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Original research article

Relationships among Characteristics of the Wave-like Pattern of Ovarian Follicular Development in White Lamphun Cows

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ABSTRACT

The aims of the current study were to characterize the pattern of ovarian follicular wave and to evaluate the relationships among length of interovulatory interval (IOI), number of follicular wave, duration of follicular growth phase, and lifespan of corpus luteum (CL) in White Lamphun cows. The dominate follicle (DF) and CL of ovulated White Lamphun cows (n=16) were scanned with an ultrasound machine and blood samples were collected from first ovulation until second ovulation. Cows with 2 follicular waves (2-wave cows) tended to have a shorter (P=0.063) length of IOI than cows with 3 follicular waves (3-wave cows). Prolonged duration of DF growth phase in first follicular wave (Wave 1) was observed more often in 2-wave cows than in 3-wave cows (P<0.05). At the end of DF growth phase in Wave 1, the concentration of progesterone was greater in 2-wave cows than in 3-wave cows (P<0.05). The 2-wave cows had a shorter length of luteal phase than 3-wave cows (P<0.05). The length of IOI was positively correlated with number of follicular wave (P<0.05) and length of luteal phase (P<0.01) but was negatively related with duration of DF growth phase in Wave 1 (P<0.05). These results demonstrate that short length of IOI in 2-wave cows is due to extended duration of DF growth phase in Wave 1 and short lifespan of CL. These data emphasized that length of IOI increased linearly with high number of follicular wave and extended lifespan of CL but decreased linearly with prolonged duration of DF growth phase in Wave 1.

Keywords: Corpus luteum; Dominant follicle; Follicular wave; Thai indigenous beef cows.

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1. Introduction

Thai native cattle (*Bos indicus*) are classified by the information of ecotypes as follows: Northern ecotype (White Lamphun), North-eastern ecotype, Central ecotype, and Southern ecotype [1]. The major group of White Lamphun cattle is raised in the upper north of Thailand, particularly Chiang Mai, Lamphun, and Lampang provinces. Nevertheless, changes in the agricultural system and increased demand of meat consumption have subsequently resulted in decreased number of the White Lamphun cattle [2]. Because of the population decreases in the number of White Lamphun cattle, the possibility of conserving typical breeds in a tropical country for future needs was considered. One possible strategy to increase population in this breed is to increase knowledge of ovarian biology for controlling the reproductive function in heifers and cows.

The ovarian follicular dynamics appear in wave pattern such as two or three waves per the interovulatory interval (IOI) [3]. The IOI period depends on the lifespan of the corpus luteum (CL) and progesterone (P_4) production from CL [4]. It seems obvious that the lifespan and function of CL is the major evaluation of the patterns of follicular waves (2 or 3 waves) [5] and the length of the estrous cycle [6] as well as the length of IOI [7]. Only the dominant follicle (DF) of the last wave has a chance to ovulate while the unovulated follicles undergo the process of atresia [8]. Even though only a few reports are available on the ovarian follicular dynamics in Thai native breeds, the data of daily ultrasonographic studies demonstrate that the IOI of North-eastern Thai native cattle [9,10] is characterized by a wave-like pattern of ovarian follicular development as was reported for Holstein (*Bos taurus*) [11], Brahman (*Bos indicus*) [12], Nelore (*Bos indicus*) [13], Angus and Senepol (*Bos taurus*) [14], and Zebu cattle (*Bos indicus*) [15].

At present, little knowledge of ovarian follicular dynamics is available for White Lamphun cattle regarding the pattern of ovarian follicular waves as well as the relationship among length of IOI, number of follicular waves, duration of follicular growth phase, and lifespan of CL. Thus, the objectives of this research were 1) to characterize the pattern of ovarian follicular waves and 2) to evaluate the relationship among the length of IOI, number of follicular wave, and duration of follicular growth phase as well as length of luteal phase in White Lamphun cows.

2. Materials and Methods

2.1 Animals

Twenty non-pregnant White Lamphun cows (*Bos indicus*) between 3 to 5 years old and with body weight (BW) of 200 to 250 kg were used in this experiment. Animals were fed corn silage from stem and leaf and were supplemented at 1.5% of BW with commercial feed containing 14% of crude protein. Cows had free access to mineral salt blocks and water. The study was approved by the Animal Ethic Committee of Chiang Mai University (No. AG004/2560[02/2560-10-12]).

