and cows, expression of sexual behaviour during the reproductive period is preceded by a 12–15-day luteal phase, during which the progesterone concentration in the blood plasma is high (Fabre-Nys and Gelez, 2007). Progesterone may decrease the expression of oestrous behaviours in females. This explains why such behaviour is rarely manifested

by pregnant females, in which the progesterone level is very high. In female domesticated ruminants, oestrous behaviours appear only after luteolysis of the corpus luteum and the resulting decrease in the progesterone level in the bloodstream (Feder and Marrone, 1977). Androgens administered during prenatal life also inhibit the expression of oestrous behaviours (Fabre-Nys and Venier, 1991). Female sheep which received androgen during the prenatal period exhibited certain spontaneous behaviours typical of males, such as mounting and nudging with the foreleg. The expression of sexual behaviour can also be negatively affected by corticosteroids, which can inhibit the release of gonadotropin-releasing hormone from the hypothalamus (Brann and Mahesh, 1991).

The importance of oestrogen and progesterone in mares has long been known and exploited for practical manipulation of the oestrous cycle (Loy et al., 1981; Curry et al., 2007). The oestrous period can be initiated by administering prostaglandins, which exert a luteolytic effect, promoting the breakdown of the corpus luteum. This decreases the level of progesterone, enabling an increase in oestrogen production from the growing ovarian follicles. This results in the expression of oestrous behaviours in females. Oestrus can be suppressed by administering exogenous progesterone or its synthetic derivatives, such as altrenogest.

The concentration of luteinizing hormone (LH) has an important role in the course of oestrous cycles and the onset of ovulation. In females of most mammalian species, ovulation occurs spontaneously, and the triggering factor is a manifold increase in the concentration of LH. This is known as the preovulatory surge in LH and usually occurs about 10–40 hours before ovulation (Cahill et al., 1998; Su et al., 2017). The preovulatory surge in LH is the result of increasing concentrations of oestrogen hormones, produced at a high rate by mature ovarian follicles during oestrus, just prior to ovulation. In females of such mammalian species there is a marked preovulatory increase in luteinizing hormone, which is essential to the initiation of the final stages of oocyte maturation and induction of ovulation. In horses, the pattern of LH secretion during the follicular phase is somewhat different. A prolonged increase in the LH level begins several days before ovulation and peaks on the day after ovulation, with a gradual return to the initial values in the mid-luteal phase (Curry et al., 2007). There are also species in which ovulation does not take place spontaneously, but is induced by stimuli generated during coitus. These include rabbits and all felids. In females with induced ovulation, oestrogens produced during oestrus do not sufficiently stimulate the LH surge through positive feedback, but sensitize the pituitary gland to respond to GnRH released from the hypothalamus in response to mechanical stimuli generated during coitus. In females of these species, the amount of LH released depends on the frequency of coitus (Wildt et al., 1980; Tsutsui et al., 2009).

During the inter-oestrus interval, the oestradiol concentration in the bloodstream of females is relatively low. It increases rapidly in the proestrus period, peaking during oestrus. This is when ovulation occurs, followed by an increase in the concentration of progesterone, produced by the corpus luteum. The sequential increase in the oestrogen level, followed by the peak concentration of progesterone, prepares the brain and physiology of the female for sexual motivation (Levine, 2015; Pfaus et al., 2015; Gotlieb et al., 2020). Outside of this period, female rodents, such as mice, rats, and hamsters, do not respond to male courtship and actively reject mating attempts. In this way, females save energy reserves for mating during maximum fertility.

The expression of sexual behaviour in males is also largely hormonally determined. The sexual behaviour of males is stimulated by androgen hormones. The most important of these is testosterone, produced in the testes by Leydig cells (Martin and Touaibia, 2020). The testosterone level determines the expression of male sexual behaviour (Vignozzi et al., 2005). Testosterone has powerful effects on the nervous system and other tissues and organs sensitive to androgens, including the prostate and penis. Androgens can act directly in the animal's brain, increasing the expression of many social behaviours, including those associated with preparation for coitus and with coitus itself. By acting on organs and tissues sensitive to androgens, including the copulatory organ, androgens indirectly shape the patterns of copulatory behaviour characteristic of each species. The effects of testosterone and its metabolites and of 5α-dihydrotestosterone in the brain direct the typical sexual preferences of males of a given species, induce sexual arousal, including penile erection, and constitute a tool for controlling the courtship and mating behaviours typical of males of a given species.

During maturation, androgens stimulate the complete development of the male sex organs (the penis and accessory sex glands), whose function and morphology in the adult animal is ensured only by an adequate influx of androgens (Murashima et al., 2015). By acting on the central nervous system, androgens stimulate the development of the male behavioural pattern. Behavioural patterns remain directly linked to behaviours in the reproductive period, such as aggressive behaviour towards other males of the same species, hierarchy fights, or behaviour during coitus (Juntti et al., 2010; Cunningham et al., 2012; Cornil et al., 2012). The development of the libido requires the production of adequate amounts of testosterone, but there are no direct links between the manifestation of libido and the level of endogenous production of androgens in a given individual (Maksimović et al., 2021; Corona and Maggi, 2022). In sexually maturing and mature males, increasing androgen production in the testes activates the male pattern of sexual behaviour and determines the level of libido (Mawhinney and Mariotti, 2013).

Androgens have been shown to be essential to the normal development and expression of the sexual behaviour of stallions. Normal sexual behaviours generally

do not develop in foals castrated before maturation (McDonnell, 1986). Castration of a mature stallion results in a reduction in androgens to a very low level, which generally leads to weakening of sexual reflexes. However, nearly normal sexual behaviour can persist long after castration, especially in experienced stallions (Line et al., 1985). Similar reactions have also been observed following castration of sexually mature rams (Parrott and Baldwin, 1984; D'Occhio et al., 1985). Testosterone is essential to the development and maintenance of the sexual behaviour of rams. Sexual activity increases with the testosterone level during maturation (Orgeur and Signoret, 1984). The expression of sexual behaviour in rams during maturation can be suppressed using GnRH agonists or by active immunization against GnRH, thus reducing the secretion of gonadotropins and limiting the development of the testes (Tilbrook et al., 1993; Brown et al., 1994).

Emotions and sexual behaviour are strongly influenced by oxytocin and vasopressin, which are involved in recognizing olfactory stimuli and have a major influence on emotions and social behaviour (Yang et al., 2018). Oxytocin, β-endorphin, prolactin and melanocortin play an important role in generating arousal. Oxytocin has been suggested to be the main factor in the appearance of affiliative behaviours and partnership bonds (Insel, 1992). Studies in animals have shown that administration of oxytocin induces erection, an effect that is clearly dependent on testosterone, while antagonists of oxytocin receptors can prevent contactless erection, considered to be an indicator of arousal. Dopamine antagonists can enhance the sexual response by increasing central oxytocinergic transmission (Argiolas, 1999). Oxytocin facilitates the movement of semen and the egg cell, stimulating smooth muscle contractility in the reproductive system (Carmichael et al., 1987). The oxytocin level has also been shown to increase following ejaculation (Krüger et al., 2003).

In order for information to be exchanged with the environment, numerous stimuli must be collected and reproduced in the central nervous system. This takes place owing to the sensory system, which processes mechanical, chemical and thermal somatosensory stimuli which act on the skin and mucous membrane. Within the sensory system, visual, auditory, gustatory and olfactory stimuli are distinguished.

During the mating season, animals receive signals from partners with their senses, with which they detect changes in the surrounding environment (Lenschow et al., 2022; Torres et al., 2023). These signals arouse the sexual interest of partners of the opposite sex. The most important senses in communication with sexual partners are sight, hearing, smell, and touch (Adamczyk et al., 2015).

The sense of sight

The sense of sight in mammals plays an enormous role in the reception of signals associated with the characteristic appearance and movements of potential sexual partners. Males generate visual signals which are perceived by females (Bielert and Van der Walt, 1982). The males of some species change their appearance during the mating season. Prior to the mating season, red deer grow antlers, whose size indicates the stag's position and importance (Malo et al., 2005). Female mammals in oestrus usually change their behaviour at the sight of a sexually mature male. They behave in a characteristic way that increases the probability of coitus (Lopez-Gatius, 2022). In most mammalian species, females at that time secrete pheromones, specific odorous substances which stimulate the activity of males (Kekan et al., 2017), and exhibit species-specific behaviours. We can observe increased motor activity, a characteristic posture (e.g. tail flagging in mares), or jumping on other females and acceptance of being jumped on (cows). These behaviours provoke aggressive efforts in males and enable the identification of a sexual partner (Chenoweth, 1983; McDonnell, 1992). Females of some rodent species perk up their ears and perform amusing "sprints" (Ferreira-Nuño et al., 2005), while female apes assume a characteristic copulatory posture. In females of many mammalian species, anatomical changes having a strong effect on males take place during oestrus. In female mink and ferrets, the vulva swells significantly during oestrus (Clapperton et al., 1988; Lindeberg, 2008). Similar changes are signs of oestrus in the females of many species of farm animals, such as cattle (Röttgen et al., 2018; Santos et al., 2022; Kuswati et al., 2022). In the females of some species of apes, readiness for mating is manifested in the swelling of special folds of skin surrounding the genitals (Du et al., 2010; Street et al., 2016). Anatomical changes and changes in the behaviour of females ready for coitus are perceived by males with their sense of sight and generate libido in them, although even sightless males have been shown to copulate normally (Fletcher and Lindsay, 1968). In individual mammalian species, the sense of sight plays a highly varied role in determining sexual behaviours and the choice of partner. In rodents, the role of sight is minor compared to the dominant sense of smell (Lenschow et al., 2022).

The other senses

Olfactory stimuli received via the sense of smell play an important role in the sexual behaviour of mammals. Females in oestrus often emit a characteristic smell, which is perceived by sexually mature males. A bitch in heat attracts dogs from the neighbourhood even if she is kept inside (Wirant and McGuire, 2004). The characteristic smell emitted by female sheep and goats in oestrus makes it easier for males to find females ready for coitus in the herd (Chenoweth, 1981). Olfactory stimuli generated by females stimulate the libido of males. Representatives of the family *Suidae* have a well-developed sense of smell which allows the males to identify and locate a female for coitus (Rekwot et al., 2001).

The sense of touch also plays an important role in generating sexual behaviours. Tactile stimuli, however, become important only when the male is in direct contact with the female. Through touch, the male obtains information on the female's readiness for coitus and stimulates her sexual behaviour. During oestrus, a sow touched by a boar freezes in a characteristic copulatory position (Pedersen, 2007; Liberles, 2014).

During the mating season, many animal species emit characteristic sounds, which are received via the sense of hearing. Sound signals are important for many mammalian species. An example is the deer rut (Charlton et al., 2007; Ciuti and Apollonio, 2016). Representatives of many mammalian species, during coitus and just before it, emit specific sounds that sexually stimulate individuals of the other sex (Reby et al., 2010; Pasch et al., 2011; Charlton et al., 2018). Female giant pandas produce high-pitched tonal vocalizations called chirps during their oestrous period (Owen et al., 2016). The songs of fin whales (*Balaenoptera physalus*), bowhead whales (*Balaena mysticetus*) and humpback whales (*Megaptera novaeangliae*) play a role in mating (Croll et al., 2002; Darling et al., 2006; Johnson et al., 2015).

