REVIEW

PHYSIOLOGICAL ASPECTS OF OVIPOSITION AND ITS ROLE IN EGG QUALITY

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Expulsion of the fully calcified egg from the reproductive tract requires coordination of the muscular activity of the shell gland with relaxation in uterovaginal sphincter. Both arginine vasotocin and prostaglandin $F_{2\alpha}$ result contraction of smooth muscle in the avian uterus through their regulation of intramuscularly Ca^{2+} concentrations. Because of increasing of phosphorus and magnesium concentrations in the shell gland fluid during the final two hours of calcification, it could be concluded that they might be involved in the termination of shell deposition. Oviposition time is strongly affected by numerous factors, including photoschedule, ovulation, surges of LH and sex steroids hormones and stress factors. In birds ovulation and oviposition are processes controlled by LH and sex steroid hormones. In fact, time of ovulation and oviposition are closely affected by lighting regimes because the open period of LH release is a response to the circadian rhythms. Exposure to stress causes hens to delay the oviposition time and adrenalin released in response to stress may suppress the uterine contractions. In the fowl, egg weight and eggshell quality characteristics vary according to oviposition time. Eggs laid in the morning were heavier than those laid later during the day but shell quality of eggs laid in the morning is not as good as that of those laid in the afternoon. In contrast, in Japanese quail, time of oviposition had no significant effect on egg weight and egg quality traits.

oviposition time; prostaglandins; arginine vasotocin; LH, lighting regimes; environmental stressors; egg weight; eggshell quality

Introduction

The avian oviduct involved in egg formation is a tubular organ responsible for the transport of the egg and the secretion of the components surrounding the yolk. It is organized into five regions: from proximal to distal, the infundibulum which receives the ovum, the magnum which secretes albumen, the isthmus which secretes precursors of the shell membranes, the red isthmus or tubular shell gland where the mammillary knobs are formed and the initial process of calcium deposition is targeted specifically at them, finally, the shell gland or uterus which adds calcium to the shell, forms the cuticle and increases the egg weight by the addition of "plumbing" fluid to the albumen (Etches, 1996; Reece, 1997). During the final few minutes before oviposition, the intensity and frequency of muscular contraction are further increased and are associated with increases in the plasma concentration of arginine vasotocin (AVT), prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$) and prostaglandin E_2 (PGE_2) (Olson et al., 1986; Shimada et al., 1987; Takahashi et al., 1994; Soh, Koga, 1999). Since both $PGF_{2\alpha}$ and AVT are known to be potent stimulators of smooth muscle contraction (Olson et al., 1978) and PGE_2 is known to cause relaxation of the uterovaginal sphincter and vagina (Verma et al., 1976; Wechsung, Houvenaghel, 1985). The prostaglandins are produced by the granulose cells of the two largest postovulatory follicles in the ovary in association with the preovulatory surges of LH (Etches, 1996).

The open period of LH release is a response to light-dark cycle, circadian rhythms (Etches et al., 1984). Furthermore, Lewis et al. (2001) postulated that light is the strongest cue for determining oviposition time in laying hens. Experiments showed that induction of premature ovulation also induced premature oviposition, although premature oviposition has no effect on the time of ovulation (Shimada et al., 1984; Shimada, Saito, 1989; Soh, Koga, 1999). Moreover, Nys et al. (1991) concluded that the increasing of shell weight and shell breaking strength were correlated with, and proportional to; time spent by the egg in the uterus. Halaj (1982) elucidated that the prolonging the time intervals of egg formation has resulted in increase of egg weight ($r = 0.069$), albumen weight ($r = 0.059$), eggshell weight ($r = 0.245$), eggshell thickness ($r = 0.223$) and shell strength ($r = 0.105$) and decreased yolk percentage ($r = -0.058$) and albumen percentage ($r = -0.015$). In these circumstances, it could be noted that time of oviposition plays a very important role in determining eggshell quality. A lot of workers indicated that eggs laid in the morning were heavier than those laid later during the day but shell quality of eggs laid in the morning is not as good as that of those laid in the afternoon (Arafa et al., 1982; Lee, Choi, 1985; Harms, 1991; Novo et al., 1997; Pavlovski et al., 2000a, b).

The main objectives of this review are therefore to demonstrate the factors, which mainly related to oviposition and also to investigate the relationship between oviposition time and egg quality traits.