2.2 Ovulating synchronization, transrectal ultrasonography, and follicular measurements

Twenty White Lamphun cows were synchronized for ovulation with hormonal protocol to initiate the IOI. To initiate the first ovulation, cows were inserted with a controlled internal drug release (CIDR; containing 1.38 g of P_4, Zoetis Limited, Thailand) for 9 days (Day -11 to Day -2) (Fig. 1). On Day -11, cows received their first injection of prostaglandin $F_{2\alpha}$ ($PGF_{2\alpha}$). Nine days later (Day -2), CIDR were removed from all cows concurrent with injections of a second $PGF_{2\alpha}$ and estradiol (Fig. 1). At 12, 24, 36, and 48 h after CIDR withdrawal, transrectal ultrasonography with a 7.5 MHz linear-array transducer (HS-

1600V; Honda electronics, Japan) was applied to determine ovulation (Fig. 1). Ovulation was determined by the absence of an ovulatory follicle (OF) ≥ 7.0 mm in diameter on ovaries [16]. Day 0 was designated as the day of the first ovulation (Fig. 1). Then, ovaries were scanned with ultrasound machines once daily from Day 0 until the second ovulation (Fig. 1). The IOI was defined as the interval from first ovulation to second ovulation.

At each ultrasound, ovarian images were recorded and sketched on ovarian charts to determine the diameter, number, and relative location of follicles (≥ 2 mm) and CL. A follicular wave was identified as a cohort of follicles that grew from 4.0 mm in diameter to an OF size of ≥ 7.0 mm in diameter [16]. The first observation of the largest follicle that was 3.0 mm in diameter followed by an increase in diameter for 4.0-5.0 mm was designated the day of follicular wave emergence [16-19]. The growth phases of DF, subordinate follicle (SF), and CL were defined as the day of DF, SF, and CL emergences to the last day of DF, SF, and CL when maximum diameters were observed [10,13]. The atretic phases of DF, SF, and CL were the last day of the growth phases until the DF, SF, and CL were no longer detectable [10,13]. Growth and atretic rates of DF, SF, and CL were calculated utilizing the diameter of DF, SF, and CL at first detection and on the day of evaluation, divided by the time of the growth or atretic phases [10,13]. Length of the luteal phase was from the day of CL emergence after first ovulation to the day of CL absence on the ovary [10,13]. The onsets of regression of DF, SF, and CL were the day previous to second consecutive day of decrease in diameter of DF, SF, and CL [20].

2.3 Blood samples and P_4 analysis

A blood sample (3 ml) was collected from each cow daily from Day 0 until second ovulation (Fig. 1) in order to analyze P_4 hormone concentrations. Immediately upon collection, the plasma samples were centrifuged 1200 × *g* for a minimum of 10 min at room temperature, and then stored at -20°C until the P_4 concentrations were measured. The plasma P_4 was analyzed in duplicate by competitive enzyme-linked immunosorbent assay. The P_4 from plasma that was extracted by petroleum ether was detected with anti-P_4 monoclonal antibody (National Center for Genetic Engineering and Biotechnology, Thailand). In duplicate plasma sample, the intra-assay coefficient of variation was 9.8% and assay sensitivity was 0.02 ng/ml.

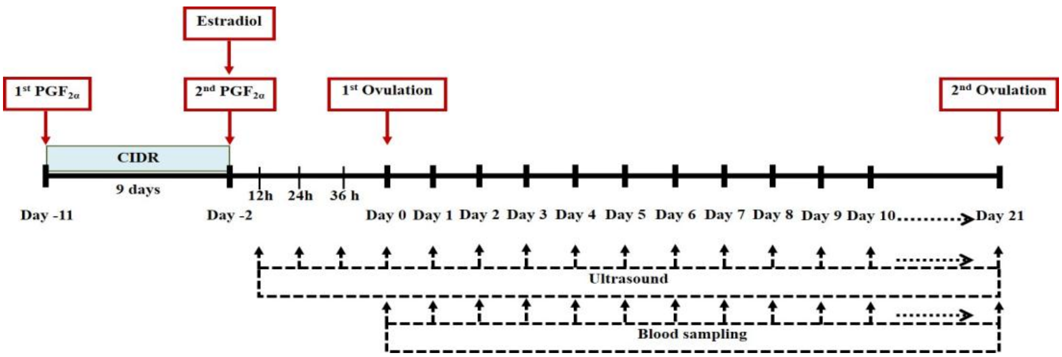

Fig. 1. Description of timing of hormonal injection, ultrasound, and blood sampling for White Lamphun cows. Abbreviations: CIDR, controlled internal drug release; $PGF_{2\alpha}$, prostaglandin $F_{2\alpha}$.