The role of induction of copulatory reflexes

Sexual behaviour can be considered into two categories: appetitive behaviours and consummatory behaviours. Appetitive sexual behaviours increase the probability of mating and are believed to reflect the individual's sexual motivations. These behaviours include approaching and examining a potential partner and showing partner preferences (Ball and Balthazart, 2008). Appetitive behaviours may be presented by members of both sexes, with certain differences specific to individual species (Jennings and De Lecea, 2020). Consummatory sexual behaviours are associated with the course of coitus. In male rodents, these will include embracing the female and inserting the penis, whereas in female rodents they mainly involve assuming the characteristic lordosis posture (stationary arching of the spine and lifting of the tail to enable coitus). Appetitive and consummatory behaviours are associated with the generation of the coitus reflex, which is meant to lead to coitus and fertilization. The coitus reflex is a logical sequence of behaviours and responses of the body, leading to coitus and fertilization. The coitus reflex is a response to sexual stimuli from individuals of the opposite sex, received by means of the senses. The senses of smell and touch are most important in the induction of the coitus reflex in individuals of both sexes, and to a lesser degree the senses of hearing and sight as well.

The coitus reflex in male mammals

Male sexual behaviour is distinguished by a high level of expression, usually much higher than in females. This is expressed in greater motor activity and a wider range of presented behaviours. The most important sexual behaviour in males is coitus with a female in oestrus. It requires the male to show complete readiness for sexual arousal and to develop behaviours associated with sexual desire in the presence of a female in oestrus – to approach the female and enter into direct contact with her (Kemp et al., 2005; Lei et al., 2021). This is followed by the act of coitus, involving the induction of a chain of reflexes, i.e. a sequence of innate reflexive behaviours, which the male can consciously influence only to a limited extent (McDonnell, 2000). The coitus reflex sequence is controlled by a centre located in the lumbar and sacral parts of the spinal cord (the erectile centre) (Steers, 1994; Giuliano and Rampin, 2000). The mating ritual of males triggers a series of reflexes determined by the libido itself and by the presence of the object inducing it. The sequence of copulatory reflexes begins with the foreplay characteristic of each species, during which the male makes eye contact with, sniffs, and touches the female (Lenschow et al., 2022). The male coitus reflex consists of the approach reflex, erection reflex, mounting reflex, reflex to search for the vulvar opening and insert the penis, and ejaculation reflex (Tarouco et al., 2009; Lucio et al., 2012; Hintze et al., 2013; Krassioukov and Elliot, 2017; Zeidan et al., 2017). Proper induction of copulatory reflexes in males is a condition for successful coitus and ejaculation. In order for mating to be successful, all copulatory reflexes should be generated in the right order and proceed without disruption. Forms of sexual behaviour vary depending on the species. In the males of most domesticated species, two main phases of mating behaviour can be observed. The first phase is manifested as an increase in libido. In the second phase, coitus takes place, beginning with copulatory movements and ending in ejaculation (Tischner et al., 1974; Waheed et al., 2015).

The approach reflex

The approach reflex is usually generated when the male approaches a female in oestrus (Inoue et al., 2019). In males of many domesticated species (e.g. in boars, bulls, stallions, and dogs), as well as in males of some wild species, the approach reflex is nonspecific and may be generated not only in the presence of a female in oestrus (Wierzbowski and Hafez, 1961; Rola et al., 2021; Woszczyło et al., 2023). This reflex may also be a response to the presence of a female not showing signs of oestrus, or even the presence of an individual of the same sex – another male (Pearce and Hughes, 1987). The approach reflex is generated in certain males when they approach an artificial object imitating an animal – a phantom. In male domestic pigs, the object of sexual interest can be a plastic phantom or a log whose shape and size are reminiscent of a sow. Initiation of coitus on the object which first triggered a reflexive sexual response generates conditioned-reflex associations, which, when repeated many times, cause these associations to be fixed as a reflex. This mechanism is exploited to teach young males to mount a phantom for semen collection for artificial insemination (Chutia et al., 2019).

A stallion with a good libido manifests his sexual interest by neighing and emitting characteristic sounds when he approaches the mare (Tischner et al., 1974). The male also displays anxiety, scratching, vocalization, intimate pre-coital activity, such as sniffing, licking, and nibbling at the biting of the hindquarters, and a characteristic flehmen response (Waheed et al., 2015). Libido in stallions is manifested year-round, although it is highest in spring and decreases in autumn or winter. Manifestations observed in he-goats include sniffing the genital region of the female, the flehmen response, nudging with the foreleg, tongue-wagging, vocalization, kicking with the front limb, and attempting to mount a female (Véliz et al., 2004). An aroused boar emits characteristic grunts, snaps its jaws, and foams at the mouth. Boar foam contains steroid pheromones (androstenone and androstenol) that induce the boar effect in gilts (Sankarganesh et al., 2022).

The erection reflex, the mounting reflex, the reflex to search for the vulvar opening and insert the penis

The mounting reflex leads the male to mount and embrace the female, after which he performs friction movements in order to locate the vagina and insert the penis (Hemsworth and Tillbrook, 2007). Tactile stimuli are important for finding the vagina (Schober, 2007). Certain coitus reflexes, such as the mounting reflex and erection reflex, can be inhibited by external stimuli: olfactory, aural, or visual. Placing a male and female rat in the same cage makes it very likely that the animals will begin to copulate. However, coitus will not take place if the male is very hungry or if there is a predator nearby arousing his fear. All animals exhibit fight or flight behaviours in situations of danger and fear. Large animals, such as mature boars or sows, may then be dangerous. The goal of the threatened animal is to avoid the object of the threat, put an end to the stimulus, and escape. For example, male cats that have been attacked many times by female cats during coitus attempts gradually lose their libido. Following a change in their surroundings and the passage of time needed to adapt, the sexual activity of such males may be restored (Steimer, 2002). Unpleasant or painful experiences associated with mating can reduce or even eliminate the libido (Mozo et al., 2015; Cojkic and Morell, 2023).

In bulls, the speed at which copulatory reflexes are induced depends on the effects of visual stimuli. The mounting reflex and erection reflex are triggered after a few seconds or longer, depending on the effect of the stimulus (Schenk, 2018). During sexual arousal, a small amount of clear, watery secretion flows from the accessory sex glands, i.e. the bulbourethral glands, flowing out of the urethra in several waves. In this way, the urethra is prepared for the flow of semen and cleansed of urine residues (Bollwein et al., 2017). In this phase, the sigmoid flexure of the penis is partially straightened, and the glans or part of it protrudes from the opening of the preputial cavity. Straightening of the sigmoid flexure of the penis and filling of the *corpora cavernosa* with blood are essential elements of erection. This is possible owing to an increased inflow of blood to the penis and a reduced outflow, due to dilation of the arteries and simultaneous constriction of the veins within the *corpora cavernosa* (Lewis et al., 1968; Simonsen et al., 2002). Protrusion and erection of the penis are mainly influenced by the parasympathetic nervous system (Giuliano and Rampin, 2004). The *corpora spongiosa* of the urethra are filled with blood as well, which clears the urethra, enabling unobstructed ejaculation. The semen moves from the ampulla of the vas deferens to the urogenital tract about two minutes after the stimuli have acted to induce arousal in the bull (Fayrer-Hosken, 1997).

In the stallion, full erection and complete protrusion of the penis do not take place immediately after the stimulus. The average time needed for an erection to take place in a young stallion after it has been led to the mating site is about three minutes, while the corresponding time in older stallions which mate with mares is 27 to 36 seconds before the mating season and 14 to 18 seconds after the mating season (Amann, 1981; Naden et al., 1990; Little and Holyoak, 1992). Before the mating season, the male is ready to mate 10–38 seconds after achieving full erection, while after the mating season, the stallion requires 42–52 seconds after the onset of erection. During direct contact between a stallion and a mare in oestrus, erection takes place after about 60 seconds. From 60 to 120 seconds elapse from the onset of erection to the mounting of the mare. About 20% of stallions exhibit the desire to mount the mare without a full penile erection. More than 70% of them ejaculate during the first mount, and about 20% during the second. In about 70% of stallions, ejaculation takes place after 5–8 copulatory thrusts (Tischner et al., 1974).

As a consequence of sexual arousal the boar extends the tip of the penis from the foreskin, approaches the sow from behind, and climbs on her, after which it inserts its penis into the vagina. However, some boars interrupt coitus, slide off the mare before beginning to ejaculate, and after a moment mount the sow again and continue coitus (Tirindelli et al., 2009; Wysokińska and Kondracki, 2014; Hook and Fisher, 2020; Kondracki et al., 2021). During coitus the boar performs energetic copulatory movements, inserting the penis into the vagina and removing it in a motion reminiscent of a corkscrew. These are known as friction movements, involving cyclical movements of the rump forwards and backwards, usually lasting up to a minute and followed by the initiation of ejaculation.

The ejaculation reflex

Proper generation of all copulatory reflexes should lead to full-fledged ejaculation. Ejaculation is preceded by friction movements (in horses, dogs, and pigs) or takes place during the single thrust after the jump (ruminants) (Kustritz, 2005; Fabre-Nys and Gelez, 2007). Semen ejaculation is the result of contraction waves of the smooth muscle of the epididymis, vas deferens and ure-

thra. First the sperm-rich portion of the semen from the tail of the epididymis is ejaculated, together with a small amount of secretion from the accessory glands (Luongo et al., 2022; Soni et al., 2022).

The ejaculation reflex in horses lasts a relatively short time – from 6 to 8 seconds. Ejaculation takes place under the influence of physical stimuli from the vagina (temperature and pressure), received by penile receptors (Tischner et al., 1974). The first phase of ejaculation in the stallion takes place at the moment of full erection and the furthest forward protrusion of the penis. Just before the first phase of ejaculation, the urethral lumen opens. Ejaculation takes place under considerable pressure (McDonnell, 2016; Houssou et al., 2020). The semen is ejaculated in 6–8 spurts, of which the first 3 or 4 contain about 80% of the sperm, while the others contain mainly mucus. The strength of ejaculation decreases in its final phase; then the erection is reversed and the penis is withdrawn from the vagina. Once ejaculation is completed, the stallion slides off the mare (Kosiniak 1975; Varner et al., 1987; Tibary, 2007).

The effect of the coitus reflex on the expression of sexual behaviour is well known in males of the domestic pig. Ejaculation in boars lasts on average from 4 to 5 minutes and depends on the individual predispositions of the boar (Bearden et al., 2004; Chutia et al., 2019; Savić and Petrovic, 2015). Ejaculation is initiated by stimuli received by nerve endings on the glans, which are stimulated by contractions of the muscles of the vas deferens (Roese and Taylor, 2006; Ersavadla et al., 2017; Schimming and Moraes, 2018). Secretions from the accessory sexual glands together with sperm are "pumped" into the urethra (Bearden et al., 2004). The first contractions of the vas deferens have considerable amplitude and strength, which decrease with subsequent contractions. When ejaculation is completed, copulatory movements cease. The boar "falls" onto the sow, salivates, and grunts, after which he slides off her. The penis becomes flaccid relatively quickly and is pulled into the foreskin (Sambraus, 1991; Tirindelli et al., 2009; Hook and Fisher, 2020). The time elapsed from the moment the boar approaches the sow until it moves off the sow is exceptionally long – longer than in the males of other species used by humans (Bravo et al., 2009; Barquero et al., 2021). Data reported by Kondracki et al. (2013) indicate that the total duration of coitus in boars used for artificial insemination, i.e. from entry into the collection pen to dismounting the phantom after ejaculation, ranges from 5 to 26 minutes, and the expression of sexual behaviour can be highly varied between individuals. Some males jump on the phantom quickly and dynamically and ejaculate after a short time. Other boars do not demonstrate a pronounced libido. They approach the phantom several times and often need several prior jumps onto it to successfully ejaculate. Most sexually mature males in a large herd can copulate at least six times a week (Hemsworth et al., 1983). Boars are able to copulate many times a day (Fraser and Broom, 1997).