Physiological mechanisms of oviposition

The regulation of oviposition is under the influence of multiple factors. Of these, the neuropeptide, AVT and prostaglandins. Indeed, plasma concentrations of $PGF_{2\alpha}$ and AVT significantly increase immediately before and during oviposition with a decrease following the expulsion of the egg in chicken (Hammond et al., 1980; Takahashi et al., 1994, 1999), quail (Hertelendy, 1974; Hertelendy et al., 1975; Soh, Koga, 1999) and in goose (Celebi, Güven, 2001). AVT and $PGF_{2\alpha}$ promote the contractile activity of the shell gland muscle, a function that is coordinate with the opening of the uterovaginal sphincter under the influence of PGE_2 and the relaxation of the vagina, allowing the egg to be expelled (Hertelendy et al., 1975; Verma et al., 1976; Hertelendy, Biellier 1978a, b; Olson et al., 1978, 1986; Wechsung, Houvenaghel, 1985; Saito et al., 1987; Shimada et al., 1987; Shimada, Molnár, 1996; Tsutsui et al., 1996). The prostaglandins are produced by the granulose cells of the two largest postovulatory follicles in the ovary in association with the preovulatory surges of LH (Etches et al., 1990; Etches, 1996). In addition, Kojisato and Shimada (1987) stated that the primary source of the increase in plasma PGF at oviposition is the theca layers of the largest preovulatory and the largest postovulatory follicles. Therefore, it could be mentioned that prostaglandins are involved in the oviposition of normal hard-shelled eggs (Hertelendy et al., 1975; Hertelendy, Biellier, 1978b; Hester et al., 1991; Hargrove, Ottinger, 1992; Soh, Koga, 1999). Simultaneously, it could be assumed that prostaglandin may be involved in the premature oviposition of some soft-shelled and shell-less eggs (Balog, Hester, 1991; Hester et al., 1991). With regard to AVT, numerous reports indicated that AVT is involved in oviposition in laying hens and it is proved that AVT has receptors in the uterus (Takahashi et al., 1992, 1994) and the injection of AVT can induce premature oviposition in laying hens (Rzasa, Ewy, 1970; Soh, Koga, 1999). At the same time, plasma levels of AVT increase at time of oviposition (Nouwen et al., 1984; Tanaka et al., 1984; Saito, Koike, 1992; Takahashi et al., 1994; Sasaki et al., 1998).

Several scientific reports were interested in the interpretation of the mood of action of prostaglandins and AVT. Shimada and Molnár (1996) proved that $PGF_{2\alpha}$ and AVT regulate calcium ion (Ca^{2+}) concentrations that are generally believed to be an essential feature of the contraction/relaxation cycle of uterine smooth muscle. The same authors indicated that $PGF_{2\alpha}$, at physiological concentrations, promotes Ca^{2+} entry into these cells whereas AVT activates the phosphoinositide cycle, generating the Ca^{2+} mobilizer and inositol triphosphate, and increasing Ca^{2+} uptake from the extracellular component. On the other side, Tsutsui et al. (1996) established that peptide avian galanin in the oviduct evokes oviposition through mechanisms of the induction of utering and vaginal contraction and this peptide may contribute as a neurotransmitter or a neuromodulator to avian oviposition.

Examination of shell deposition reveals that the concentration of phosphorus increases in the shell gland fluid during the final two hours of calcification; both phosphorus-containing proteins and phosphorus have been implicated in this process (Nys et al., 1991). These results comply with Soh and Koga (1999) who established that the intravenous and intrauterine injection with phosphate solution induced oviposition and secretion of shell pigment from the shell gland in Japanese quail. Moreover, Nys et al. (1986) revealed that concentrations of inorganic phosphorus in the plasma were increased during the period of shell formation and decreased when calcification was suppressed. Conversely, both Choi et al. (1981) and Ogawa et al. (1999) reported that serum inorganic phosphorus level 3 hr prior to the estimated time of oviposition did not change at different times of the day. In turkey, plasma phosphorus was the lowest at oviposition and remained relatively low until 6 hr postoviposition but values at 18 and 24 hr postoviposition were higher (Manley et al., 1982) and also the similar pattern was found in the laying chicken (Miles et al., 1984). On the other side, data reported by Miller et al. (1977a, b) and Mongin and Sauveur (1979) indicated that plasma inorganic phosphorus fluctuates during the day. At the same time, the increase in magnesium in the shell gland fluid at the end of calcification and the observation that the outer layers of the egg shell contain higher amounts of magnesium have been taken as evidence to implicate this ion in the termination of shell deposition (Arad et al., 1989). It has also been noted that both total and inorganic magnesium concentrations decreased before oviposition in both the guinea fowl and the chicken (Ogawa et al., 1999). In addition, Waddell et al. (1991) showed that plasma concentrations of calcium and magnesium decreased during shell formation in all birds.