2.4 Statistical analysis

Data were analyzed with ANOVA using the general linear model (GLM) procedure of SAS (SAS Institute, Inc., Cary, NC, USA). The proportions of cows with appearance of different follicular wave patterns were analyzed using chi-square analysis [21]. The differences between the means (length of IOI, day of follicular wave emergence, duration of follicular wave, and DF, SF, CL as well as P_4 characteristics) were evaluated using the Student's *t-test* [21]. Differences in P-value $\leq$ 0.05 were considered significant, and a 0.05 < P-value < 0.10 was considered a tendency [22]. The information is presented as mean ± SEM. Simple linear correlations between the length of IOI, number of follicular wave, duration of follicular growth phase, and length of luteal phase were evaluated using PROC CORR of SAS.

3. Results and Discussion

3.1 Proportion of cows appearing 2 and 3 follicular waves and average length of IOI

At the end of hormonal protocol for ovulation synchronization, 4 of the cows were excluded from the ovarian follicular analysis due to anovulation. Thus, 16 of the ovulated cows were included to analyze follicular patterns. The numbers of ovulated White Lamphun cows having 2 follicular waves (2-wave cows) had greater (P<0.05) proportion than cows having 3 follicular waves (81.3% vs. 18.8%). The 2-wave cows tended to have a shorter (P=0.063) length of IOI than the 3-wave cows (19.8 ± 0.5 days vs. 22.7 ± 0.9 days).

The results of White Lamphun cows are consistent with the findings on patterns of ovarian follicular dynamics reported by Rhodes et al. [12] and Figueiredo et al. [13] who reported that a predominance of 2 ovarian follicular waves was 66.7% in Brahman heifers (*Bos indicus*) and 83.3% in Nelore (*Bos indicus*) cows. In *Bos taurus* beef cattle (Angus × Simmental and Hereford × Angus), most heifers and cows had 2 follicular waves during the estrous cycle before breeding [17]. Although the length of IOI in White Lamphun cows tended to be shorter in 2-wave patterns compared with 3-wave patterns, the average length of IOI decreased significantly in the 2-wave pattern of northeastern Thai indigenous (*Bos indicus*) heifers [12]. Investigations in Holstein (*Bos taurus*) heifers have shown that the length of IOI was longer in 3-wave patterns than 2-wave patterns (22.8 ± 0.6 days vs. 20.4 ± 0.3 days) [12]. On the one hand, in the comparisons between 2-wave and 3-wave patterns in beef cattle, Hereford-cross heifers with 2-wave patterns had a longer length of IOI than heifers with 3-wave patterns (22.5 ± 0.3 days vs. 19.8 ± 0.2 days) [23].

3.2 Ovarian follicular wave and DF characteristics of cows appearing 2 and 3 follicular waves

The ovarian follicular dynamic in White Lamphun cows was characterized by 2 follicular waves (2-wave cows; Fig. 2A) and 3 follicular waves (3-wave cows; Fig. 2B).

