Endocrine changes during pregnancy, parturition and the early post-partum period in the llama (*Lama glama*)*

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Summary. Mean ($\pm$ s.d.) pregnancy length for the 14 llamas in this study was 350 ± 4.5 days. Plasma progesterone concentrations increased by 5 days after mating and remained elevated (>2.0 ng/ml) throughout most of pregnancy. At about 2 weeks before parturition, plasma progesterone concentrations began to decline, dropped markedly during the final 24 h before parturition, and returned to basal concentrations (<0.5 ng/ml) by the day of parturition. The combined oestrone + oestradiol-17 β and oestradiol-17 β concentrations varied between 6 and 274 pg/ml and 4 and 114 pg/ml, respectively, during the first 9 months of pregnancy. Concentrations increased between 9 months after mating and the end of pregnancy with peak mean concentrations of 827 ± 58 (s.e.m.) pg oestrone + oestradiol-17 β /ml (range: 64–1658) and 196 ± 10 pg oestradiol-17 β /ml (31–294) during the last week of pregnancy. Concentrations then declined to 87 ± 14 pg oestrone + oestradiol-17 β /ml (7–488) and 25 ± 5 pg oestradiol-17 β /ml (2.5–142) during the first week *post partum*. Plasma cortisol concentrations varied between 2.6 and 51.9 ng/ml (14.0 ± 0.5) from mating until 2 weeks before parturition when the concentrations began to decline. Only a slight increase in plasma cortisol concentrations was observed in association with parturition. Plasma triiodothyronine concentrations varied between 0.5 and 4.5 ng/ml (1.9 ± 0.1) throughout pregnancy and the periparturient period. Plasma thyroxine concentrations varied between 21.3 and 91.5 ng/ml (56.5 ± 0.8) from mating until about 39 weeks of pregnancy when they began to decline, from 43.0 ± 5.3 ng/ml at 15 days *pre partum* to 23.5 ± 5.5 ng/ml immediately before parturition, but then increased to 52.8 ± 3.9 ng/ml by 1 day *post partum*.

Keywords: llama; pregnancy; *post partum*; progesterone; oestrogen; parturition

Introduction

The hormonal changes associated with pregnancy, parturition and the post-partum period in the llama (*Lama glama*) are poorly defined. A detailed understanding of the normal hormonal changes observed during these periods will allow better management, treatment, or prevention of fertility problems in this species.

The endocrine changes occurring during pregnancy, parturition, and the early post-partum period have been studied in numerous species (Wagner *et al.*, 1974; Bazer & First, 1983). A decline in serum progesterone concentration before parturition occurs in the cow (Fairclough *et al.*, 1975a; Hunter *et al.*, 1977), ewe (Chamley *et al.*, 1973; Thompson & Wagner, 1974), pig (Molokwu & Wagner, 1973; Robertson & King, 1974), goat (Thorburn *et al.*, 1972), and dromedary camel, a

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species phylogenetically related to the llama (Elias *et al.*, 1984b). In contrast, progesterone concentrations in women and other primates decline during or shortly after parturition (Llauro *et al.*, 1968; Csapo *et al.*, 1971). A rise in glucocorticoid concentrations preceding parturition has been reported in the cow (Adams & Wagner, 1970; Smith *et al.*, 1973), ewe (Thompson, 1973; Thompson & Wagner, 1974), and pig (Ash & Heap, 1975; First & Bosc, 1979). Total serum oestrogen and oestradiol-17 β concentrations have been observed to increase in several species before parturition (Bedford *et al.*, 1972), including the cow (Stabenfeldt *et al.*, 1970; Peterson *et al.*, 1975; Hoffman *et al.*, 1977), ewe (Bedford *et al.*, 1972; Thompson, 1973), and pig (Wagner & Oxenrider, 1971; Guthrie *et al.*, 1972; Molokwu & Wagner, 1973). Elias *et al.* (1984b) and Agarwal *et al.* (1987) reported a similar increase in oestrogen concentrations in the camel 2 days before parturition. Soliman *et al.* (1963) suggested that thyroid hormones increased during late pregnancy in the cow, while Heshmat *et al.* (1984) reported that plasma triiodothyronine and thyroxine concentrations in the dromedary camel increased throughout pregnancy.