Indomethacin and acetylsalicylic acid (ASA), the active ingredient of aspirin, have been evaluated as antiprostaglandin. Indomethacin, an inhibitor of prostaglandin synthetase, will block uterine muscle electromyographic activity (Shimada et al., 1986; Takahashi et al., 1994). Furthermore, Sasaki et al. (1998) reported that in hens that were administrated indomethacin, oviposition was delayed for several hours and the same result was postulated by Soh and Koga (1999) in Japanese quail. At the same time, ASA inhibits PGH syntheses or cyclo-oxygenase, an enzyme that converts arachidonic acid into prostaglandin (Balog, Hester, 1991;

McDaniel et al., 1993). Recently, ASA was fed to laying hens and breeders to improve egg quality due to its antiprostaglandin properties (Balog, Hester, 1991; Balog et al., 1993; McDaniel et al., 1993; Ebeid, 1999). Results showed that feeding 0.05% ASA decreased the incidence of soft-shelled (SS) and shell-less (SL) eggs in aged layer breeders (Balog, Hester, 1991). On the other hand, McDaniel et al. (1993) showed no effect on HS, SS, or SL egg production and all levels of dietary ASA resulted in significant decreases in specific gravity, shell thickness, shell weight, and percentage shell.

Based on these results, it is clear that oviposition appears to be accomplished by co-ordination of several mechanisms. Both AVT and $PGF_{2\alpha}$ result in contraction of smooth muscle in the avian uterus through their regulation of intracellular Ca^{2+} concentrations. Also, peptide avian galanin in the oviduct may contribute as a neurotransmitter or a neuromodulator to avian oviposition. Phosphorus and magnesium could be involved in the termination of shell deposition.

Factors affecting oviposition

The relationship between photoschedule and time of oviposition has been illustrated for a flock of chickens subjected to 14L : 10D. It is evident that the first eggs were laid during the first hours of illumination and that the model time of lay occurs about 5 hr after the down signal (Etches et al., 1984). Where the periods of darkness are of equal or nearly equal duration, causing ovipositions to occur at all times of the sunny day. Usually, these photoperiods are avoided because eggs may remain in the house for long periods of time (Etches, 1990). Ovipositions occur at all times of the day when hens are held in constant light or constant darkness (Bhatti, 1987). Whereas, under photoschedules 14L : 10D to 17L : 7D, hens usually lay their eggs in the early morning hours of the photophase (Etches et al., 1984; Etches, Schoch, 1984). On the other hand, under many photoschedules, however, hens lay their eggs in the dark. For example, hens in 14L : 7D photoschedules lay many eggs immediately after dusk and hens in 14L : 14D lay all of their eggs in darkness (Etches, 1990). Similarly, Patterson (1997) indicated that 50% of the 33-week-old flock's eggs were laid within 13 hr of the beginning of the dark cycle, while in the 76-week-old flock oviposition was delayed by another 30–60 min. Moreover, mean oviposition time was advanced relatively to dusk by approximately 0.5 hr for each 1 hr extension of the photoperiod (Lewis et al., 1995). Furthermore, under intermittent lighting regimes, such as 14 (0.25L : 0.75D) : 10D, approximately 75% of eggs are laid in periods of darkness (Lewis et al., 1995).