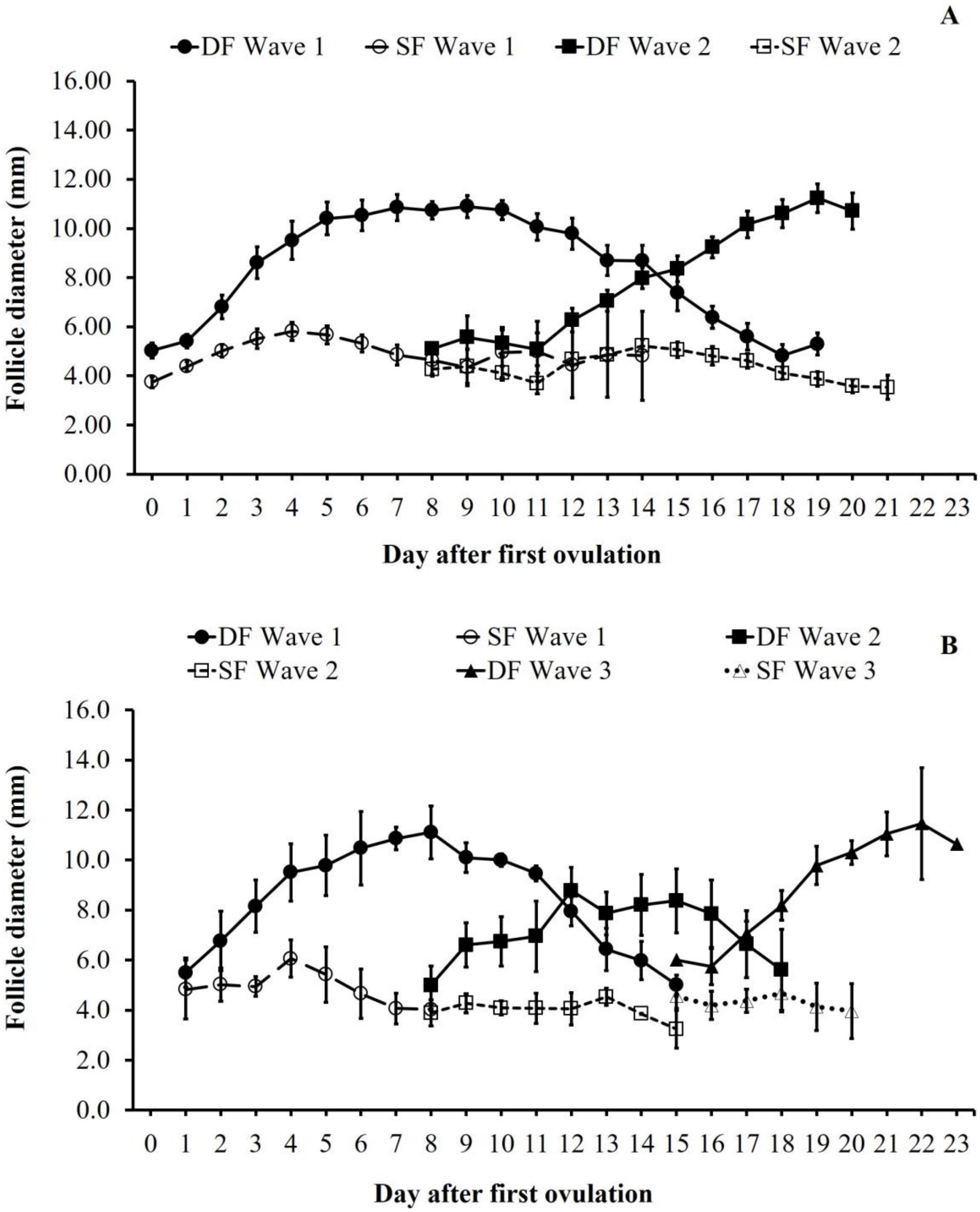

Fig. 2. Daily diameters of DF and SF in first wave (Wave 1) and second wave (Wave 2) of ovulated White Lamphun cattle appearing 2 follicular waves (2-wave cows; n=13) (A). Daily diameter of DF and SF in Wave 1, Wave 2, and third wave (Wave 3) of cows appearing 3 follicular waves (3-wave cows; n=3) (B). Abbreviations: DF, dominant follicle; SF, subordinate follicle.