Sexual reflexes preceding coitus influence the ejaculatory performance of males. This is exploited in the acquisition of semen from male domestic animals for artificial insemination (Chenoweth, 1983). Walking bulls around one by one before collecting semen amplifies the approach reflex and results in ejaculates of greater volume and containing more sperm (Presicce et al., 1993; Schenk, 2018; Kowalczyk et al., 2021). Increased ejaculatory performance is also obtained when prior to semen collection the bull makes one or two attempts to jump the phantom without the use of the artificial vagina (Hafs et al., 1962; Pongsiri et al., 2020). Ejaculatory performance may be linked to the male's libido level. Ahmad et al. (2005) found that bulls with greater libido produce ejaculates of better quality and a higher sperm concentration, and they are more successful at fertilization than individuals with low libido. Ejaculate quantity and quality can be influenced by stimulating the sexual behaviour of males (Pound et al., 2002; Levis and Reicks, 2005). Boars climbing onto the phantom several times before ejaculating become more aroused and produce ejaculates containing more sperm than boars ejaculating after the first climb onto the phantom (Maryse and Signoret, 1984; Sambraus, 1991; Tirindelli et al., 2009; Wysokińska and Kondracki, 2014). The level of libido of boars, measured as the time elapsed from the boar's entry into the semen collection pen to the start of ejaculation, is fairly clearly associated with certain physical characteristics of the ejaculate. Boars that need the most time to begin ejaculation have been shown to produce ejaculates with a higher concentration and number of sperm (Kondracki et al., 2021). Studies in boars have shown that the physical characteristics of the ejaculate depend on the time elapsed from the boar's entry into the collection pen to its successful mounting of the phantom and on the time from its entry into the pen to the start of ejaculation (Szostak and Sarzyńska, 2011). This research also showed that an increase in the time from the boar's entry into the pen to its successful mounting of the phantom, as well as an increase in the time from its entry into the pen to the start of ejaculation, is associated with a reduction in ejaculate volume and sperm motility, but an increase in the sperm concentration in the ejaculate. In addition, boars with a high libido were shown to produce ejaculates with more beneficial traits than boars exhibiting lower sexual activity (Szostak and Sarzyńska, 2011; Kondracki et al., 2013).

The coitus reflex in females

The coitus reflex in females usually has lower expression than in males, but is very important for the fertilization process. Reflexes generated by aroused females serve three main purposes: to send a signal of readiness for coitus, to stimulate the coitus reflex in the male, and to facilitate the act of coitus and the fertilization process (Beach, 1976; Barelli et al., 2008; Veening et al., 2015).

Females ready to be fertilized manifest a set of signs of readiness for coitus, characteristic of each species. These signs involve changes in appearance, especially

the appearance of the external sex organs, changes in motor activity (a significant increase), emission of characteristic sounds, and excretion of odorous substances (pheromones) (Reith and Hoy, 2018; Crabtree, 2022; Xu et al., 2023). During oestrus in females the vulva increases in size, which is correlated with a high oestrogen level. The elevated oestrogen level increases the flow of blood through the vagina and vulva, causing the vulva to swell (Sykes et al., 2012). During oestrus females lose their appetite, run, jump on other females, and become noisy, and even aggressive. This is stimulating to males, prompting them to approach and copulate. Sexual reflexes stimulate the libido of females (Kemp et al., 2005; Curry et al., 2007; Salleh et al., 2021). As a consequence of sexual arousal, the vestibular glands located in the vaginal vestibule begin to copiously secrete mucus, facilitating the act of coitus (Dubinskaya et al., 2021). Reflexes generated during coitus stimulate the pituitary gland of females to increase the secretion of oxytocin. This stimulates contractions of the uterine muscle, which are important for transporting semen in the female reproductive tract (Kunz et al., 1998).

The sexual activity of a boar is influenced by the behaviour of the sow, which depends on the phase of the oestrous cycle. During the luteal phase, sows may ignore the presence of a boar (Kemp et al., 2005; Jose et al., 2018). In the oestrogen phase of the oestrous cycle, oestrogen hormones cause an increase in sexual activity in females (Ford, 1982, 1985; Kotwica et al., 1995; Maina and Katz, 1999; Ka et al., 2018). The level of oestrogen hormones in the blood of the sow is highest during the period immediately preceding ovulation. Then the sow displays the characteristic set of behaviours known as oestrus. The expression of sexual behaviour in sows is stimulated by the presence of a boar (Kemp et al., 2005). Sows manifest sexual behaviours more clearly in the presence of a boar, when they assume a characteristic posture with the spine arched (lordosis), facilitating the male's copulatory activity. These behaviours have a strong effect on the boar, enhancing his sexual activity. In natural mating, the boar holds his head just above the head of the sow and emits characteristic grunts. The mouth of the aroused boar secretes abundant foam rich in pheromones, which are stored in the submandibular gland. Pheromones enhance sexual arousal in the sow and stimulate her coitus reflex, which is conductive to effective fertilization (Grigoriadis et al., 2000; Gerritsen et al., 2005; Pedersen, 2007; Coombes et al., 2018). Boars exhibiting greater activity in the manifestation of certain sexual behaviours, such as head-butting the underbelly of the sow, are more effective at achieving fertilization (Hemsworth et al., 1978). Perhaps hitting this area with the head stimulates the release of oxytocin in the pituitary gland, thereby facilitating the transport of sperm in the sow's reproductive tract. This allows more sperm to reach the oviduct, which translates to more effective fertilization. Expression of the sexual behaviour of a boar increases if the mating pen has a larger area, a dry, non-slippery floor, and a shape similar to an octagon (Jongman et al., 1996).

Sows in the proestrus phase exhibit increased anxiety and increased exploratory activity. They become more aggressive and may bite their companions. Their physical activity increases in proestrus, and they spend less time recumbent (Pedersen, 2007). At this time sows attempt to find a boar and remain near him. As proestrus progresses, the sow gradually shows a reduced tendency to avoid the boar when it pushes or nudges her in the genital area. Some sows or gilts react to such contact by urinating. The changes taking place in the body of gilts and sows during oestrus cause changes in the external sexual organs. The vulva swells, the mucous membranes take on a pink colour, and mucus mixed with blood flows from the vagina (Beach, 1976). Once the sow has become tolerant to mounting, mating may take place. Coitus in pigs usually lasts several minutes. During oestrus the sow assumes a copulatory posture and raises her ears. The number of acts of coitus during oestrus may range from 1 to 10. Some females show little activity between copulations, while others actively interact with the male, sniffing his genitalia (Horrell and Kilgour, 1985; Soede and Kemp, 1997). Some sows, when in contact with a less active or less experienced male (usually young), may vigorously push and prod the boar and sniff his genitalia. In metoestrus, sows and gilts react with aversion to various forms of tactile stimulation undertaken by the boar and to efforts to mount them (Hurnik, 1987).

Mares show willingness to copulate at the age of about 12–18 months, after reaching sexual maturity. Mares in the proestrus phase are not yet ready to accept a male. At this time, the mare responds to the male's presence by squealing and tossing her hindquarters, which is a signal to the stallion to walk away. As proestrus progresses, mares gradually show increasing tolerance for the male's courtship. Stallions are observed to sniff the vicinity of the mare's vulva and raise their upper lip (flehmen response). The mare urinates more frequently and exhibits "winking" of the vulva (Stachurska et al., 2023). The stallion often spends time near the mare, licking the urine she has passed. Sometimes the male urinates in the same place as the female. During proestrus, mares which do not have access to stallions show interest in other horses in their vicinity. These mares may exhibit aggressive behaviour more often and rest for shorter periods (Crowell-Davis, 2007). In oestrus proper, the mare accepts the stallion. During oestrus in mares, the most characteristic sign of the desire to copulate is the copulatory posture adopted in response to the presence of a male. In the copulatory posture, the mare's hind legs are set slightly apart and bent. The forelegs are moved forward slightly, the neck is stretched with the head raised, and the tail is raised and moved to the side. Winking of the vulva is common (Asa et al., 1979). During coitus, the male mounts the female with his penis erect, using his forelegs to hold on to her sides just behind her hips, sometimes gently catching hold of the back of her neck

with his teeth. During the pre-ejaculatory movements, mares sometimes moan, while stallions emit characteristic grunts. Outside of oestrus, the mare avoids the approaching stallion, resists the stallion's court attempts, and behaves aggressively towards the male, e.g. by kicking him. In this situation, the mare exhibits anxiety and emits squeaking sounds (McDonnell, 1986, 2000; Crowell-Davis, 2007).

The sexual behaviour of cows is less strongly manifested than in bulls. The periestrous period in cows can be divided into three phases: proestrus, oestrus proper, and metoestrus. The proestrus phase usually lasts from 1 to 3 days. It can be difficult to distinguish proestrus from oestrus. Characteristic elements of the cow's behaviour at this time include anxiety, decreased appetite, and reduced rumination time. The cow urinates more often and lifts her tail. The vulva is congested and swollen, and mucus flows from it (Boer et al., 2010; Roelofs et al., 2010). Cows actively participate in courtship. They rub against the bull and sniff and lick his body. In the final hours of the proestrus phase, cows become restless and more interested in their surroundings. They look for contact, rub against other cows, and lick them. At this time the cow can be observed to jump on other individuals, rest her head on them, push them with her head, and sniff their hindquarters (Williamson et al., 1972; Hurnik 1987). The cow in oestrus searches for a male, and when she comes across one she prepares for coitus by standing still. The most characteristic sign of oestrus is tolerance of mounting. In metoestrus, the sexual activity of cows decreases and the desire for coitus disappears. The labia become pale and shrunken, although viscous, shiny mucus may still appear (Hurnik, 1987; Reith and Hoy, 2018).

In female sheep, increased anxiety is observed at the start of the proestrus phase. If a male is close by, females in oestrus will try to get closer to him. It appears that females are particularly attracted to mature and energetic males (Lindsay and Robinson, 1961; Maldonado et al., 2021). However, if there is no ram nearby, sheep may not show behaviours associated with searching for a partner, or they may not exhibit them distinctly enough to be noticed. A female sheep taking part in courtship rubs her head and neck against the ram's body. Vigorous tail-wagging and the lordosis posture are more common in older ewes. When the male initiates contact with the female's sexual organs, she may urinate (Gelez et al., 2003; Fabre-Nys and Gelez, 2007). A ewe in oestrus actively searches for a male, rubs her neck and torso against a male she comes across, blocks his path, surrounds him, sniffs his testicles, and nudges him vigorously with her neck. While the male sniffs her she stands still, shaking her tail, and then allows him to mount her. During coitus the female bends her head back in a characteristic manner. Oestrus usually lasts from 18 to 36 hours. In metoestrus, the male leaves the female when her sexual sensitivity wanes, and she then avoids the male. If no other female is in oestrus at the same time, the ram may continue to show interest in her for a short time, grazing or resting nearby (Hulet et al., 1962; Banks, 1964; Simitzis et al., 2006).