The purpose of this study was to characterize the changes in plasma progesterone, triiodothyronine, thyroxine and cortisol, and serum oestradiol-17 β and total oestrogen concentrations during pregnancy, parturition and the early post-partum period in the llama.

Materials and Methods

Animals. Fourteen 4–8-year-old, multiparous, healthy, female (136–150 kg body weight) and 3 intact male (5–12 years of age) llamas from a commercial herd in the Willamette Valley of Oregon were used in the study. Animals were fed a combination of grass hay and allowed free access to pasture. Trace-mineral salt mix and water were available *ad libitum*. Following breeding practices used by the farm operator, the animals were mated twice at 6-h intervals to 1 of the 3 males. The males were separated from the females for the remainder of the study. The day of mating was designated Day 0.

Blood sampling. Blood samples were collected from mid-July 1987 to August 1988. Samples were collected every other day for the first 30 days after mating and then at 7-day intervals between 30 and 60 days of pregnancy. Starting 60 days after mating, samples were collected at monthly intervals until the end of the 10th month of pregnancy; one sample was collected at 10.5 months, and then 3 times per week until 1 week *post partum*. Animals that failed to conceive as determined by serum progesterone determinations and the birth of a live offspring were not included in the study. Blood was collected into evacuated serum and EDTA tubes (Becton-Dickinson, Rutherford, NJ, USA) by puncture of the internal jugular vein. The EDTA samples were placed on ice and centrifuged within 2 h of collection. Plasma was stored at -20°C until analysed. Serum samples were allowed to clot at room temperature for 30 min, centrifuged, and the serum stored at -20°C until analysed.

Progesterone assay. The direct-reading solid-phase assay (Diagnostic Products Corporation, Los Angeles, CA, USA) was validated for use in the llama by evaluating recoveries following the addition of known amounts of progesterone to llama samples. After addition of 0.5, 2.0 and 10.0 ng progesterone to a llama plasma pool containing <0.5 ng progesterone/ml, mean recoveries were $92.0\% \pm 2.0\%$, $99.0\% \pm 14.0\%$ and $105.0\% \pm 7.0\%$, respectively. After addition of 50, 100 and 200 μl llama plasma pooled from 3 samples, progesterone concentrations of 1.3 ± 0.2 , 2.1 ± 0.1 , 3.9 ± 1.6 ng/ml, respectively, were measured. All assays were conducted using a sample volume of 100 μl plasma using incubation times and protocols outlined by the manufacturer. Parallelism between the log-logit plotted standard curve and the variable added volumes of llama plasma was evaluated by comparison of regression slopes using a Student's *t* test. The slopes did not differ ($P > 0.05$). Reported antibody cross-reactivity was 100% with progesterone, 2.0% with 20 α -dihydroprogesterone, 1.7% with 11-deoxycorticosterone, 2.4% with 11-deoxycortisol, and 1.3% with 5 β -pregnan-3,20-dione. All other tested steroids had <1.0% cross-reactivity. Samples were run in a total of 17 assays with intra- and interassay coefficients of variation of 6% and 16%, respectively. The assay sensitivity was 0.1 ng/ml and represented approximately 91% binding relative to the B_0 tubes.