The days of first wave (Wave 1) and second wave (Wave 2) emergences were not significant (P>0.05) between 2-wave cows and 3-wave cows (Table1). There was no significant difference (P>0.05) in durations of Wave 1 and Wave 2 between 2-wave cows and 3-wave cows (Table 1). The diameter of DF at wave emergence and the growth rates of DF in Wave 1 and Wave 2 did not differ (P>0.05) between 2-wave cows and 3-wave cows (Table 1). The maximum size of DF in Wave 1 did not differ (P>0.05); yet the maximum diameter of DF in Wave 2 tended to increase significantly (P=0.082) between 2-wave cows and 3-wave cows (Table 1). Day at maximum diameter of DF in Wave 1 tended to be longer (P=0.068) for 2-wave cows than 3-wave cows and the interval from the day of wave emergence to the day of maximum diameter of DF in Wave 2 was extended more (P<0.05) in 2-wave cows than 3-wave cows (Table 1). Duration of DF growth phase in Wave 1 was extended (P<0.05) in 2-wave cows compared with 3-wave cows (Table 1). Duration of DF growth phase in Wave 2 (P=0.066) and time at onset of DF atresia in Wave 1 (P=0.068) tended to be longer for 2-wave cows than 3-wave cows (Table 1). In Wave 1, there was no significant difference (P>0.05) in atretic rate and duration of atretic phase of DF between 2-wave cows and 3-wave cows (Table 1).

Table 1. Follicular wave and DF characteristics in first wave (Wave 1), second wave (Wave 2), and third wave (Wave 3) of White Lamphun cattle appearing 2 and 3 follicular waves (2-wave cows and 3-wave cows).

Follicular wave characteristics	Ovarian follicular wave								
	Wave 1			Wave 2			Wave 3		
	2-wave cows	3-wave cows	P	2-wave cows	3-wave cows	P	2-wave cows	3-wave cows	P
Day of wave emergence (day)	0.62 ± 0.37	1.00 ± 0.58	0.606	10.31 ± 0.41	9.00 ± 0.48	0.323	-	15.33 ±0 .33	-
Duration of wave (days)	16.23 ± 0.62	14.00 ± 1.53	0.281	8.54 ± 0.35	9.33 ± 1.20	0.584	-	6.33 ± 0.67	-
Diameter of DF at wave emergence (mm)	4.94 ± 0.24	4.77 ± 0.08	0.515	4.79 ± 0.20	4.92 ± 0.46	0.818	-	5.45 ± 0.56	-
Maximum diameter of DF (mm)	11.90 ± 0.51	11.42 ± 0.96	0.686	11.85 ± 0.32	8.84 ± 0.97	0.082	-	11.88 ± 0.93	-
Day at maximum diameter of DF (day)	8.77 ± 0.58	7.00 ± 0.58	0.068	18.69 ± 0.46	14.00 ± 1.00	0.026	-	21.33 ± 1.20	-
Growth rate of DF (mm/day)	0.96 ± 0.14	1.12 ± 0.17	0.503	0.86 ± 0.06	0.80 ± 0.05	0.526	-	1.11 ± 0.12	-
Duration of DF growth phase (days)	8.08 ± 0.66	6.00 ± 0.58	0.045	8.46 ± 0.31	5.00 ± 1.00	0.066	-	6.67 ± 0.33	-
Onset of DF atresia (day)	9.77 ± 0.58	8.00 ± 0.58	0.068	-	15.00 ± 0.48	-	-	-	-
Atretic rate of DF (mm/day)	-0.87 ± 0.10	-0.94 ± 0.21	0.778	-	-0.98 ± 0.28	-	-	-	-
Duration of DF atretic phase (days)	7.15 ± 0.70	7.00 ± 1.73	0.940	-	3.33 ± 0.88	-	-	-	-

Abbreviation: DF, dominant follicle

The results of the present study elucidate follicular dynamics in White Lamphun cows, in which prolonged duration of DF growth phase in Wave 1 is observed more often in 2-wave cows than in 3-wave cows. Although concentration and frequency of the luteinizing hormone (LH) were not evaluated in this experiment, Stock et al. [24], Savio et al. [25] and Ireland et al. [26] stated that a high frequency of LH pulses is necessary during the early luteal phase of the estrous cycle to maintain the life span of DF [26]. Investigations in cattle have indicated that the growth phase of DF is associated with a high frequency of LH pulses [27,28] and the life span of DF is extended by an increase in frequency of LH pulses [28-30]. Presumably, prolonged duration of DF growth phase may be due to a high frequency of LH pulses during development of Wave 1 in White Lamphun cows that have 2 follicular waves and may explain the delayed emergence of the following wave in 2-wave cows. Although there were no statistically significant differences in the onset of DF atresia in Wave 1, delay in the onset of DF atresia in Wave 1 appeared in 2-wave heifers and was related to a following delay in the day at DF maximum diameter in Wave 2, and early onset of CL atresia [24].