Numerous studies were interested in investigating the relationship between ovulation and oviposition. In birds ovulation and oviposition are processes controlled by LH and sex steroid hormones (Gilbert, 1971). Surges of LH and progesterone (P_4) have been observed between 4 and 7 hr before ovulation in laying hens (Senior, Cunningham, 1974; Shodono et al., 1975), quail (Doi et al., 1980; Wakabyashi et al., 1996), duck hens (Wilson et al., 1982) and 2–8 hr before ovulation in laying turkey hens (Mashaly et al., 1976; Proudman et al., 1984; Liu et al., 2001). In a series of studies, ovulation of the largest and most mature ovarian follicles occurred 15–30 min after oviposition in turkey hens (Wolford et al., 1964) and less than 15 min after oviposition in the guinea fowl (Ogawa et al., 1996; Panhéleux et al., 1999). Many studies have been concluded that the induction of premature ovulation also induced premature oviposition (Shimada et al., 1984; Shimada, Saito, 1989; Soh, Koga, 1999). Likewise, Etches et al., (1990) interpreted that the granulosa cells of the largest preovulatory follicle are the major intraovarian source of prostaglandin and that production of PGF2 is associated with the preovulatory surges of gonadotropins and steroid hormones preceding oviposition.

Environmental stressors, such as relocation, exposure to unfamiliar conspecifics and removal of nest sites, can cause hens to delay oviposition (Hughes et al., 1986; Watt, Solomon, 1988; Reynard, Savory, 1997, 1999). In addition, Mills et al. (1991) demonstrated that disturbance of hens increased oviposition intervals and the incidence and degree of shell whitening. It has been suggested that adrenalin released in response to stress may delay oviposition by suppressing uterine contractions (Hughes, Black, 1976). Simultaneously, studies confirmed that exogenous adrenalin causes delaying in the time of oviposition (Sykes, 1955; Crossley, 1983).

It is evident, therefore, that the time of oviposition is restricted to the lighting regime. Rather, the timing of oviposition is the overt physiological consequence of a circadian rhythm restricting the preovulatory surge of LH because the circadian rhythm controls a threshold in the neuroendocrine events that culminate in the generation of the pre-ovulatory surge of LH and sex steroid hormones. Thus, oviposition and ovulation is strongly related to each other and induction of premature ovulation also induced premature oviposition. Furthermore, exposure to stress causes hens to delay the oviposition time by reason of releasing adrenalin.

Oviposition time and egg quality

Egg quality of laying hens is influenced by several factors, including hen's age, strain, nutrition and time of oviposition. Time of oviposition plays a vital physiological role in determining eggshell quality because the amount of shell deposited is a linear function of time spent in the shell gland after plumping, and therefore thickness, should reflect the length of the interval (Belyavin et al., 1987). In the fowl, egg weight and eggshell quality characteristics vary according to oviposition

time. Numerous studies indicated that eggs laid early in the morning were heavier than eggs laid during the later periods of the day (Halaj, 1974; Washburn, Potts, 1975; Choi et al., 1981; Arafa et al., 1982; Lee, Choi, 1985; Harms, 1991; Novo et al., 1997; Patterson, 1997; Pavlovski et al., 2000a; Aksoy et al., 2001; Ledvinka et al., 2002; Ebeid et al., 2003). A possible explanation for this result could be found in Choi et al. (1981) who indicated that when a bird lays the first egg is usually the heaviest and generally there is a gradual decrease in the weight of the subsequent eggs. The first egg of a sequence is usually laid relatively early in the day and the remainder of the eggs are generally laid later on each following day. Therefore, a greater proportion of the eggs laid in the early morning of any given day should be the first eggs of the sequence and heavier than the eggs laid during the later periods of the day. The authors assumed that the heavier eggs laid early in the morning were mainly due to the greater percentage of the first eggs of the sequence in a clutch among those laid early in the morning. These findings are consistent with those of Xu Lairen and Yang Ning (1999) who confirmed that the first egg in a clutch was laid before 12:00 hr for 89.33% of all layers and the last egg in a clutch tended to be laid in the afternoon (71.2%). Furthermore, Washburn and Potts (1975) showed that the eggs laid at 10:00 hr when shell quality was poorer was greater than at later periods when shell quality was better. This might suggest that egg weight is a factor involved in the relationship of time of oviposition to shell strength.