Cortisol assay. The solid-phase commercial assay (Diagnostic Products Corporation) was validated for use in the llama by evaluating recoveries following the addition of cortisol to llama plasma samples. After addition of 4.0, 8.0 and 40.0 ng cortisol/ml to llama plasma containing <5 ng cortisol/ml, mean recoveries were $99.0\% \pm 1.0$, $104.0\% \pm 0.6$ and $90.0\% \pm 2.0$, respectively. After addition of 25, 50 and 100 μl llama plasma pooled from 3 samples, cortisol concentrations of 26.0 ± 3.0 , 48.0 ± 4.0 , and 94.0 ± 2.0 ng/ml, respectively, were measured. All assays were conducted using a sample volume of 50 μl . Parallelism between the log-logit plotted standard curve and the variable added volumes of llama plasma was evaluated as previously outlined. The slopes of the regression lines did not differ ($P < 0.05$). Reported antibody cross-reactivity was 100% with cortisol, 1.4% with corticosterone, 0.25% with deoxycortisol and 1.5% with 11-deoxycorticosterone. All other tested endogenous steroids had <0.1% cross-reactivity. The assay was run under conditions specified by the manufacturer. Samples were run in a total of 9 assays with an

intra- and interassay coefficients of variation of 9% and 10%, respectively. The assay sensitivity was 5 ng/ml and represented approximately 84% binding relative to the B_0 tubes.

Assays for oestradiol-17 β and oestrone + oestradiol-17 β . Serum oestradiol-17 β and combined oestrone + oestradiol-17 β concentrations were measured using commercial radioimmunoassay kits (Radioassay Systems Laboratories, Carson, CA, USA) validated for use in the llama. Before measurement by RIA, samples were extracted by mixing 800 μ l serum with 8 ml of a ethyl acetate:hexane (3:2, v:v) mixture. The mixture was vortex-mixed, and the organic phase containing the conjugated oestrogens removed by aspiration. The aqueous phase was dried under nitrogen at 40°C, and reconstituted with 2.4 ml assay buffer (0.1 M-phosphate-buffered saline with gelatin, pH 7.9) before overnight storage at 4°C. Each assay tube contained 0.5 ml of the diluted sample, 0.1 ml 125 I-labelled oestrogen-17 β and 0.1 ml of either anti-oestrone + oestradiol-17 β or anti-oestradiol-17 β antiserum (depending on the assay). After incubation for 90 min at room temperature, 400 μ l anti-rabbit-IgG in 3% polyethylene glycol were added and incubated for an additional 60 min at room temperature. The samples were centrifuged at 1500 g for 30 min, the supernatant was decanted and the tubes dried and counted in a gamma counter equipped with automated data-reduction facilities (Cobra, Packard Instrument Corporation, Chicago, IL, USA). In initial studies, extraction efficiency was evaluated by adding trace amounts of [3 H]oestradiol-17 β to serum and measuring the activity following the extraction procedure. Due to the high and consistent recoveries ($91 \pm 3\%$), assay values were not corrected for extraction efficiency. Serum blank values were subtracted from assayed samples. The minimum detectable oestradiol-17 β and oestrone + oestradiol-17 β concentrations for both assays were 2.5 pg/ml and represented approximately 80 and 88% binding, respectively, relative to the B_0 tubes.

Oestrone + oestradiol-17 β assay. The assay was validated for use in the llama by evaluating recoveries following the addition of known amounts of oestradiol-17 β to llama samples. Following the addition of 50, 100 and 200 pg oestradiol-17 β /ml to llama serum containing 83 pg total oestrogen/ml mean recoveries were $96.0 \pm 10.0\%$, $88.2 \pm 19.0\%$ and $94.0 \pm 13.0\%$, respectively. After addition of 250, 500 and 1000 μ l serum pooled from 3 animals, total concentrations of 45 ± 4 , 76 ± 12 and 139 ± 12 pg/ml, respectively, were measured. The slope of the regression lines fitted to the standard curve and the added volumes of llama serum did not differ ($P > 0.05$). Reported antibody cross-reactivity was 100% with oestradiol-17 β , 9% with oestriol, 7% with oestradiol-17 α , and 100% with oestrone. All other tested treated steroids had $<0.01\%$ cross-reactivity. All assays were conducted using a sample volume of 800 μ l. Samples for total oestrogen were run in a total of 10 assays with intra- and interassay coefficients of variation of 6% and 14%, respectively.