In goats, sexual interaction consists of courtship and coitus. The most important function of courtship is to induce sexual arousal in both the male and the female. In some females in proestrus, viscous, clear mucus flows from the vagina (Fatet et al., 2011). The male sniffs the female's genitalia and manifests the flehmen response. Over the course of courtship, the female goat becomes increasingly sensitive to the male. Urination and tail-wagging become more frequent. The female becomes increasingly restless and bleats more often. If there is a male nearby, the she-goat will attempt to get closer to him. Eating and resting time is reduced. Some females rub against various object in their surroundings (Ladewig et al., 1980; Haulenbeek and Katz, 2011). In female goats in oestrus, anxiety is clearly visible, bleating and vigorous tail-wagging are frequent, and the vulva is red. The sexual behaviour of female goats depends on their age. Young she-goats initially run from the male, while older ones compete for him, are more anxious, and frighten off their rivals in various ways. Female goats in oestrus urinate more frequently. In this stage they are especially sensitive to the odour of males. In the copulatory position, the hind legs of female goats are set slightly apart, and the forelegs are stretched out to some extent. The head and neck may be slightly lowered (Ichimaru et al., 2008; Endo et al., 2016). In metoestrus, the females' interest in the male wanes, and they often assume a recumbent position. The purpose of this strategy is to avoid coitus or attempt to rest following the increase in physical activity (Hurnik, 1987).

In dogs, copulatory behaviour involves the male mounting his partner from behind, while the female assumes a proactive position – lordosis, in which the pelvis is tilted back (with a characteristic bending of the lumbar spine), the tail is bent sideways, and the external genitalia are exposed (Fox, 1971). A typical proestrus period takes place in females, characterized by swelling and hyperaemia of the vulva and bloody discharge from the pudendal cleft, containing pheromones. In the proestrus phase, the female shows greater interest in males than usual, but does not yet accept partners (Holst and Phemister, 1975). In the ovulation phase, the female assumes a standing position, remaining motionless with her tail raised or held at the side of the perineum, while the male sniffs the vulvar area and attempts to mount her. During the proestrus phase the vulva becomes increasingly swollen and is often coated with a serous, reddish secretion (Christie and Bell, 1972; Skliarov et al., 2022). At the start of this phase, the female avoids the male, turns to the side, crouches or runs away, or sometimes barks or growls when the male touches her genitalia. Over time, the female becomes more tolerant of physical contact. She urinates more frequently or adopts a posture as for urination. The proestrus phase lasts from 2 to 12 days and gradually transitions to oestrus, when ovulation takes place. At this time the male is accepted by the female

(tolerance). During oestrus proper, the vulva becomes flaccid, and the vaginal discharge becomes paler and less copious (Beach and LeBoeuf, 1967; Holst and Phemister, 1975). If the male does not achieve intromission, the female may actively stimulate him, sniffing his genitalia, rubbing against him, and resuming the copulatory position. During penetration, the dog's penis broadens in the vagina, preventing its removal. Then the male with its penis in the vagina turns around and remains joined to her for about 30-40 minutes. The penis is then turned 180 degrees laterally. Ejaculation takes place at this time, and the female's reproductive system gradually enters metoestrus (Pal, 2011). The male and female separate only when the vaginal muscles relax and the bulbus glandis contracts. During metoestrus, after coitus, the female no longer tolerates physical contact with the male. Some females may react with regression to physical contact by the male (Hart, 1967; Hurnik, 1987).

In female cats, proestrus is characterized by anxiety and more frequent walking and vocalization. Female cats kept in the home are observed to spend less time resting and more time moving about the home (Kędzierski, 2009). This behaviour most likely indicates the search for a sexual partner. It is usually accompanied by caterwauling and rubbing of the head, neck and sides against doorframes and furniture. In the presence of a male, the female will crouch multiple times with her back arched (lordosis). At this stage the female does not yet tolerate the male's attempts to mount her. The proestrus phase usually lasts 1 to 2 days (da Silva et al., 2006). The cat in oestrus lies down and rolls on the ground, caterwauling. A male in close proximity to the female makes a squeaking sound, to which the female may respond with aversion, by hissing and snarling. If the female accepts the male, the front part of her body drops to the ground, while the rear part of the body is raised high and the tail bends to the side. The male responds to this signal of permission by grabbing a fold of skin on the back of the female's neck with his teeth and mounting her, followed by coitus lasting a few seconds. This act ends with the male's quick withdrawal and escape, because feline females experience pain at this time and react aggressively. After a short time, the female again begins to show interest in the male, and after 5–15 minutes coitus can take place again. Ten acts of coitus can take place within about two hours. During metoestrus, the female's sexual sensitivity passes and she does not tolerate any form of mounting by the male (Fox and Bekoff, 1975; Houpt, 1997).

Sexual behaviour and social behaviour of mammals

Males and females of most wild animal species live in separate groups or lead a solitary lifestyle for most of the year, meeting only during the mating season (Farstad, 1998). Then sexual contact takes place between females in oestrus and one or more males (Xia et al., 2021). The choice of sexual partners, however, is not accidental, and is subject to rules specific to each species and resulting from the sexual behaviour of the species. In wild sheep and goats, bison, and many other mammalian species, males fight one another for access to females during mating season. At this time a specific hierarchy is formed, preferring the dominant individual, which mates with most of the females ready for reproduction. The dominant position is usually occupied by the male whose strength and experience exceed those of his competitors. In the mating season, some males even mate with several females in a single day. This may lead to physical exhaustion in dominant males and deterioration of the quality of their semen. The fertility of the dominant individual is of great importance. If the dominant male is infertile or his fertility is reduced, the effectiveness of mating and the number of fertilized females may be negatively affected (Fabre-Nys and Gelez, 2007; Wroblewski et al., 2009).

Sexual activity influences the way of life and social position of the animal and the intensity and manifestation of sexual behaviour. Male pampas deer (*Ozotoceros bezoarticus*) live harmoniously side by side for most of the year, but with the start of the mating season, when they must acquire and hold territory for mating, they not only separate but become aggressive towards one another (Morales-Piñeurúa and Ungerfeld, 2012). A dominant male vervet monkey has a better chance with an attractive female than a subordinate male. His chances of access to food are greater as well. A female vervet monkey forming a relationship with a dominant male benefits from his position in the herd hierarchy, but generally only while the relationship lasts (Isbell and Young, 1993).

Sexual behaviour is genetically determined, but can be influenced by experience (Lucio et al., 2013; Kondracki et al., 2021). Female guinea pigs raised in isolation show less variety of sexual behaviour than those raised in a group. Males raised in isolation or without physical contact with other animals also show reduced sexual activity upon reaching sexual maturity (Hemsworth et al., 1978; Hemsworth and Beilharz, 1979). Copulatory experience seems to be more important for males than for females. There is no doubt that the copulatory experience and sexual skills of males increase with age (Rhen and Crews, 2002). The scope of acquisition of these skills depends not only on experience, but also on the cognitive capacity of the brain of a given individual. Therefore the influence of sexual experience on the reproductive capacity of males shows high individual variation and may have either stimulatory or diminishing effects (Kondracki et al., 2021).

The sexual behaviour of males is closely linked to manifested libido and the presence of the object triggering sexual responses. Male sexual behaviour is characterized by a dominant position, characteristic body movements, and a characteristic posture during coitus. The male usually climbs onto the female from behind, and the female assumes the lordosis position, with a characteristic arching of the spine during coitus (Pfaff et al., 2008). Females of some species (apes, alpacas, and felids), however, receive males in a recumbent position. The posture

of the female depends on the behaviour of the male. One form of male behaviour is an aggressive posture in which females are forced to copulate. Aggressive behaviour in males may also be directed towards females of another species inhabiting the same environment (Harris et al., 2010). Three forms of sexual coercion are known: forced coitus, in which the faster and stronger male holds down the female during coitus; continual disturbance of the female with attempts at coitus; and intimidation of the female when she attempts to avoid coitus with the male (Clutton-Brock and Parker, 1995).

Certain sexual behaviours proceed similarly in males of different species. These include sniffing the genitals of females, characteristic tongue movements, striking the ground with the forelimb, and emitting characteristic sounds (Fraser and Broom, 1997; Kongsted and Hermansen, 2008). Certain behaviours are specific only to a given species or related species. Male deer assume a characteristic posture and gait during courtship (Morales-Piñeurúa and Ungerfeld, 2012). Tomcats become aggressive and sometimes nibble at females. Male giraffes recognize whether a female is in oestrus by the taste of her urine (Pratt and Anderson, 1985). Free-range male donkeys approach the female many times and then withdraw before ultimately approaching and engaging in coitus, with the expression of male sexual behaviour stimulated by the behaviour of the female (Henry et al., 1998). Sexually aroused boars emit a short series of characteristic grunts, snap their jaws, salivate, urinate frequently, sniff the reproductive organs and head of the sow (Signoret, 1970; Tanida et al., 1989; Grigoriadis et al., 2000), and hit her abdomen with their snout.

Conclusion

Throughout evolution, animals have developed species-specific sexual behaviours aimed at leading to coitus and successful fertilization. Mechanisms and strategies of sexual behaviour are different in males and females, due to their different roles in the process of transferring genes to the next generation. In the female strategy of sexual behaviour, it is important to attract all potential partners, but only in order to obtain the best one. The male strategy of sexual behaviour in most mammalian species involves fertilization of the largest possible number of young, healthy females, which guarantees that a large number of offspring will be reared. It is not only the generation of a set of characteristic reflexes that is important, but also the expression with which they are manifested. Through their sexual behaviour animals signal their readiness for coitus and stimulate individuals of the other sex to copulate. Expression of sexual behaviour determines the strength of this effect, the course of coitus, the transport of gametes in the female reproductive tract, and consequently fertilization. Animals belonging to the same species may differ in their expression of sexual behaviour. Some males respond quickly and dynamically to sexual stimuli, quickly jump onto the phantom or begin coitus, and ejaculate after a short time. Other males do not demonstrate a pronounced libido. They approach the phantom or female several times and need to climb onto the phantom or female several times in order to ejaculate. Differences in the expression of sexual behaviour are also observed in females. In domesticated animals, this makes it difficult to identify signs of oestrus and choose the optimum moment for mating or artificial insemination in order to achieve conception. Stimuli from potential sexual partners, received by the senses, play a fundamental role in generating sexual behaviour. They trigger a series of copulatory reflexes, which should be generated in the right order and proceed without disruption for successful coitus and fertilization to take place. The sexual behaviour of an individual influences its position in the herd. In general, individuals with high expression of sexual behaviour typical of a given species occupy a dominant position. The dominant status gives an advantage not only in the search for mating partners, but also in access to food and expression of preferred social behaviour.

References

Adamczyk K., Górecka-Bruzda A., Nowicki J., Gumułka M., Molik E., Schwarz T., Earley B., Klocek C. (2015). Perception of environment in farm animals – a review. Ann. Anim. Sci., 15: 565−589.

Ahmad M., Asmat M.T., Rehman N.U. (2005). Relationship of testicular size and libido to age and season in Sahiwal bulls. Pak. Vet. J., 25: 67−70.

Amann R.P. (1981). A review of anatomy and physiology of the stallion. J. Equine Vet. Sci., 1: 83−105.

Angelini F., Ghiara G. (1984). Reproductive modes and strategies in vertebrate evolution. Ital. J. Zool., 51: 121−203.

Argiolas A. (1999). Neuropeptides and sexual behaviour. Neurosci. Biobehav. Rev., 23: 1127−1142.