3.3 Luteal characteristics and P_4 concentrations of cows that have 2 and 3 follicular waves

The luteal phase of White Lamphun cows that have 2 follicular waves had shorter ($P<0.05$) length compared with cows with 3 follicular waves (Table 2). The maximum diameter of CL in 2-wave cows had greater size ($P=0.05$) than in 3-wave cows (Table 2). The growth rate of CL was significantly greater ($P<0.05$) in 2-wave cows than in 3-wave cows (Table 2). The 2-wave cows tended to have a shorter day at maximum diameter of CL ($P=0.052$) and day at onset of CL atresia ($P=0.052$) than the 3-wave cows (Table 2). The 2-wave cows and the 3-wave cows had similar ($P>0.05$) durations of CL growth phase and atretic phase as well as atretic rate of CL (Table 2).

At the end of DF growth phase in Wave 1, the concentration of plasma P_4 was higher ($P<0.05$) in 2-wave cows compared with 3-wave cows (Table 2). The concentration of plasma P_4 at the end of DF growth phase in Wave 2 was greater ($P<0.05$) in 3-wave cows compared with 2-wave cows (Table 2). However, the maximum concentration of P_4, day at maximum concentration of P_4, and day at concentration of P_4 <1.0 ng/ml did not differ ($P>0.05$) between the two groups (Table 2).

These results from White Lamphun cows are consistent with the ovarian follicular dynamics and luteal dynamics during the IOI in *Bos indicus* and *Bos taurus* reported by Chasombat et al. [10], Ginther et al. [19], Taylor and Rajamahendran [20], and Townson et al. [5]; who stated that the short lifespan of CL was observed in cattle with the 2-wave pattern. In the comparisons between 2-wave and 3-wave cows, it seems that the extension of CL lifespan by 2.8 days caused an increase in appearance of 3 follicular waves, as observed in this study. As described, the enlargement of the length of CL by 2 to 3 days resulted in atresia of DF in Wave 2 and subsequent emergence of Wave 3 [5]. As proposed in the bovine valuable model to explain the hormonal controlling the time of CL regression (luteolysis), Araujo et al. [6] indicated that estradiol and oxytocin, as well their receptors, directly control the lifespan of CL by regulation of exogenous $PGF_{2\alpha}$ from the uterus, in which $PGF_{2\alpha}$ stimulates the regression of CL. At the onset of luteolysis, estradiol (from DF of Wave 2) of 2-wave pattern increases its concentration and high estradiol binding to uterine estradiol receptor can result in stimulation of synthesis of uterine oxytocin receptor, which results in an increase in oxytocin-induced secretion of uterine $PGF_{2\alpha}$ [6,31-33]. In the present study, plasma concentration of P_4 was low at the end of DF growth phase in Wave 2 of 2-wave cows (0.24 ng/ml); however, circulating P_4 concentration at the end of DF growth phase in Wave 2 was still higher than 1.0 ng/ml in 3-wave cows. Based on this P_4 concentration of Wave 2, it is strongly implied that the short-lived CL was present in White Lamphun cows with the 2-wave pattern.

As resulted in this study of White Lamphun cows, the average concentration of plasma P_4 was approximately 1.19 ng/ml at the end of DF growth phase in Wave 1 and prolonged duration of DF growth phase (approximately 8.08 days) was found in Wave 1 of 2-wave cows. We may therefore speculate that extended duration of DF growth phase in Wave 1 under sub-luteal concentration of P_4 and shortened lifespan of CL are the major reasons for the appearance of a 2-wave pattern in White Lamphun cows. On the ovarian mechanism, the DF appearance at the initiation of sub-luteal level of P_4 proceeds to grow and an increase in secretion of estradiol from follicular cells [34-38]. Investigation in the heifer model receiving exogenous P_4 administration found that sub-luteal concentrations (1.0 to 2.0 ng/ml) of blood P_4 stimulate an increase in the frequency of LH pulses and subsequent extended growth of DF [38]. On the other hand, in the comparisons between 2-wave and 3-wave cows in this experiment, it seems that insufficient P_4 (approximately 0.66 ng/ml) to suppress the frequency of LH pulses during Wave 1 may be the cause of DF regression in 3-wave cows. As stated earlier, Abreu et al. [39] reported that 3-wave cows have a lower concentration of P_4 during late follicular growth.

