Artykuł przeglądowy *Review*

Biological and clinical significance of anti-Müllerian hormone in the reproduction of domestic animals

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Summary

The anti-Müllerian hormone (AMH) is a member of the transforming growth factor-β superfamily discovered in 1953 by Alfred Jost. The AMH is a 140 kDa dimetric glycoprotein, corresponding to 553-575 amino acids. The AMH protein is encoded by the *AMH* gene located in chromosome 7 in cattle, horses and goats, chromosome 5 in sheep and chromosome 2 in pig. The action of AMH is carried out through two receptors, AMH receptor type I (AMHR1) and AMH receptor type II (AMHR2). In males, the AMH is secreted by Sertoli cells in testes and plays a fundamental role in the regression of Müllerian ducts in male embryo. In its absence Müllerian ducts develop into female inner reproductive organs. In females the AMH is produced by the granulosa cells of growing follicles and is supposed to be involved in oocyte maturation and follicle development. In the last decade, AMH has been the subject of great interest in veterinary medicine as a potential diagnostic tool in animal reproduction. The purpose of this review paper is to provide an overview of the research on the use of AMH in domestic animal reproduction.

Keywords: anti-Müllerian hormone, reproduction, domestic animals

The anti-Müllerian hormone (AMH) is a member of the transforming growth factor-β superfamily discovered in 1953 by Alfred Jost. The AMH is a 140 kDa dimetric glycoprotein (corresponding to 553-575 amino acids) consisting of two identical subunits linked by sulfide bridges and characterized by the N-terminal dimer (pro-region) and C-terminal dimer (TGF-β domain) (16, 70). It is believed that N-terminal domain enhances the activity of the C-terminal domain in which resides the bioactivity of the molecule (70). The AMH protein is encoded by the *AMH* gene. The gene is located in chromosome 7 in cattle, horses and goats, chromosome 5 in sheep and chromosome 2 in pig (28, 63). The AMH signaling pathway needs two receptors, AMH receptor type I (AMHR1) and AMH receptor type II (AMHR2), both composed of a single transmembrane domain and an intracellular domain with serine-threonine kinase activity (17, 63). The ligand binds to primary type AMHR2 that is the specific receptor as it has no other ligand. AMHR2 dimerizes to the secondary type AMHR1 allowing signal transduction (16). An activated receptor complex phosphorylates and activates cytoplasmic Smad proteins that translocate to the nucleus and directly or indirectly affect gene expression (63, 70). The *AMHR2* gene is specifically expressed in the gonads and in the mesenchymal cells adjacent to the paramesonephric ducts (70). The first described function of AMH was the suppression of the development of Müllerian ducts during embryogenesis in males (15, 50). In its absence Müllerian ducts develop into female inner reproductive organs. In the last decade, AMH has been the subject of great interest in veterinary medicine as a potential diagnostic tool in animal reproduction. Numerous studies have investigated the usefulness of AMH determination in serum samples and several clinical applications of AMH have been described.

Secretion and role of AMH in males

In males, the AMH is secreted by Sertoli cells in the testes. Sertoli cells are the earliest cell type that appear in the embryonic testis and more than 75% of the gonadal mass in the prepubertal testis is composed of Sertoli cells (69). During the fetal period the AMH secreted by immature Sertoli cells is responsible for the regression of the Müllerian ducts in the male fetus during the sexual differentiation process (15, 50). The Müllerian ducts form the base for the development

of the oviductus, the uterus and the cranial part of the vagina in females. According to data from human medicine, Müllerian ducts regression requires activation of the β-catenin pathway in Müllerian duct mesenchymal cells (15). The AMH signaling pathway activates the expression of multiple *Wnt* genes, which leads to the accumulation of β-catenin and its translocation to the nucleus. In the nucleus, β-catenin activates the expression of *Osterix* genes, which are involved in apoptosis and Müllerian duct regression (15). The AMH production begins in the fetal male gonad when Sertoli cells begin to differentiate. During puberty Sertoli cells mature, which is associated with arresting their proliferation and a progressive decrease in AMH expression and secretion (15). After puberty, testosterone inhibits AMH production through the androgen receptor (AR) that is expressed by mature Sertoli cells and in adult male individuals, AMH concentrations are low (1, 24). Testosterone is the major regulator of Sertoli cell maturation and AMH production (52). The increase in testosterone levels is always accompanied by a decrease in AMH levels (13). In the fetus and neonate, AMH is not down regulated by testosterone due to the lack of AR in Sertoli cells (52). Testosterone has an inhibitory effect on AMH production by inhibiting the transcription of NF-kB and thus suppress the transcriptional activation of *AMH* gene (69). FSH regulates of Sertoli cell number and transcriptionally activates AMH production in the absence of androgen signaling (69). During the initial stages of fetal development, AMH expression and secretion is triggered by the *SOX9* gene, without the participation of gonadotropins (15).