Oestradiol-17 β assay. The assay was validated for use in the llama by evaluating recoveries after spiking of unknown llama samples. Following the addition of 50, 100 and 200 pg oestradiol-17 β /ml to pooled llama serum containing 24 pg oestradiol-17 β /ml, mean recoveries were $102.0 \pm 14\%$, $96.0 \pm 19\%$ and $95.0 \pm 9.0\%$, respectively. After addition of 250, 500 and 1000 μ l of serum pooled from 3 animals, oestradiol-17 β concentrations of 29 ± 4 , 60 ± 11 and 113 ± 11 pg/ml, respectively, were measured. The slope of the regression lines fitted to the standard curve and the added volume of llama serum did not differ ($P > 0.05$). Reported antibody cross-reactivity was 100% with oestradiol-17 β , 6.5% with oestriol, 5.2% with oestradiol-17 α , 0.55% with oestrone, and 0.38% with equilin. All other tested steroids had $<0.01\%$ cross-reactivity. All assays were conducted using a sample volume of 800 μ l. Samples were run in a total of 10 assays with intra- and interassay coefficients of variation of 5% and 16%, respectively.

Triiodothyronine and thyroxine assays. The direct-reading solid-phase assays (Diagnostic Products Corporation, Los Angeles, CA, USA) have been previously validated for use in the llama (Smith *et al.*, 1989). The sensitivities for the assays were 0.2 ng/ml triiodothyronine and 10 ng thyroxine/ml. Binding at these concentrations represented approximately 83% binding relative to the B_0 tubes for both assays. Samples were run in a total of 5 assays with intra- and interassay coefficients of 4.5%, 9.1% and 6.0%, 8.9% for the triiodothyronine and thyroxine assays, respectively.

Statistical procedures. Hormone concentrations and variance are reported as the mean and the standard error of the mean (s.e.m.), respectively. Temporal changes in hormone concentrations during the last 2 weeks of pregnancy were evaluated by fitting a linear regression to the data. The null hypothesis that the regression slope was equal to 0 was tested using a Student's *t* test. The data collected between Days 1 and 7 *post partum* were tested in the same manner. Analysis of the data was performed using the Statistical Applications System (SAS) program (version 6.0) running on a microcomputer.

Results

The 14 animals in the study had a pregnancy of 350 ± 4.5 days (standard deviation) (range: 346–359 days). All animals had normal unassisted deliveries.

Changes in plasma progesterone, serum oestradiol-17 β and combined oestrone + oestradiol-17 β concentrations during the first 35 days after conception are shown in Fig. 1. Mean progesterone, oestradiol-17 β , combined oestrone + oestradiol-17 β , triiodothyronine, thyroxine and cortisol concentrations from conception until 1 week *post partum* are shown in Fig. 2. To facilitate visualization of the data during periods of frequent sampling, data from samples collected within a 7-day period

were pooled (mean = 18; range: 5–37 samples/datum point). Due to the variability in the length of pregnancy, the changes in hormone concentrations from individual animals were more pronounced than indicated in Fig. 2. To examine more clearly the endocrine changes associated with parturition, the day of parturition for each animal was defined as Day 0. Hormone concentrations for the 15 days before parturition and the first 7 days *post partum* are shown in Fig. 3, plotted relative to the day of parturition. Each datum point represents a mean of 6 observations (range: 3–11 samples/datum point).

Fig. 1. Mean ($\pm$ s.e.m.) plasma progesterone, and serum oestradiol-17 β , and combined oestrone + oestradiol-17 β concentrations from Day 0 (day of mating) to Day 35 of pregnancy in the llama (N = 14).