3.4 The linear correlation among the length of IOI, number of ovarian follicular wave, duration of DF growth phase, and lifespan of CL

The length of IOI was positively correlated with number of follicular waves ($r=0.590$, $P<0.05$) (Fig. 3A) and length of the luteal phase ($r=0.704$, $P<0.01$) (Fig. 3B); however, there was a negative correlation between the length of IOI and duration of DF growth phase in Wave 1 ($r=-0.596$, $P<0.05$) (Fig. 3C). The number of follicular waves demonstrated a significant positive correlation with length of luteal phase ($r=0.558$, $P<0.05$) (Fig. 3D). However, the number of follicular wave did not correlate ($P>0.05$) with duration of DF growth phase in Wave 1 (Fig. 3E). There was no correlation ($P>0.05$) between duration of DF growth phase and length of luteal phase (Fig. 3F).

Our findings are in agreement with a previous study on Brahman heifers (*Bos indicus*), which showed that the length of IOI increased linearly with the number of follicular waves [12] . In agreement with previous studies, the average length of IOI greatly corresponds to the length of luteal phase [5,7,19,20] and the number of ovarian follicular waves [3,12,40,41] in cattle. For this reason, it is strongly implied that the number of follicular waves and the lifespan of CL are directly related to the length of IOI in White Lamphun cows. Interestingly, in White Lamphun cows, there was an inverse correlation between the length of IOI and the duration of DF growth phase in Wave 1. In accordance with Jaiswal et al. [3] and Jaiswal [41], one of the main factors to regulate the length of IOI is the growth period of DF in Wave 1. Taken together, it seems that the extended growth phase of DF in Wave 1 may also directly regulate the pattern of 2 follicular waves in White Lamphun cows.

Table 2. Luteal characteristics and P_4 concentrations of White Lamphun cattle appearing 2 and 3 follicular waves (2-wave cows and 3-wave cows).

Luteal characteristics and P_4 concentrations	Ovarian follicular wave		
	2-wave cows	3-wave cows	P
Length of the luteal phase (days)	15.85 ± 0.58	19.00 ± 0.58	0.007
Maximum diameter of CL (mm)	17.56 ± 0.53	16.25 ± 0.29	0.050
Days at maximum diameter of CL (day)	8.77 ± 0.83	11.67 ± 0.88	0.052
Growth rate of CL (mm/day)	1.37 ± 0.17	0.83 ± 0.08	0.011
Duration of CL growth phase (days)	6.15 ± 0.93	8.33 ± 0.88	0.130
Atretic rate of CL (mm/day)	-0.64 ± 0.09	-0.78 ± 0.14	0.442
Duration of CL atretic phase (days)	8.54 ± 0.92	9.67 ± 0.67	0.344
Onset of CL atresia (day)	9.77 ± 0.83	12.67 ± 0.88	0.052
Maximum concentration of P_4 during the IOI (ng/ml)	1.90 ± 0.23	1.84 ± 0.20	0.866
Days at maximum concentration of P_4 during the IOI (day)	12.46 ± 0.45	13.00 ± 1.00	0.659
Days at concentration of $P_4 < 1.0$ ng/ml (day)	14.92 ± 0.42	15.00 ± 0.58	0.919
Concentration of P_4 at the end of DF growth phase in first follicular wave (Wave 1) (ng/ml)	1.19 ± 0.06	0.66 ± 0.14	0.038
Concentration of P_4 at the end of DF growth phase in second follicular wave (Wave 2) (ng/ml)	0.24 ± 0.04	1.09 ± 0.16	0.030
Concentration of P_4 at the end of DF growth phase in third follicular wave (Wave 3) (ng/ml)	-	0.13 ± 0.06	-

Abbreviations: CL, corpus luteum; DF, dominant follicle; IOI, interovulatory interval; P_4, progesterone