Clinical usefulness of AMH in reproduction of male domestic animals

Determination of castration status in males. In males, castration eliminates the source of AMH, that are Sertoli cells in testes, causing a reduction in circulating AMH concentration (50). Many studies have shown that an assessment of serum AMH levels can be used in determining the presence or absence of testes in dogs (50, 60), cats (9), calves (37) and stallions (20). In comparison to intact males, castrated males had undetectable or significantly lower serum AMH concentrations. It was established, that the elimination half-life of the serum AMH after castration is 2.85 days in male dogs (13), 1.5 days in stallions (20), and approximately 2 days in bull calves (64).

Detection of cryptorchidism. Cryptorchidism is one of the most prevalent congenital reproductive abnormalities in males (6, 19, 56). It is defined by the failure of one or both testes to descend from the abdominal cavity into the scrotal sac or failure to retain their normal position in the scrotum (6, 56). Cryptorchidism has a higher risk of testicular neoplasia (particularly Sertoli cell tumour and seminoma) and spermatic cord torsion; therefore, retained testes should be surgically removed (6, 56). According to available literature, serum AMH is a potential biomarker for detection cryptorchid testis in humans (52), bovines (37), equines (20), and dogs (29, 34, 50). Measurement of serum AMH concentration seems to be an accurate and rapid diagnostic method to distinguish between neutered and bilateral abdominal cryptorchid male animals. Significantly higher AMH concentrations have been observed in dogs with bilateral/unilateral inguinal or abdominal cryptorchidism compared with castrated and intact dogs (29, 34, 50). The study in horses showed that serum AMH level in geldings was below the detectable limit of the assay, whereas in cryptorchid stallions the level of AMH was higher than in stallions with descended testes (20). The reason for the higher AMH concentrations in males with cryptorchidism seems to be the high amount of immature Sertoli cells in these gonads (50, 68).

AMH as a marker of Sertoli cell tumour. Sertoli cell tumour is one of the testicular neoplasms, that occur relatively often in male animals, especially in dogs (41). Signs often associated with this tumour include feminization, hyperpigmentation or bilateral alopecia and are related to estrogen production by the tumour (8, 51). Bone marrow hypoplasia is a life-threatening condition associated with estrogen production of Sertoli cell tumours (42). It has been found that there are higher estradiol levels in the dogs with Sertoli cells tumours compared to other types of testicular tumours (42). However, analysis of estradiol may give inconclusive results due to large variations among individuals (33). Therefore, a more reliable diagnostic marker is needed. The results of studies on serum AMH concentration in dogs with Sertolli cell tumours are promising, and indicate that AMH may be useful as diagnostic marker for canine Sertoli cell tumours (8, 33). According to these studies all dogs with Sertoli cell tumours have significantly increased serum AMH concentrations compared to that in healthy dogs (8, 33). After surgical removal of the tumour the concentration of AMH dropped to very low values.

AMH as a marker of semen quality. Recently, studies have also been undertaken on the use of AMH as a marker of semen quality in dogs (23). Obtained findings showed moderate negative correlation between serum AMH concentration and semen total motility, progressive motility and normal morphology. An AMH concentration of 5.54 μg/L was found to be an optimal cut-off point value to obtain the greatest summation of sensitivity (86%) and specificity (63%) to predict semen quality. These findings suggest that the serum AMH concentration may be a potential marker to predict which dogs would require further semen analysis.