Lee and Choi (1985) and Harms (1991) concluded that egg was heaviest in the early morning and there was a steady decline in egg weight until 15:45 hr and it increased thereafter. This result was confirmed by Patterson (1997) and demonstrated that eggs laid progressively later in the day were lower in weight and egg weights were higher in the morning and declined by 2–9 g/egg/day between 05:00 and 18:00 hr. The similar findings were obtained by Pavlovski et al. (2000a) and Aksoy et al. (2001) who showed that collection time had a significant ($P < 0.05$) effect on the egg weight of white and brown layers and the heaviest eggs were determined at the first collection time (09:00 hr) and the lightest eggs at the last time (15:00 hr). Whilst, Choi et al. (1981) and Novo et al. (1997) showed that egg mass significantly declined with oviposition time, Ayorinde and Olagbuyiro (1991) revealed that egg weight did not differ significantly among eggs laid at different time.

Regarding to shell quality attributes, a number of studies (Roland, Harms, 1974; Cipera, 1976; Roland, 1978b; Arafa et al., 1979, 1982; Lee, Choi, 1985; Yannakopoulos et al., 1994; Oguike, 1995; Pavlovski et al., 2000b) have shown that eggs had better shell quality characteristics if are laid in the afternoon than in the morning. It has also been reported that shell strength of eggs laid in the morning is not as good as that of those laid in the afternoon (Roland et al., 1973a; Potts, Washburn, 1974; Washburn, Potts, 1975; Choi et al., 1981; Pavlovski et al., 2000a). Furthermore, it is proved that shell deformation decreased while shell breaking force, shell thickness, shell mass and specific gravity increased with increasing oviposition time (Cipera, 1976; Arafa et al., 1979; Harms, 1991; Yannakopoulos et al., 1994; Pavlovski et al., 2000a, b). On the other hand, Aksoy et al. (2001) declared that although the measured shell weight was not affected by the collection time, it was highest at the first collection (09:00 hr). These results are in correspondence with Halaj and Szoby (1977) who elucidated that the mass, percentage, thickness and strength of the shell is highest in eggs collected early in the morning and late in the afternoon. Furthermore, Halaj (1974), Harms (1991) and Ebeid et al. (2003) established that shell percentage was somewhat higher in eggs laid in the morning at 06:00 hr (10.36%) and at 10:00 hr (10.32%) and it significantly decreased at 14:00 hr (10.08%). Other shell quality assessments, shell strength, shell deformation and shell thickness were not significantly affected by time of oviposition (Ebeid et al., 2003).

A number of investigators argued the reasons, which conduct to the improvement of shell quality in afternoon eggs. Roland et al. (1973a) pointed out that the improvement in shell quality of eggs laid in the afternoon was because an increase in photoperiod makes it possible for hens to consume calcium for a greater percentage of time during the process of shell formation. During the dark, much of the calcium for shell formation must be provided from the skeleton and it may be that this process is less effective in some way in such provision than from the diet. Furthermore, Roland et al., (1973b) also demonstrated that hen's digestive tract contain less total calcium in the early morning hours (06:00 hr) than in the late afternoon (20:00 hr), and that when hens were fed a diet containing 3.57% calcium (dry weight basis) the small intestine contained a lower percent calcium in the early morning than in the late afternoon. Another investigation was reported by Roland (1978a, 1981) who examined the positions of eggs in the oviduct by killing hens and concluded that although there is individual birds variation, much of the difference in the interval between ovipositions of morning and evening eggs is not due to the time eggs spends in the oviduct, but is instead due to delay in ovulation. However, Belyavin et al. (1987) declared that the generally thicker shell has been associated with, on average; a smaller size has been taken as evidence that longer formation time is accounted for by residence in the shell gland rather than elsewhere in the tract. Other studies by Roland and Harms (1974) indicated that even though eggs laid during the afternoon were lighter than morning eggs, the difference in egg weight would not explain the improvement in shell quality of afternoon eggs for three reasons. Firstly, when shell qualities of morning and afternoon eggs of the same weights were compared, afternoon eggs had the

better shell. Secondly, egg weight did not continue to decrease in the afternoon as shell quality increased. Thirdly, even though afternoon eggs weighed less, they had more total shell than the morning eggs. Another point of view was investigated by Roland (1978b) who tested the hypothesis that eggs laid during the afternoon could be rounder, thus requiring less shell to maintain shell quality; however, it was found that even though eggs laid during the afternoon were rounder than morning eggs, the difference was not large enough to explain the variation in shell quality. Simultaneously, Roland (1978c) showed that the greatest percentage of the misshapen eggs were laid during the morning hours from 06:00 to 10:00 hr and the incidence of misshapen eggs was very low and constant after 10:00 hr. Also, most of the body-checked eggs were laid between 06:00 and 08:00 hr with few being laid after 08:00 hr.