Asa C.S. (1979). Sociosexual behaviour and the ovulatory cycle of ponies (*Equus caballus*) observed in harem groups. Horm. Behav., 13: 49−65.

Ball G.F., Balthazart J. (2008). How useful is the appetitive and consummatory distinction for our understanding of the neuroendocrine control of sexual behavior? Horm. Behav., 53: 307−311.

Banks E.M. (1964). Some aspects of sexual behaviour in domestic sheep, *Ovis aries*. Behaviour, 23: 249−278.

Barelli C., Heistermann M., Boesch C., Reichard U.H. (2008). Mating patterns and sexual swellings in pair-living and multimale groups of wild white-handed gibbons, *Hylobates lar*. Anim. Behav., 75: 991−1001.

Barquero V., Roldan E.R.S., Soler C., Yaniz J., Camacho M., Valverde A. (2021). Predictive capacity of boar sperm morphometry and morphometric subpopulations on reproductive success after artificial insemination. Animals, 11: 920.

Beach F.A. (1976). Sexual attractivity, proceptivity, and receptivity in female mammals. Horm. Behav., 7: 105−138.

Beach F.A., LeBoeuf B.J. (1967). Coital behaviour in dogs. I. Preferential mating in the bitch. Anim. Behav., 15: 546−558.

Bearden H.J., Fuquay J.W., Willard S.T. (2004). Appl. Anim. Reprod., 6th edition. Pearson Prentice-Hall, Upper Saddle River, NJ, USA.

Ben-Ari E.T. (2000). Choosy Females: Exploring the role of cryptic female choice in sexual selection and battles over paternity. BioScience, 50: 8−12.

Bielert C., Van der Walt L.A. (1982). Male chacma baboon (*Papio ursinus*) sexual arousal: mediation by visual cues from female conspecifics. Psychoneuroendocrinology, 7: 31–48

Blaustein J.D. (2008). Neuroendocrine regulation of feminine sexual

behavior: Lessons from rodent models and thoughts about humans. Annu. Rev. Psychol., 59: 93−118.
Boer H.M., Veerkamp R.F., Beerda B., Woelders H. (2010). Estrous behaviour in dairy cows: identification of underlying mechanisms and gene functions. Animal, 4: 446−453.
Bollwein H., Janett F., Kaske M. (2017). Effects of nutrition on sexual development of bulls. Anim. Reprod., 14: 607−613.
Borge K.S., Tønnessen R., Nødtvedt A., Indrebø A. (2011). Litter size at birth in purebred dogs – A retrospective study of 224 breeds. Theriogenology, 75: 911−919.
Brann D.W., Mahesh V.B. (1991). Role of corticosteroids in female reproduction. FASEB J., 5: 2691−2698.
Bravo P.W., Moscoso R., Alarcon V., Ordonez C. (2009). Ejaculatory process and related semen characteristics. Arch. Androl., 48: 65−72.
Brown B.W., Mattner P.E., Carroll P.A., Holland E.J., Paull D.R., Hoskinson R.M., Rigby R.D. (1994). Immunization of sheep against GnRH early in life: effects on reproductive function and hormones in rams. J. Reprod. Fertil., 101: 15−21.
Cahill D.J., Wardle P.G., Harlow C.R., Hull M.G. (1998). Onset of the preovulatory luteinizing hormone surge: diurnal timing and critical follicular prerequisites. Fertil. Steril., 70: 56−59.
Carmichael M.S., Humbert R., Dixen J., Palmisano G., Greenleaf W., Davidson J.M. (1987). Plasma oxytocin increases in the human sexual response. J. Clin. Endocrinol. Metab., 64: 27−31.
Charlton B.D., Reby D., McComb K. (2007). Female red deer prefer the roars of larger males. Biol. Lett., 3: 382−385.
Charlton B.D., Martin-Wintle M.S., Owen M.A., Zhang H., Swaisgood R.R. (2018). Vocal behaviour predicts mating success in giant pandas. Royal Soc. Open Sci., 5: 181323.
Chenoweth P.J. (1981). Libido and mating behaviour in bulls, boars, and rams: a review. Theriogenology, 16: 155−177.
Chenoweth P.J. (1983). Sexual behaviour of the bull: a review. J. Dairy Sci., 66: 173−179.
Chenoweth P.J., Landaeta-Hernandez A.J. (1998). Genetic influences on reproductive and maternal behavior in livestock. In: Genetics of Animal Behavior, Grandin T. (ed.). Academic Press, New York, pp. 145−165.
Christensen A., Bentley G.E., Cabrera R., Ortega H.H., Perfito N., Wu T.J., Micevych P. (2012). Hormonal regulation of female reproduction. Horm. Metab. Res., 44: 587−591.
Christie D.W., Bell E. (1972). Studies of canine reproductive behaviour during the normal oestrous cycle. Anim. Behan., 20: 621−631.
Chutia T., Ahmed F.A., Lalrintluanga K., Kalita G., Gali J.N., Roychoudhury P., Mayengbam P., Chaudhary J.K. (2019). Training and libido assessment in boar during semen collection. Haryana Vet., 58 (S.I.): 50−52.
Ciuti S., Apollonio M. (2016). Reproductive timing in a lekking mammal: male fallow deer getting ready for female estrus. Behav. Ecol., 27: 1522−1532.
Clapperton B.K., Minot E.O., Crump D.R. (1988). An olfactory recognition system in the ferret *Mustela furo* L. (Carnivora: Mustelidae). Anim. Behav., 36: 541−553.
Clutton-Brock T. H., Parker G. A. (1995). Sexual coercion in animal societies. Anim. Behav., 49: 1345−1365.
Cojkic A., Morrell J.M. (2023). Animal welfare assessment protocols for bulls in artificial insemination centres: requirements, principles, and criteria. Animals, 13: 942.
Colegrave N. (2012). The evolutionary success of sex. EMBO Rep., 13: 774−778.
Colledge W.H. (2013). The neuroendocrine regulation of the mammalian reproductive axis. Exp. Physiol., 98: 1519−1521.
Comninosa A.N., Dhillo W.S. (2018). Emerging roles of kisspeptin in sexual and emotional brain processing. Neuroendocrinology, 106: 195−202.
Coombes H.A., Stockley P., Hurst J.L. (2018). Female chemical signalling underlying reproduction in mammals. J. Chem. Ecol., 44: 851−873.
Cornil C.A., Ball G.F., Balthazart J. (2012). Rapid control of male typical behaviours by brain-derived estrogens. Front. Neuroendocrinol., 33: 425−446.
Corona G., Maggi M. (2022). The role of testosterone in male sexual function. Rev. Endocr. Metab. Disord., 23: 1159−1172.
Crabtree J.R. (2022). A review of oestrus suppression techniques in mares. Equine Vet. Educ., 3: 141−151.
Creel S., Creel N.M., Mills M.G.L., Monfort S.L. (1997). Rank and reproduction in cooperatively breeding African wild dogs: behavioural and endocrine correlates. Behav. Ecol., 8: 298−306.
Croll D.A., Clark C.W., Acevedo A., Tershy B., Flores S., Gedamke J., Urban J. (2002). Only male fin whales sing loud songs. Nature, 417: 809.
Crowell-Davis S. L. (2007). Sexual behavior of mares. Horm. Behav., 52: 12−17.
Csermely D. (1984). Comparative ethology of reproductive strategies in animals. Ital. J. Zool., 51: 223−241.
Cunningham R.L., Lumia A.R., McGinnis M.Y. (2012). Androgen receptors, sex behaviour, and aggression. Neuroendocrinology, 96: 131−140.
Curry M.R., Eady P.E., Mills D.S. (2007). Reflections on mare behaviour: Social and sexual perspectives. J. Vet. Behav., 2: 149−157.
Da Silva T.F.P., da Silva L.D.M., Uchoa D.C., Monteiro C.L.B., Thomaz L.A. (2006). Sexual characteristics of domestic queens kept in a natural equatorial photoperiod. Theriogenology, 66: 1476−1481.
Darling J.D., Jones M.E., Nicklin C.P. (2006). Humpback whale songs: do they organize males during the breeding season? Behaviour, 143: 1051−1101.
Dewsbury D.A. (1972). Patterns of copulatory behavior in male mammals. Q. Rev. Biol., 47: 133.
Dixson A.F. (2018). Copulatory and postcopulatory sexual selection in primates. Folia Primatol., 89: 258−286.
D'Occhio M.J., Galil K.A.A., Brooks D.E., Setchell B.P. (1985). Differential effects of gonadectomy on sensitivity to testosterone of brain centres associated with gonadotrophin negative feedback and with mating behavior in rams. J. Endocrinol., 104: 69−75.
Du Y., Fan T.Y., Tan Y., Xiong Z., Wang Z. (2010). Seasonal changes in the reproductive physiology of female rhesus macaques (*Macaca mulatta*). J. Am. Assoc. Lab. Anim. Sci., 49: 289−293.
Dubinskaya A., Guthrie T., Anger J.T., Eilber K.S., Berman J.R. (2021). Local genital arousal: mechanisms for vaginal lubrication. Curr. Sex. Health Rep., 13: 45−53.
Endo N., Rahayu L.P., Arakawa T., Tanaka T. (2016). Video tracking analysis of behavioural patterns during estrus in goats. J. Reprod. Develop., 62: 115−119.
Ersavadla R., Nalla R., Gudepu P., Mekala L. (2017). Histological studies on penis of the boar (*Sus scrofa domesticus*). Int. J. Livest. Res., 7: 80−85.
Evans A.C.O., Walsh S.W. (2012). The physiology of multifactorial problems limiting the establishment of pregnancy in dairy cattle (Review). Reprod. Fert. Develop., 24: 233−237.
Fabre-Nys C., Gelez H. (2007). Sexual behavior in ewes and other domestic ruminants. Horm. Behav., 52: 18−25.
Fabre-Nys C., Venier G. (1991). Sexual differentiation of sexual behaviour and preovulatory LH surge in ewes. Psychoneuroendocrinology, 16: 383−396.
Farstad W. (1998). Reproduction in foxes: current research and future challenges. Anim. Reprod. Sci., 53: 35−42.
Fatet A., Pellicer-Rubio M.T., LeBoeuf B. (2011). Reproductive cycle of goats. Anim. Reprod. Sci., 124: 211−219.
Fayrer-Hosken R. (1997). Anatomy and physiology of the bull's reproductive system. Vet. Clin. North Am. Food Anim. Pract., 13: 195−202.
Feder H.H., Marrone B.L. (1977). Progesterone: its role in the central nervous system as a facilitator and inhibitor of sexual behavior and gonadotropin release. Ann. N.Y. Acad. Sci., 286: 331−354.
Ferreira-Nuño A., Morales-Otal A., Raúl G., Paredes G., Velázquez-Moctezuma J. (2005). Sexual behavior of female rats in a multiple-partner preference test. Horm. Behav., 47: 290−296.
Fewell G.D., Meredith M. (2002). Experience facilitates vomeronasal and olfactory influence on Fos expression in medial preoptic area during pheromone exposure or mating in male hamsters. Brain Res., 941: 91−106.
Fletcher I.C., Lindsay D.R. (1968). Sensory involvement in the mating behavior of domestic sheep. Anim. Behav., 16: 410−414.