Secretion and role of AMH in females

In females the AMH is produced by the granulosa cells of growing follicles and is supposed to be involved in oocyte maturation and follicle development (46). Ovarian AMH production is much lower and more stable throughout life, compared to the testis (52). In females AMH production starts as early as the initial selection of ovarian follicular waves (5). After production begins in the pre-antral follicles, AMH production gradually decreases as the follicles develop (5). After binding to its receptor, AMH decreases the responsiveness of follicles to FSH, inhibiting the recruitment of primordial follicles into the pool of growing follicles (5, 63). The inhibitory effect of AMH on follicular sensitivity to FSH can play a role in the process of dominant follicle selection (17). In females, FSH and bone morphogenetic proteins are the main regulators of AMH production. *In vitro* studies have shown that FSH inhibited AMH production by granulosa cells and bone morphogenetic proteins, produced by the oocyte and theca, can enhance secretion of AMH by these cells (54). Similarly, *AMH* gene expression has been decreased by FSH and increased by bone morphogenetic proteins (54). Although study by Scheetz et al. (57) showed the dose-dependent effect of FSH on the AMH response in bovine granulosa cell culture. According to this study, FSH increases *AMH* gene expression and protein secretion in bovine granulosa cells at low concentrations, but inhibits them at higher concentrations. It is suggested that the inhibitory actions of FSH on AMH expression and protein production may be mediated, at least in part, by high intrafollicular estradiol concentrations that result from increased expression of *CYP19A1* gene in the granulosa cells of the large antral follicles when they develop to the preovulatory stage (44).

The circulating level of AMH secreted in females may change in various species due to many factors including age, stage of reproductive cycle, pregnancy, size of the animal or breed (66). In females serum AMH level is almost undetectable during the prepubertal period and then rapidly increases with the onset of puberty, reflecting the initial recruitment of primordial follicles (70). Analysis of AMH concentrations in mares grouped by 5-year intervals of age showed AMH concentrations to be higher in mares aged 5-10 and 10-15 years than 0-5 years of age and lower in mares after 20 years of age (62). Another study showed that the concentration of AMH in mares reaches its peak level at around 16-18 years, and then the level of AMH declines with increasing age (11). Hollinshead et al. (32) reported a decline in the AMH concentration in female dogs older than 4 years.

Significant changes in the AMH concentration throughout the estrus cycle have been found in female dogs (2, 46, 68). In the study by Walter et al. (68) the serum AMH concentration significantly increases from late anestrus up to 6 days before ovulation and significantly decreases starting 3 days before ovulation. A further significant decrease occurred from the last days of estrus to metestrus and middle anestrus. Nagashima et al. (46) found a significant increase in AMH concentration nine to four days before the preovulatory LH surge followed by a decline before ovulation. Alkan et al. (2) demonstrated in female dogs the highest serum AMH values in proestrus and significantly higher serum AMH concentrations in proestrus and estrus compared to diestrus and anestrus. Interestingly, in female cats, higher serum AMH concentrations have been observed in anestrus and inter-estrus than in estrus (27). In cows, on the other hand, the AMH level is static both during the natural and synchronized estrus cycles (26, 47, 59).

In pregnant cows the serum AMH level increases during the first 3 months of gestation and then decreases until parturition (44). Postpartum, AMH concentration decreases significantly and it remains at this level until the next pregnancy. In turn, in mares pregnancy has no effect on AMH secretion (4).

The concentration of serum AMH in giant breeds of female dogs was significantly lower than in small-sized, medium sized and large-sized dogs (32). Walter et al. (68) found the significantly higher AMH concentrations in the Beagles than in the Labrador crossbreeds in the same phase of estrus cycle. The serum AMH concentrations were higher in beef heifers than in dairy females (47). Jerseys cows had higher AMH levels than Holstein-Jersey crossbred cows, and the crossbred cows had higher AMH levels than Holsteins cows (53).

Clinical usefulness of AMH in reproduction of female domestic animals

Ovarian reserve testing. In females, AMH is produced by granulosa cells mainly from pre-antral and early antral follicles (14). The antral follicular population (AFP) is greatly variable among individuals. Therefore, reliable laboratory methods to predict AFP could be useful to select donor-females for use in reproductive biotechnology and for genomic selection of animals with greater reproductive potential (14). The serum AMH concentration decreases gradually as the number of growing follicles diminishes. This makes AMH a good marker for assessing a female's reproductive potential expressed by ovarian reserve (17). It has been shown that AMH is a reliable endocrine marker of AFP in cows (54), mares (21), and sheep (65). A single measurement of serum AMH concentration on any day of the estrus cycle enables predicting the number of morphologically healthy follicles and oocytes and potential fertility of individual young adult female (35, 59).