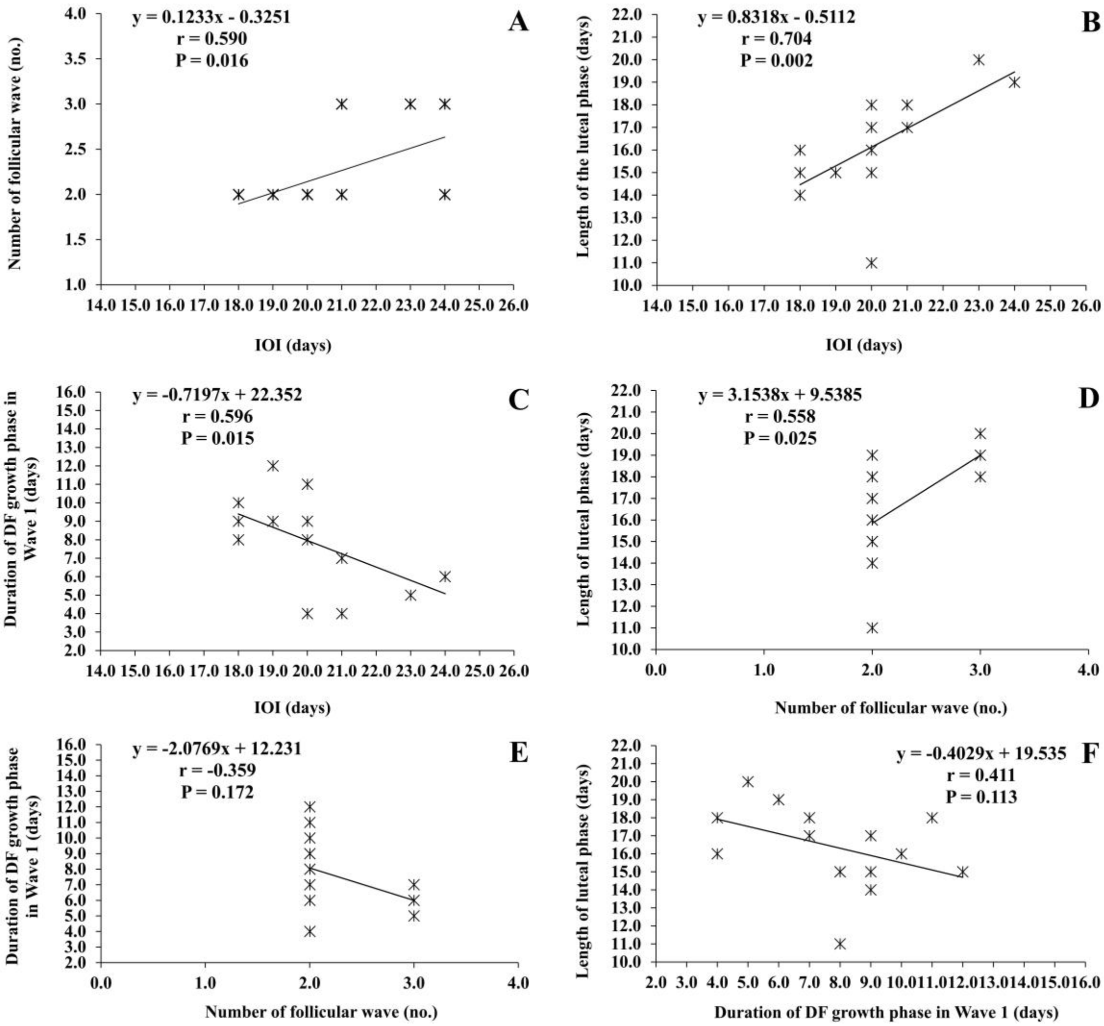

Fig. 3. The linear correlation among the length of IOI, number of ovarian follicular wave, duration of DF growth phase in first follicular wave (Wave 1), and length of luteal phase in 2-wave cows and 3-wave cows (n=16). Abbreviations: DF, dominant follicle; IOI, interovulatory interval.

4. Conclusion

The data highlight that differences between White Lamphun cows having 2 and 3 follicular waves can be partially explained by differences in the length of IOI and duration of DF growth phase in Wave 1, as well as lifespan of CL. It appears that the short length of IOI in White Lamphun cows with the 2-wave pattern is due to the extended duration of DF growth phase in Wave 1 and short lifespan of CL. Furthermore, the data emphasize that the length of IOI increased linearly with high numbers of follicular waves and extended length of luteal phase, but decreased linearly with prolonged duration of DF growth phase in Wave 1.

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