Ford J.J. (1982). Testicular control of defeminization in the male pigs. Biol. Reprod., 27: 425.
Ford J.J. (1985). Reevaluation of the role of progesterone in stimulating sexual receptivity in estrogen-treated gilts. J. Anim. Sci., 61: 36−43.
Fox M.W. (1971). Socio-infantile and socio-sexual signs in canids: a comparative and ontogenetic study. Zeitsch. Tierpsychol., 28: 185−210.
Fox M.W., Bekoff M. (1975). The behaviour of dogs. In: The behaviour of domestic animals, 3rd Edition, Hafez E.S.E. (ed.). Bailliere Tindall, London.
Fraser A.F., Broom D.M. (1997). Farm animal behaviour and welfare. CAB International, Oxon, U.K., pp. 33−45.
Garces-Restrepo M.F., Peery M.Z., Reid B., Pauli J.N. (2017). Individual reproductive strategies shape the mating system of tree sloths. J. Mammal., 98: 1417−1425.
Gelez H., Lindsay D.R., Blache D., Martin G.B., Fabre-Nys C. (2003). Temperament and sexual experience affect female sexual behaviour in sheep. Appl. Anim. Behav. Sci., 84: 81−87.
Gerritsen R., Langendijk P., Soede N.M., Kemp B. (2005). Effects of (artificial) boar stimuli on uterine activity in estrous sows. Theriogenology, 64: 1514−1525.
Ginther O.J. (1992). Reproductive biology of the mare. Basic and applied aspects (2nd ed.). Equiservices, Cross Plains, WI, pp. 31−33.
Giuliano F., Rampin O. (2000). Central noradrenergic control of penile erection. Int. J. Impot. Res., 12 (Suppl. 1): 13−19.
Giuliano F., Rampin O. (2004). Neural control of erection. Physiol. Behav., 83: 189−201.
Gotlieb N., Moeller J., Kriegsfeld L.J. (2020). Development and modulation of female reproductive function by circadian signals. In: Developmental neuroendocrinology, Wray S., Blackshaw S. (eds). Cham: Springer, pp. 413−446.
Górski K., Kondracki S., Wysokińska A. (2017). Effects of season on semen parameters and relationships between selected semen characteristics in Hypor boars. Turk. J. Vet. Anim. Sci., 41: 563−569.
Grigoriadis D.F., Edwards S.A., English P.R., Davidson F.M. (2000). The reproductive behaviour of pigs in a dynamic service system for gilts. Appl. Anim. Behav. Sci., 66: 203−216.
Hafs H.D., Knisely R.C., Desjardins C. (1962). Sperm output of dairy bulls with varying degrees of sexual preparation. J. Dairy Sci., 45: 788.
Harris H.S., Oates S.C., Staedler M.M., Tinker M.T., Jessup D.A., Harvey J.T., Miller M.A. (2010). Lesions and behavior associated with forced copulation of juvenile Pacific harbor seals (*Phoca vitulina richardsi*) by southern sea otters (*Enhydra lutris nereis*). Aquat. Mamm., 36: 219−229.
Hart B.L. (1967). Sexual reflexes and mating behaviour in the male dog. J. Comp. Physiol. Psychol., 64: 388–399.
Haulenbeek A.M., Katz L.S. (2011). Female tail wagging enhances sexual performance in male goats. Horm. Behav., 60: 244−247.
Heitor F., Oom M.M., Vicente L. (2006). Social relationships in a herd of Sorraia horses: Part II. Factors affecting affiliative relationships and sexual behaviors. Behav. Processes, 73: 231−239.
Hemsworth P.H., Beilharz R.G. (1979). The influence of restricted physical contact with pigs during rearing on the sexual behaviour of the male domestic pig. Anim. Prod., 29: 311−314.
Hemsworth P.H., Tilbrook A.J. (2007). Sexual behaviour of male pigs. Horm. Behav., 52: 39−44.
Hemsworth P.H., Findlay J.K., Beilharz R.G. (1978). The importance of physical contact with other pigs during rearing on the sexual behaviour of the male domestic pig. Anim. Prod., 27: 201−207.
Hemsworth P.H., Winfield C.G., Hansen C., Makin A.W. (1983). The influence of isolation from females and mating frequency on the sexual behaviour and semen quality of young post-pubertal boars. Anim. Prod., 37: 49−52.
Henry M., Lodi L. D., Gastal M.M.F.O. (1998). Sexual behavior of domesticated donkeys (*Equus asinus*) breeding under controlled or free range management systems. Appl. Anim. Behav. Sci., 60: 263−276.
Herbison A.E. (2020). A simple model of estrous cycle negative and positive feedback regulation of GnRH secretion. Front. Neuroendocrinol., 57: 100837.
Hintze S., Scott D., Turner S., Meddle S.L., D'Eath R.B. (2013). Mounting behaviour in finishing pigs: stable individual differences are not due to dominance or stage of sexual development. Appl. Anim. Behav. Sci., 146: 69−80.
Hoffman J.I., Boyd I.L., Amos W. (2003). Male reproductive strategy and the importance of maternal status in the Antarctic fur seal *Arctocephalus gazella*. Evolution, 57: 1917−1930.
Hollander-Cohen L., Golan M., Levavi-Sivan B. (2021). Differential regulation of gonadotropins as revealed by transcriptomes of distinct LH and FSH cells of fish pituitary. Int. J. Mol. Sci., 22: 6478.
Holst P.A., Phemister R.D. (1975). Temporal sequence of events in the estrus cycle of the bitch. Anim. J. Vet. Res., 36: 705−706.
Hook K.A., Fisher H.S. (2020). Methodological considerations for examining the relationship between sperm morphology and motility. Mol. Reprod. Dev., 87: 633−649.
Horrell R.I., Kilgour R. (1985). Oestrous behaviour. In: Ethology of farm animals, Fraser A.F. (ed.). Amsterdam, Elsevier.
Houpt K.A. (1997). Sexual behaviour problems in dogs and cats. Vet. Clin. North Am. Small Anim. Pract., 27: 601−615.
Houssou H., Bouzebda-Afri F., Bouzebda Z., Benidir M. (2020). Evaluation of sexual behavior of stallion (Arabian versus Barb) during breeding season in Algeria. Indian J. Anim. Res., 54: 1078−1082.
Hulet C.V., Blackwell R.L., Ercanbrack S.K., Price D.A., Wilson L.O. (1962). Mating behaviour of the ewe. J. Anim. Sci., 21: 870−874.
Hurnik J.F. (1987). Sexual behaviour of female domestic mammals. Vet. Clin. N. Am-Food A., 3: 423−461.
Hurtado-Gonzales J.L., Uy J.A.C. (2010). Intrasexual competition facilitates the evolution of alternative mating strategies in a colour polymorphic fish. BMC Evol. Biol., 10: 391.
Ichimaru T., Mogi K., Ohkura S., Mori Y., Okamura H. (2008). Exposure to ram wool stimulates gonadotropin-releasing hormone pulse generator activity in the female goat. Anim. Reprod. Sci., 106: 361−368.
Igbokwe C.O. (2009). The role of main olfactory and vomeronasal systems in animal behavior and reproduction. Anim. Research Int., 6: 1093−1101.
Inoue S., Yang R., Tantry A., Davis C., Yang T., Knoedler J.R., Wei Y., Adams E.L., Thombare S., Golf S.R., Neve R.L., Tessier-Lavigne M., Ding J.B., Shah N.M. (2019). Periodic remodelling in a neural circuit governs timing of female sexual behaviour. Cell, 179: 1393−1408.
Insel T.R. (1992). Oxytocin: a neuropeptide for affiliation: evidence from behavioural, receptor autoradiographic, and comparative studies. Psychoneuroendocrinology, 17: 3−35.
Isbell L.A., Young T.P. (1993**)**. Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. Behav. Ecol. Sociobiol., 32: 377−385.
Jennings K.J., De Lecea L. (2020**)**. Neural and hormonal control of sexual behavior. Endocrinology, 161: 113.
Johnson H.D., Stafford K.M., George J.C., Ambrose W.G.J., Clark C.W. (2015). Song sharing and diversity in the Bering-Chukchi-Beaufort population of bowhead whales (*Balaena mysticetus*) (spring 2011). Mar. Mamm. Sci., 31: 902−922.
Jongman E.C., Hemsworth P.H., Galloway D.B. (1996**)**. The influence of conditions at the time of mating on the sexual behavior of male and female pigs. Appl. Anim. Behav. Sci., 48: 143−150.
Jose P.C., Ethel G.G., Ignacio P.G., Ulises M.C., Leonel A.R., Ricardo V.P. (2018). Induction and synchronization of estrus with exogenous hormones and sexual biostimulation in multiparous sows at weaning. Abanico Vet., 8: 88−97.
Juntti S.A., Tollkuhn J., Wu M.V., Fraser E.J., Soderborg T., Tan S., Honda S.I., Harada N., Shah N.M. (2010). The androgen receptor governs the execution, but not programming, of male sexual and territorial behaviours. Neuron, 66: 260−272.
Ka H., Seo H., Choi Y., Yoo I., Han J. (2018). Endometrial response to conceptus-derived estrogen and interleukin-1β at the time of implantation in pigs. J. Anim. Sci. Biotechnol., 9: 44.
Kekan P.M., Ingole S.D., Sirsat S.D., Bharucha S.V., Kharde S.D., Nagvekar A.S. (2017). The role of pheromones in farm animals – a review. Agric. Rev., 38: 83−93.
Kemp B., Soede N.W., Langendijk P. (2005). Effects of boar contact