AMH as a marker of longevity, productivity and embryo production. AMH produced by growing

follicles from the beginning of folliculogenesis until reproductive senescence can be female's reproductive lifetime marker (17). Jimenez-Krassel et al. (36) found that the concentration of AMH in dairy heifers was positively correlated with their productive life in the herd. The heifers with a low level of AMH had fewer lactations and a significantly shorter productive herd life compared to those with a high level of AMH. These findings indicate AMH as a useful tool for predicting the success of heifers as cows in the herd and facilitating the decision to make early culling (5).

The measurement of AMH concentration can be useful for predicting of the effects of superovulation and embryo production during embryo transfer and selection of donors producing a high number of embryos (5). The cows with higher responses to superovulation had significantly higher mean AMH concentrations throughout the estrus cycle (54). A positive correlation was found between the plasma AMH concentration and the number of transferable embryos produced by the donors-cows (45). AMH measurements were also used successfully as a predictive marker for the superovulatory response in goats (43), sheep (40) and mares (22).

AMH as a marker of female fertility. Few studies have investigated the usefulness of AMH as a fertility marker in domestic animals. The results of such studies in cows are conflicting. One study reported that high AMH dairy cows had higher pregnancy rates following first service and a lower incidence of pregnancy loss between day 30 and 65 of gestation (53). Other studies showed that the circulating AMH concentration had no effect on the reproductive parameters in dairy cows (36). The study by Lahoz et al. (39) revealed that plasma AMH concentration might be a reliable marker of the ovarian status of prepubertal ewe lambs, reflecting their ability to respond to eCG stimulation. Moreover, these authors stated, that fertility at first mating was 34.8% higher in ewes with high plasma AMH concentrations than in those with low AMH concentrations. A Study on female dogs showed no effect of AMH concentration on the whelping rate; however, within each breed size category, the female dogs with higher serum AMH concentrations had significantly larger litter sizes compared to those with lower AMH values (32). For each 1 ng/mL increase in AMH concentrations, litter size increased by 0.3 pups/litter.

Determination of female neuter status. In veterinary practice, there are situations requiring confirmation or exclusion of the presence of functional gonadal tissues in females, especially in female dogs and female cats when their reproductive history is unknown. The diagnostic methods currently used to determine the gonadal status of females, including analyses of ovarian steroid hormones, vaginal cytology, ultrasonography and exploratory surgery, have many limitations. Therefore, it may be difficult to definitively determine whether a female has active ovaries or not. Due to the ovarian origin of AMH, its reduction is expected after removal of the gonads. A significant reduction of serum AMH concentration has been found in female dogs and female cats 10 days after ovariohysterectomy (7, 13, 48, 49). According to many studies, a single measurement of serum AMH concentration, using the available AMH assays, can clearly distinguish between intact and spayed females and can be a good alternative for current methods (9, 48, 49, 68). The mean AMH concentrations, measured by available ELISA kits, in spayed females were undetectable or significantly lower than those in intact female dogs (3, 9, 48, 49, 60, 68). Although, false positive AMH levels can occur in spayed dogs (3), in intact females occasionally low serum AMH concentrations were observed similar to spayed animals as well as (3, 49, 60). Moreover, prepubertal intact female dogs frequently have low serum AMH (49). Place et al. (49) reported that probability of correctly identifying female dogs with removed ovaries was 93.8% and female cats 100%. Alm and Holst (3) showed that 88% intact and 98% spayed female dogs were correctly identified using AMH assay. Themmen et al. (60) examined AMH levels in blood samples of intact and spayed female dogs using the canine AMH ELISA assay. They found that using cut-off values of 1.1 ng/mL, all spayed female dogs were correctly identified. Concentrations of AMH were higher in cyclic (0.96 ng/mL) and pregnant mares (0.72 ng/mL) than in ovariectomized mares (0.06 ng/mL) (4).