With respect to the effect of oviposition time on egg shape index, eggs laid in the afternoon have a higher shape index (rounder) and are smaller than eggs laid in the morning (Washburn, Potts, 1975; Roland, 1978b). This result has been confirmed by Ebeid et al., (2003) and it is noted that egg shape index was significantly ($P < 0.05$) higher in eggs laid in the morning at 06:00 hr (77.21%) and at 10:00 hr (77.32%) and it decreased at 14:00 hr (76.66%). Conversely, Ayorinde and Olagbuyiro (1991) demonstrated that egg shape index was not significantly affected by different times of lay. Halaj and Packa (1977) elucidated that the highest occurrence of non-standard eggs (double-yolks, small, pointed, spherical, elongated and ring-like) was in the most intensive period of egg-laying (9:00 to 11:00 hr).

Halaj (1974) revealed that the eggs laid in the morning have a slightly higher yolk percentage than the eggs laid in the afternoon. However, Yannakopoulos et al., (1994) proved that time of oviposition had no significant effect on yolk weight. However, time of oviposition had a significant effect on albumen weight when egg weight remind constant. Afternoon eggs have significantly ($P < 0.05$) more albumen than morning eggs. This could be due to the fact that afternoon egg absorbs more albumen during formation, which in turn does not contribute to an increase of its weight. Likewise, Pavlovski et al. (2000b) concluded that eggs laid in the afternoon showed lower value of Haugh Units. Contrarily, Ebeid et al., (2003) reported that Haugh Units were higher in eggs laid in the afternoon at 14:00 hr (76.87) and it is significantly ($P < 0.01$) decreased at 10:00 hr (74.23) and at 06:00 hr (73.88).

In Japanese quail, Altan and Ouz (1995, 1997) reported that egg weight did not change with oviposition time. This result agrees with that of Harms et al. (1983) who proved that egg weight in Japanese quail did not differ with the oviposition time. Erensayin and Camci (2002) investigated the effects of oviposition time on egg weight, shape index, shell thickness, albumen index, yolk index and Haugh Units in Japanese quail and they concluded that time of oviposition had no significant effect on egg quality characteristics.

Based on the previous observations, in laying hens, eggs laid in the afternoon weigh less than eggs laid in the morning but shell characteristics were higher in eggs laid in the afternoon. But in Japanese quail, time of oviposition has no influence on egg weight and egg quality traits.

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Fyziologické aspekty ovipozice vajec a její role v kvalitě vajec.

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Vypuzení vejce z pohlavního ústrojí slepic vyžaduje koordinaci svalové aktivity a činnosti žláz s vnitřní sekrecí. Kontrakce svalů dělohy u ptáků je výsledkem vlivu arginin vazotocinu a prostaglandinu $F_{2\alpha}$ na intramuskulární koncentraci Ca^{2+}. Během posledních dvou hodin tvorby skořápky dochází ke zvýšení koncentrace fosforu a hořčíku ve žlázách produkujících hmotu skořápky, což může ovlivnit dobu snesení vejce. Doba snesení vejce je významně ovlivněna řadou faktorů, jako jsou délka světla, ovulace, sekrece LH a pohlavních steroidních hormonů a stres. U ptáků je ovulace a ovipozice řízena sekrecí LH a pohlavními hormony. Doba ovulace a snesení vejce rovněž souvisí se světelným režimem, protože uvolnění LH je vázáno na cirkadiální rytmus. Stres u slepic způsobuje posunutí doby snesení vejce a adrenalin vyvolává děložní kontrakce. Dobou snesení vejce je rovněž ovlivněna hmotnost vejce a ukazatele kvality skořápky. Vejce snesená ráno bývají těžší než vejce snesená později během dne, ale kvalita skořápky vajec snesených ráno není taková jako u vajec snesených odpoledne. Naproti tomu u japonských křepelek nejsou dobou snesení vejce hmotnost ani kvalita vajec ovlivněny.

ovipozice; prostaglandiny; arginin vazotocin; LH; světelné režimy; stres; hmotnost vajec; kvalita skořápky

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