and housing conditions on estrus expression in sows. Theriogenology, 63: 643−656.
Kędzierski W. (2009). Mechanism of the action of estrogens on nerve-centers in the brain that regulate the sexual behavior of females (in Polish). Med. Weter., 65: 674−678.
Kondracki S., Iwanina M., Wysokińska A.., Górski K. (2013). The use of sexual activity measurements to assess ejaculatory performance of boars. Arch. Tierz., 56: 106.
Kondracki S., Iwanina M., Wysokińska A., Banaszewska D., Kordan W., Fraser L., Rymuza K., Górski K. (2021). The usefulness of sexual behaviour assessment at the beginning of service to predict the suitability of boars for artificial insemination. Animals, 11: 3341.
Kongsted A.G., Hermansen J.E. (2008). The mating behavior and reproduction performance in a multi-sire mating system for pigs. Theriogenology, 69: 1139−1147.
Kosiniak K. (1975). Characteristics of the successive jets of ejaculated semen of stallions. J. Reprod. Fertil., 23: 59−61.
Kotwica G., Sobczak J., Koziorowski M. (1995). Effects of opioid peptides, indomethacin and age on oxytocin and prolactin release during mating in sows. Reprod. Domest. Anim., 30: 257−263.
Kowalczyk A., Gałęska E., Czerniawska-Piątkowska E., Szul A., Hebda L. (2021). The impact of regular sperm donation on bulls' seminal plasma hormonal profile and phantom response. Sci. Rep., 11: 11116.
Krassioukov A., Elliott S. (2017). Neural control and physiology of sexual function: effect of spinal cord injury. Top Spinal Cord Inj. Rehabil., 23: 1−10.
Krüger T.H.C. Haake P., Chereath D., Knapp W., Janssen O.E., Exton M.S., Schedlowski M., Hartmann U. (2003). Specificity of the neuroendocrine response to orgasm during sexual arousal in men. J. Endocrinol., 177: 57−64.
Kunz G., Noe M., Herbertz M., Leyendecker G. (1998). Uterine peristalsis during the follicular phase of the menstrual cycle: effects of oestrogen, antioestrogen and oxytocin. Hum. Reprod. Update, 4: 647−654.
Kustritz M.V.R. (2005). Reproductive behavior of small animals. Theriogenology, 64: 734−746.
Kuswati A.N., Prasetyo D., Yekti A.P.A., Susilawati T. (2022). The relationship of estrous character with conception rate in Madura cattle. J. Ilmu-ilmu Peternakan, 32: 407−415.
Kvarnemo C. (2018). Why do some animals mate with one partner rather than many? A review of causes and consequences of monogamy. Biol. Rev., 93: 1795−1812.
Ladewig J., Price E.O., Hart B.L. (1980). Flehmen in male goats: Role in sexual behaviour. Behav. Neural Biol., 30: 312−322.
Lee V.H.Y., Lee L.T.O., Chow B.K.C. (2008). Gonadotropin-releasing hormone: regulation of the GnRH gene. FEBS J., 275: 5458−5478.
Lei K., Zong C., Du X., Teng G., Feng F. (2021). Oestrus analysis of sows based on bionic boars and machine vision technology. Animals, 11: 1485.
Lenschow C., Mendes A.R.P., Lima S.Q. (2022). Hearing, touching, and multisensory integration during mate choice. Front. Neural Circuits, 16: 943888.
Levine J.E. (2015). Neuroendocrine control of the ovarian cycle of the rat. 4th Ed. Elsevier, pp. 1199−1257.
Levis D.G., Reicks D.L. (2005). Assessment of sexual behavior and effect of semen collection pen design and sexual stimulation of boars on behavior and sperm output – a review. Theriogenology, 15: 630−642.
Lewis J.E., Walker D.F., Beckett S.D., Vachon R. (1968). Blood pressure within the corpus cavernosum penis of the bull. J. Reprod. Fert., 17: 155−156.
Liberles S.D. (2014). Mammalian pheromones. Ann. Rev. Physiol., 76: 151−175.
Lindeberg H. (2008). Reproduction of the female ferret (*Mustela putorius furo*). Reprod. Domest. Anim., 43: 150−156.
Lindsay D.R., Robinson T.J. (1961). Studies of the efficiency of mating in the sheep. II. Effect of freedom of rams, paddock size and age of ewes. J. Agric. Sci., 57: 137−140.
Line S.W., Hart B.L., Sanders L. (1985). Effect of prepubertal versus postpubertal castration on sexual and aggressive behaviour in male horses. J. Am. Vet. Med. Assoc., 186: 249−251.
Little T.V., Holyoak G.R. (1992). Reproductive anatomy and physiology of the stallion. Vet. Clin. North Am. Equine Pract., 8: 1−29.
Lopez-Gatius F. (2022). Revisiting the timing of insemination at spontaneous estrus in dairy cattle. Animals, 12: 3565.
Lott D.F. (1981). Sexual behaviour and intersexual strategies in American Bison. Z. Tierpsychol., 56: 97−114.
Loy R.G., Pemstein R., O'Canna D., Douglas R.H. (1981). Control of ovulation in cycling mares with ovarian steroids and prostaglandin. Theriogenology, 15: 191−200.
Lucio R.A., Cruz Y., Pichardo A.J., Fuentes-Morales M.R., Fuentes-Farias A.L., Molina-Ceron M.L., Gutierrez-Ospina G. (2012). The physiology and ecophysiology of ejaculation. Trop. Subtrop. Agroecosyst., 15: 113−127.
Lucio R.A., Tlachi-Lòpez J.L., Eguibar J.R., Agmo A. (2013). Sperm count and sperm motility decrease in old rats. Physiol. Behav., 110–111: 73−79.
Luongo C., Llamas-Lopez P.J., Hernandez-Caravaca I., Matas C., Garcia-Vazquez F.A. (2022). Should all fractions of the boar ejaculate be prepared for insemination rather than using the sperm rich only? Biology, 11: 210.
Maccoby E.E. (1991). Different reproductive strategies in males and females. Child Dev., 64: 676−681.
Maina D., Katz L.S. (1999). Scent of a ewe: transmission of social cues affects ram sexual performance. Biol. Reprod., 60: 1373−1377.
Maksimović N., Hristov S., Milovanović A., Barna T., Stojanov I., Cekić B., Milošević-Stanković I. (2021). Development of sexual behaviour in ram lambs and its correlation to serum testosterone. Large Anim. Rev., 27: 31−34.
Maldonado J.G., Valverde G.R., De Lara R.R., Sanchez J.G., Ruiz J.A. (2021). Ram sexual preferences and estrus behaviour expression in ewes with different reproductive status. Turk. J. Vet. Anim. Sci., 45: 1074−1079.
Malo A.F., Roldan E.R., Garde J., Soler A.J., Gomendio M. (2005). Antlers honestly advertise sperm production and quality. Proc. Royal Soc. B, 272: 149−157.
Martin L.J., Touaibia M. (2020). Improvement of testicular steroidogenesis using flavonoids and isoflavonoids for prevention of late onset male hypogonadism. Antioxidants, 9: 237.
Maryse B.J., Signoret P. (1984). Sex play and behavioural sexualization in the pig. Reprod. Nutr. Dev., 24: 507−513.
Mawhinney M., Mariotti A. (2013). Physiology, pathology and pharmacology of the male reproductive system. Periodontol 2000, 61: 232−251.
McDonnell S. (1986). Reproductive behavior of the stallion. Vet. Clin. North Am. Equine Pract., 2: 535−555.
McDonnell S.M. (1992). Normal and abnormal sexual behaviour. Vet. Clin. North Am. Equine Pract., 8: 71−89.
McDonnell S.M. (2000). Reproductive behaviour of stallions and mares: comparison of free-running and domestic in-hand breeding. Anim. Reprod. Sci., 60−61: 211−219.
McDonnell S.M. (2016). Revisiting clinical stallion sexual behavior: applying ethology in the breeding shed. J. Equine Vet. Sci., 43: 18−22.
Molloy P.P., Gage M.J.G. (2006). Evolution: Vertebrate reproductive strategies get mixed up. Curr. Biol., 16: 876−879.
Morales-Piñeurúa J.T., Ungerfeld R. (2012). Pampas deer (*Ozotoceros bezoarticus*) courtship and mating behavior. Acta Vet. Scand., 54: 54−60.
Morali G., Beyer C. (1979). Neuroendocrine control of mammalian estrous behavior. In: Endocrine control of sexual behaviour, Beyer C. (ed.). Raven Press, New York, pp. 33−75.
Mozo R., Galeote A.I., Alabart J.L., Fantova E., Folch J. (2015). Evaluating the reproductive ability of breeding rams in North-Eastern Spain using clinical examination of the body and external genitalia. BMC Vet. Res., 11: 289.
Muller M.N., Mitani J.C. (2005). Conflict and cooperation in wild chimpanzees. Adv. Study Behav., 35: 275−331.
Murashima A., Kishigami S., Thomson A., Yamada G. (2015). Androgens and mammalian male reproductive tract development. Biochim. Biophys. Acta Gene Regul. Mech., 1849: 163−170.