Detection of ovarian remnant syndrome. The ovarian remnant syndrome (ORS) is a specific complication of ovariohysterectomy or ovariectomy related to functional residual ovarian tissue (12). ORS is a result of failure to remove some or all of an ovary during ovariohysterectomy or ovariectomy. Clinical signs of ORS typically mimic those of proestrus or estrus and include vulvar swelling, sero-sanguineous vaginal discharge, and attraction to males (58). The diagnosis of ORS is mainly based on clinical symptoms, vaginal cytology (in the follicular phase), hormonal analysis (estradiol and progesterone or provocative progesterone testing with hCG or GnRH), ultrasound and exploratory laparotomy (12, 48, 58). However, these methods, except exploratory laparotomy, often require repetitive analyses and are inadequate for definitive diagnosis as well as being costly. Some studies have indicated that measurement of serum AMH concentration in a single blood sample using ELISA kit could be useful tool for diagnosis of ORS in dogs and cats (2, 48, 49, 61). It has been found that the mean serum AMH concentration in female dogs with ORS was similar to that in unspayed female dogs and significantly higher compared to that in the spayed female dogs (48, 49, 61). Alkan et al. (2) found that serum AMH concentrations in ORS group were higher than in anestrus group, and significantly lower compared to the proestrus and estrus groups. Flock et al. (27) reported significantly higher mean

AMH concentrations in queens with ORS (0. 6 ng/mL) compared to that in spayed queens (≤ 0.01 ng/mL) and significantly lower compared to intact queens (8.95 ng/mL). However, Gozer et al. (30) found no difference between the queens with ORS and the intact queens in terms of serum AMH concentration.

AMH as a marker of granulosa cell tumour. Granulosa cell tumour (GCT) is the most common tumour of the ovary in domestic animals (41). The GCT originates from the sexual cords of the ovary and can be hormonally active leading to hyperestrogenism. This tumour can be malignant, especially in female cats (25, 41). Early diagnosis of GCT and then ovariectomy could prevent metastasis as well as such other diseases as pyometra, skin lesions and bone marrow hypoplasia associated with hyperestrogenism caused by estrogen production by the GCT. Significantly higher values of AMH have been found in cows (26), mares (4, 10), queens (31) and female dogs (67) affected by GCT than in females with healthy ovaries. Moreover, the AMH values in female dogs with GCT were significantly higher than the AMH values in female dogs with ovarian cysts or ovarian neoplasm other than GCT (67). In humans, serum AMH concentration was used in diagnosis GCT with a sensitivity ranging between 76 and 93% (17).

AMH as a novel biomarker for detecting bovine freemartinism. Freemartinism is a well described disorder in cattle. This anomaly occurs in heifers born from heterosexual twin pregnancies, resulting in an underdeveloped reproductive system and ultimately sterility. It is a result of the vascular anastomoses between the placentas of the heterosexual twin fetuses and an inhibiting effect of males hormones on the development of the reproductive system (38). In the freemartin heifers, inhibition of genital organs development causes minimal ovarian reserves in these animals (18). Koca et al. (38) investigated circulating levels of AMH in healthy Holstein heifers that had reached puberty and in freemartin heifers of the same breed and age. The study showed that the mean AMH levels in healthy animals were approximately 14 times higher than in freemartin animals. These authors concluded that AMH could be used as a reliable biomarker for identifying Holstein freemartin animals. Rota et al. (55) found that newborn males and freemartins have very high concentrations of AMH (over 700 ng/ml). Conversely, plasma AMH concentrations were always below 120 ng/ml in females. While values remained stable in males for the first five months of life, they sharply decreased in the freemartins within the first fortnight, and reach female levels, which demonstrates that AMH is originated in the male twin.

Conclusion

In last decade, numerous studies have been conducted to determine the usefulness of AMH measurement in serum samples as a diagnostic tool in domestic animal reproduction. The findings of these studies indicate that serum AMH determination can have many important clinical applications, in both male and female domestic animals, including the determination of the neuter status of animals and the accurate diagnosis of ORS, cryptorchidism, Sertoli cell tumour and granulosa cell tumour. Moreover, the circulating AMH level can be useful for the assessing of ovarian reserve, predicting of the effects of embryo production during embryo transfer and detecting bovine freemartinism. The availability of AMH ELISA assays makes AMH an attractive marker that can be determined by commercial laboratories and used in veterinary practice to examine the gonadal status of domestic animals, especially for detecting active gonadal tissue in stallions, and in both sexes of dogs and cats.

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