Plasma progesterone concentrations increased by 5 days after mating (Fig. 1) and remained > 2.0 ng/ml until 15 days before parturition (Fig. 3). Between 15 and 1 days *pre partum*, progesterone concentrations declined significantly ($P < 0.001$) from a mean concentration of 3.8 ± 0.8 to 1.4 ± 0.2 ng/ml. Between Day 1 *pre partum* and the day of parturition, progesterone concentrations further declined to 0.4 ± 0.1 ng/ml. During the first week post-partum progesterone concentrations remained low (< 0.5 ng/ml) and did not change significantly ($P > 0.05$).

Plasma cortisol concentration remained relatively constant (14.0 ± 9.0 ng/ml) through most of pregnancy. Cortisol concentration increased slightly (26.0 ± 4.1 ng/ml) at Week 45 of pregnancy and then declined to earlier concentrations. Between 15 and 1 days *pre partum*, cortisol concentration decreased significantly ($P < 0.01$) from a mean concentration of 18.7 ± 5.1 to 11.7 ± 2.3 ng/ml. There was a slight but non-significant increase in cortisol concentrations on the day of parturition. Cortisol concentration did not change significantly with time during the post-parturient period ($P > 0.05$).

Fig. 2. Mean ($\pm$ s.e.m.) plasma progesterone, cortisol, triiodothyronine and thyroxine and serum oestradiol-17 β and combined oestrone + oestradiol-17 β concentrations between mating and parturition in the llama (N = 14).

Combined oestrone + oestradiol-17 β concentrations remained relatively constant (67.0 ± 5.0 pg/ml) from mating until 36 weeks of pregnancy, then increased, and reached peak concentrations of 827.0 ± 58.0 pg/ml at 49 weeks after mating. The combined oestrone + oestradiol-17 β concentrations remained elevated during the 2 weeks *pre partum* until 24 h *pre partum* when they declined significantly ($P < 0.05$) to 171.0 ± 87.0 pg/ml at parturition. The concentrations of oestrone + oestradiol-17 β after parturition remained stable at 76.0 ± 11.0 pg/ml during the first week *post partum* ($P > 0.05$).

Serum oestradiol-17 β concentrations were also reasonably constant (18.0 ± 21.0 pg/ml) from mating until about Week 37 of pregnancy, then increased to a maximum concentration of 196.0 ± 10.0 pg/ml at Week 48 after mating. No significant changes ($P > 0.05$) were observed during the 2 weeks *pre partum* until the day of parturition when oestradiol-17 β concentrations declined rapidly to 42.0 ± 26.0 pg/ml on the day of parturition. During the next 7 days, concentrations remained low (25.4 ± 4.9 pg/ml) and did not vary significantly ($P > 0.05$).

Plasma triiodothyronine concentrations averaged 1.9 ± 0.9 ng/ml (0.5–4.4 ng/ml) between mating and parturition. No significant changes ($P > 0.05$) were observed during pregnancy or the periparturient period. Thyroxine concentrations did not vary substantially until Week 41 of pregnancy (58.1 ± 0.9 ng/ml) (21.3–91.5), then declined ($P < 0.02$) to a minimum concentration of 24.0 ± 5.0 ng/ml 1 day before parturition. Starting 1 day *pre partum*, thyroxine concentrations then increased again to 53.0 ± 4.0 ng/ml by 1 day *post partum*. The thyroxine concentration did not vary significantly ($P > 0.05$) during the first week *post partum*.

Fig. 3. Mean ($\pm$ s.e.m.) plasma progesterone, cortisol, triiodothyronine and thyroxine and serum oestradiol-17 β and combined oestrone + oestradiol-17 β concentrations from 15 days before to 7 days after parturition in the llama ($N = 14$). Day 0 (broken vertical line) was the day of parturition.