Naden J., Amann R.P., Squires E.L. (1990). Testicular growth, hormone concentrations, seminal characteristics and sexual behaviour in stallions. J. Reprod. Fertil., 88: 167−176.
Orgeur P., Signoret J.P. (1984). Sexual play and its functional significance in the domestic sheep (*Ovies aries* L.). Physiol. Behav., 33: 111−118.
Owen M.A., Swaisgood R.R., Zhou X., Blumstein D.T. (2016). Signalling behaviour is influenced by transient social context in a spontaneously ovulating mammal. Anim. Behav., 111: 157−165.
Pal S.K. (2011). Mating system of free-ranging dogs (*Canis familiaris*). Int. J. Zool., 1: 1−10.
Parrott R.F., Baldwin B.A. (1984). Sexual and aggressive behaviour of castrated male sheep after injection of gonadal steroids and implantation of androgens in the hypothalamus: a preliminary study. Theriogenology, 21: 533−542.
Pasch B., George A.S., Campbell P., Phelps S.M. (2011**)**. Androgen-dependent male vocal performance influences female preference in Neotropical singing mice. Anim. Behav., 82: 177−183.
Pearce G.P., Hughes P.E. (1987). An investigation of the roles of boar-component stimuli in the expression of proceptivity in the female pig. Appl. Anim. Behav. Sci., 18: 287−299.
Pedersen L.J. (2007). Sexual behaviour in female pigs. Horm. Behav., 52: 64−69.
Pfaff D.W., McEwen B.S. (1983). Actions of estrogens and progestins on nerve cells. Science (New York), 219: 808−814.
Pfaff D.W., Kow L.M., Loose M.D., Flanagan-Cato L.M. (2008). Reverse engineering the lordosis behavior circuit. Horm. Behav., 54:347−354.
Pfaus J.G., Jones S.L., Flanagan-Cato L.M., Blaustein J.D. (2015). Female sexual behavior. In: Knobil and Neill's physiology of reproduction. 4th ed. Vol 2., Plant T., Zeleznik A. (eds). Elsevier, pp. 2287−2370.
Pianka E.R. (1970). On r- and K-selection. Am. Nat., 104: 592−597.
Pongsiri W., Rungruangsak J., Pant S.D., Stephen C.P. (2020). The effect of false mount on quality of frozen-thawed semen in *Bos indicus* beef bulls. J. Vet. Med. Sci., 82: 673−677.
Pound N., Javed M.H., Ruberto C., Shaikh M.A., Del Valle A.P. (2002). Duration of sexual arousal predicts semen parameters for masturbatory ejaculates. Physiol. Behav., 76: 685−689.
Pratt D. M., Anderson V. H. (1985). Giraffe social behavior. J. Nat. Hist., 19: 771−781.
Presicce G.A., Brockett C.C., Cheng T., Foote R.H., Rivard G.F., Klemm W.R. (1993). Behavioral responses of bulls kept under artificial breeding conditions to compounds presented for olfaction, taste or with topical nasal application. Appl. Anim. Behav. Sci., 37: 273−284.
Price E.O. (1987). Male sexual behavior. Vet. Clin. North Am. Food Anim. Pract., 3: 405−422.
Price P.W. (1973). Strategies for egg production. Evolution, 28: 76−84.
Reby D., Charlton B.D., Locatelli Y., McComb K. (2010). Oestrous red deer hinds prefer male roars with higher fundamental frequencies. Proc. Royal. Soc. B., 277: 2747−2753.
Reith S., Hoy S. (2018). Review: Behavioral signs of estrus and the potential of fully automated systems for detection of estrus in dairy cattle. Animal, 12: 398−407.
Rekwot P.I., Ogwu D., Oyedipe E.O., Sekoni V.O. (2001). The role of pheromones and biostimulation in animal reproduction. Anim. Reprod. Sci., 65: 157−170.
Resko J.A., Perkins A., Roselli C.E., Stellflug J.N., Stormshak F.K. (1999). Sexual behaviour of rams: male orientation and its endocrine correlates. J. Reprod. Fertil. Suppl., 54: 259−269.
Reznick D., Bryant M.J., Bashey F. (2002). r- and K-selection revisited: the role of population regulation in life-history evolution. Ecology, 83: 1509−1520.
Rhen T., Crews D. (2002). Variation in reproductive behaviour within a sex: neural systems and endocrine activation. J. Neuroendocrinol., 14: 517−531.
Rittschof C.C., Hilber S.A., Tudor M.S., St Mary C.M. (2012). Modeling male reproductive strategies and optimal mate number in an orb-web spider. Behav. Ecol., 23: 1−10.
Roelofs J., López-Gatius F., Hunter R.H.F., van Eerdenburg F.J.C.M., Hanzen C. (2010). When is cow in estrus? Clinical and practical aspects. Theriogenology, 74: 327−344.
Roese G., Taylor G. (2006). Basic pig husbandry – the boar. Primefact, 2: 1−6.
Rola L.D., Buzauskas M.E., Melo L.M., Chaves M.S., Freitas V.J.F., Duarte J.M.B. (2021). Assisted reproductive technology in neotropical deer: a model approach to preserving genetic diversity. Animals, 11: 1961.
Röttgen V., Becker F., Tuchscherer A., Wrenzycki C., Düpjan S., Schön P.C., Puppe B. (2018). Vocalization as an indicator of estrus climax in Holstein heifers during natural estrus and superovulation. J. Dairy Sci., 101: 2383−2394.
Salleh S.M., Basri A.M.H., Yaakub H. (2021). Study of sexual behaviours with different types of estrus synchronization protocols in Boer goats. Anim. Reprod., 18: e20200038.
Sambraus H.H. (1991). Comparison of reproductive behavior of farm animals. Tierarztl. Prax., 19: 8−13.
Sankarganesh D., Kirkwood R.N., Nagnan-Le Meillour P., Angayarkanni J., Achiraman S., Archunan G. (2022). Pheromones, binding proteins, and olfactory systems in the pig (*Sus scrofa*): An updated review. Front. Vet. Sci., 9: 989409.
Santos C.A.D., Landim N.M.D., Araújo H.X.D., Paim T.D.P. (2022). Automated systems for estrous and calving detection in dairy cattle. Agri Eng., 4: 475−482.
Savić R., Petrović M. (2015). Effect of photoperiod on sexual activity of boar. R. Bras. Zootec., 44: 276−282.
Schenk J.L. (2018). Review: Principles of maximizing bull semen production at genetic centres. Animal, 12: 142−147.
Schimming B.C., Moraes G.N. (2018). Morphological analysis of the elastic and collagen fibres in the ram penis. Pesq. Vet. Bras., 38: 2159−2165.
Schober J.M. (2007). The neurophysiology of sexual arousal. Best Pract. Res. Clin. Endocrinol. Metab., 21: 445−461.
Schulte-Hostedde A.I., Millar J.S., Gibbs H.L. (2004). Sexual selection and mating patterns in a mammal with female-biased sexual size dimorphism. Behav. Ecol., 15: 351−356.
Seminara S.B., Crowley W.F. Jr. (2008). Kisspeptin and GPR54: discovery of a novel pathway in reproduction. J. Neuroendocrinol., 20: 727−731.
Signoret J.P. (1970). Swine behaviour in reproduction. Proceedings of a symposium on effect of disease and stress on reproductive efficiency in swine. Extension Services, University of Nebraska, College of Agriculture, Lincoln, Nebraska, USA: 28−45.
Simitzis P.E., Deligeorgis S.G., Bizelis J.A. (2006). Effect of breed and age on sexual behaviour of rams. Theriogenology, 65: 1480−1491.
Simonsen U., Garcia-Sacristan A., Prieto D. (2002). Penile arteries and erection. J. Vasc. Res., 39: 283−303.
Skliarov P., Holubiev O., Mylostyvyi R. (2022). Determining the optimal insemination time of bitches. FAVE, Secc. Cienc. Vet., 21: e0005.
Soede N.M., Kemp B. (1997). Expression of oestrus and timing of ovulation in pigs. J. Reprod. Fertil., 52: 91−103.
Soni K.K., Jeong H.S., Jang S. (2022). Neurons for ejaculation and factors affecting ejaculation. Biology, 11: 686.
Stachurska A., Kędzierski W., Kaczmarek B., Wiśniewska A., Żylińska B., Janczarek I. (2023). Variation of physiological and behavioural parameters during the oestrous cycle in mares. Animals, 13: 211.
Stearns S.C. (1976). Life-history tactics: a review of the ideas. Q. Rev. Biol., 51: 3−47.
Steers W.D. (1994). Neuroanatomy and neurophysiology of erection. Sex. Disabil., 12: 17−27.
Steimer T. (2002). The biology of fear- and anxiety-related behaviors. Dialogues Clin. Neurosci., 4: 231−249.
Street S.E., Cross C.P., Brown G.R. (2016). Exaggerated sexual swellings in female nonhuman primates are reliable signals of female fertility and body condition. Anim. Behav., 112: 203−212.
Su H.W., Yi Y.C., Wei T.Y., Chang T.C., Cheng C.M. (2017). Detection of ovulation, a review of currently available methods. Bioeng. Transl. Med., 16: 238−246.
Sykes D.J., Couvillion J.S., Cromiak A., Bowers S., Schenck E., Crenshaw M. (2012). The use of digital infrared thermal imaging to detect estrus in gilts. Theriogenology, 78: 147−152.

Szostak B., Sarzyńska J. (2011). The influence of the breed and age on the libido of insemination boars. Acta Sci. Pol., Zootech., 10: 103−110.

Tanida H., Murata Y., Tanaka T., Yoshimoto T. (1989). Mounting efficiencies, courtship behavior and mate preference of boars under multi-sire mating. Appl. Anim. Behav. Sci., 22: 245−253.

Tarouco A.K., Freitas C.C., Neves A.P., Gregory R.M., Mattos R.C. (2009). Sexual and social behaviors of pony stallions and mares. Anim. Reprod., 6: 534−544.

Thimonier J., Mauléon P. (1969). Variations saisonnières du comportement d'oestrus et des activités ovarienne et hypophysaire chez les ovins. Ann. Biol. Anim. Biochim. Biophys., 9: 233−250.

Tibary A. (2007). Stallion reproductive behaviour. In: Current Therapy in Equine Reproduction, Samper J.C., Pycock J.F., McKinnon A. (eds). Saunders Elsevier, St. Louis, USA, pp. 174−175.

Tilbrook A.J., Galloway D.B., Williams A.H., Clarke I.J. (1993). Treatment of young rams with an agonist of GnRH delays reproductive development. Horm. Behav., 27: 5−28.

Tirindelli R., Dibattista M., Pifferi S., Menini A. (2009). From pheromones to behavior. Physiol. Rev., 89: 921−956.

Tischner M., Kosiniak K., Bielański W. (1974). Analysis of the pattern of ejaculation in stallions. J. Reprod. Fert., 41: 329−335.

Topaloglu A.K., Tello J.A., Kotan L.D., Ozbek M.N., Yilmaz M.B., Erdogan S., Gurbuz F., Temiz F., Millar R.P., Yuksel B. (2012). Inactivating KISS1 mutation and hypogonadotropic hypogonadism. N. Engl. J. Med., 366: 629−635.

Torres M.V., Ortiz-Leal I., Sanchez-Quinteiro P. (2023). Pheromone sensing in mammals: a review of the vomeronasal system. Anatomia, 2: 346−413.

Tsutsui K., Saigoh E., Ukena K., Teranishi H., Fujisawa Y., Kikuchi M., Ishii S., Sharp P. J. (2000). A novel avian hypothalamic peptide inhibiting gonadotropin release. Biochem. Biophys. Res. Commun., 275: 661−667.

Tsutsui T., Higuchi C., Soeta M., Oba H., Mizutani T., Hori T. (2009). Plasma LH, ovulation and conception rates in cats mated once or three times on different days of oestrus. Reprod. Domest. Anim., 44 (Suppl. 2): 76−78.

Varner D.D., Blanchard T.L., Love C.C., Garcia M.C., Kenney R.M. (1987). Effects of semen fractionation and dilution ratio on equine spermatozoa motility parameters. Theriogenology, 28: 709−723.

Veening J.G., de Jong T.R., Waldinger M.D., Korte S.M., Olivier B. (2015). The role of oxytocin in male and female reproductive behaviour. Eur. J. Pharmacol., 753: 209−228.

Véliz F.G., Vèlez, L.I., Flores J.A., Durate G., Poindron P., Malpaux B. (2004). Previous segregation between sexes is not a requisite to successful male effect in an estrous female goat. Anim. Reprod. Sci., 92: 300−309.

Vignozzi L., Corona G., Petrone L., Filippi S., Morelli A.M., Forti G., Maggi M. (2005). Testosterone and sexual activity. J. Endocrinol. Invest., 28: 39−44.

Waheed M.M., Ghoneim I.M., Abdoub M.S. (2015). Sexual behavior and hormonal profiles in arab stallions. J. Equine Vet. Sci., 35: 499−504.

Wallen K., Zehr J.L. (2004). Hormones and history: the evolution and development of primate female sexuality. J. Sex. Res., 41: 101−112.

Weir B.J., Rowlands I.W. (1973). Reproductive strategies of mammals. Annu. Rev. Ecol. Evol. Syst., 4: 139−163.

Wierzbowski S., Hafez E.S.E. (1961). Analysis of copulatory reflexes in the stallion. Proc. Fourth International Congress Animal Reproduction. The Hague, 2: 176−179.

Wildt D.E., Seager S.W., Chakraborty P.K. (1980). Effect of copulatory stimuli on incidence of ovulation and on serum luteinizing hormone in the cat. Endocrinology, 107: 1212−1217.

Williamson N.B., Morris R.S., Blood D.C., Cannon C.M., Wright P.J. (1972). A study of oestrous behaviour and oestrus detection methods in a large commercial dairy herd. II. Oestrous signs and behaviour patterns. Vet. Rec., 91: 58−62.

Wirant S.C., McGuire B. (2004). Urinary behavior of female domestic dog (*Canis familiaris*): influence of reproductive status, location, and age. Appl. Anim. Behav. Sci., 85: 335−348.

Wodzicka-Tomaszewska M., Kilgour R., Ryan M. (1981). "Libido" in the larger farm animals: a review. Appl. Anim. Ethol., 7: 203−238.

Woszczyło M., Szumny A., Knap P., Jezierski T., Nižański W., Kokocińska A., Skwark M.J., Dzięcioł M. (2023). The influence of mammal semen collection in male trained dogs (*Canis familiaris*), in the presence or absence of a female in estrus, on the concentration of cortisol, oxytocin, prolactin and testosterone. PLoS ONE, 18: e0278524.

Wroblewski E.E., Murray C.M., Keele B.F., Schumacher-Stankey J.C., Hahn B.H., Pusey A.E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. Anim. Behav., 77: 873−885.

Wysokińska A., Kondracki S. (2014). Assessment of sexual activity levels and their association with ejaculate parameters in two-breed hybrids and purebred Duroc and Pietrain boars. Ann. Anim. Sci., 14: 559−571.

Xia W., Grueter C.C., Ren B., Zhang D., Yuan X., Li D. (2021). Determinants of harem size in a polygynous primate: reproductive success and social benefits. Animals, 11: 2915.

Xu Z., Sullivan R., Zhou J., Bromfield C., Lim T.T., Safranski T.J., Yan Z. (2023). Detecting sow vulva size change around estrus using machine vision technology. Smart Agric. Technol., 3: 100090.

Yang L., Comninos A.C., Dhillo W.S. (2018). Intrinsic links among sex, emotion, and reproduction. Cell. Mol. Life Sci., 75: 2197−2210.

Zeidan A.E.B., El-Sharabassy A.A., Meklawy M.Y., El-Nady I.A. (2017). Sexual behaviour of Arabian stallions as affected by age and season of the year under the Egyptian environmental conditions. J. Anim. Poultry Prod., Mansoura Univ., 8: 79−82.

Received: 5 X 2023
Accepted: 17 VII 2024