Discussion

Plasma progesterone concentrations in the llama were significantly elevated by 5 days after mating and remained high during pregnancy. The mean progesterone concentrations (3.0–4.5 ng/ml) were similar to those reported for many other species during the same stage of pregnancy. Progesterone concentrations during the first month after mating have been reported to vary between 6 and 12 ng/ml in the pig (Killian *et al.*, 1973; Ash & Heap, 1975), 2 and 10 ng/ml in the cow (Pope *et al.*, 1969; Evans & Wagner, 1976), 2 and 3 ng/ml in the ewe (Basset *et al.*, 1969), and 3 and 7 ng/ml (Elias *et al.*, 1984b; Agarwal *et al.*, 1987) in the dromedary camel.

Progesterone concentrations in the llama declined slightly between 18 and 27 weeks of pregnancy. A similar transitory decline in progesterone concentrations has been observed in the dromedary camel at 21 weeks of pregnancy (Elias *et al.*, 1984b). The physiological significance of this observation is unknown, as the role of the placenta in steroidogenesis in the llama has not been elucidated. The regulatory mechanism(s) associated with the gradual decline in progesterone concentrations during the 2 weeks before parturition is also unknown. A similar pre-partum decline has been observed in the dromedary camel, although the time course of the decline is different. In the camel, progesterone production has been reported to decline starting at 5 months of pregnancy (Elias *et al.*, 1984b). The final decline in plasma progesterone concentrations began 24–48 h pre

partum, temporal changes similar to those reported in some other species (Bassett *et al.*, 1969; Pope *et al.*, 1969; Stabenfeldt *et al.*, 1972; Chamley *et al.*, 1973; Smith *et al.*, 1973; Challis *et al.*, 1974; Robertson & King, 1974; Ash & Heap, 1975; Baldwin & Stabenfeldt, 1975; Fairclough *et al.*, 1975b; Hunter *et al.*, 1977).

Alpacas have substantial serum concentrations of 20 α -dihydroprogesterone in addition to progesterone (Fernandez-Baca *et al.*, 1970). Due to the low cross-reactivity of the primary antiserum for 20 α -dihydroprogesterone (2.0%), changes in serum concentrations of 20 α -dihydroprogesterone during pregnancy could not be evaluated. The physiological importance, if any, of this progesterone metabolite in the llama is unknown.

Substantial changes in cortisol concentration during pregnancy and parturition have been previously reported for many domestic species including the cow, ewe, pig and goat (Adams & Wagner, 1970; Chamley *et al.*, 1973; Smith *et al.*, 1973; Thompson & Wagner, 1974; Baldwin & Stabenfeldt, 1975; Hunter *et al.*, 1977). Scott *et al.* (1984), working with the rhesus macaque, reported similar stable cortisol concentration in the maternal circulatory system before and during parturition. The llama may be similar to the rhesus monkey exhibiting only minor changes in cortisol concentrations during the periparturient period. This is in contrast to work in the ewe, sow and cow in which substantial increases in maternal corticosteroid concentrations occurred before parturition (Adams & Wagner, 1970; Chamley *et al.*, 1973; Killian *et al.*, 1973; Molokwu & Wagner, 1973; Smith *et al.*, 1973). One possible explanation for the absence of a dramatic periparturient increase in glucocorticoid concentrations in the llama may have been the relatively low sampling frequency during this period (3 samples per week). A periparturient increase in cortisol could easily have been missed. There is no obvious explanation for the decline in mean glucocorticoid concentrations observed during the 2 weeks immediately *pre partum*.

Changes in serum oestrone and oestradiol-17 β concentrations reported in this study are similar to those reported for the pig (Guthrie *et al.*, 1972; Molokwu & Wagner, 1973), cow (Henricks *et al.*, 1972), and ewe (Chamley *et al.*, 1973). Oestrogen concentrations have previously been reported to increase during pregnancy in other camelids. Agarwal *et al.* (1987), working with dromedary camels, reported that oestradiol-17 β concentrations increased progressively during pregnancy from a basal concentration of 20 pg/ml at 2–3 months of pregnancy to about 450 pg/ml during the final stage of gestation. Elias *et al.* (1984a) reported that the oestradiol-17 β concentrations in the dromedary camel had increased dramatically from 338 pg/ml at 10 months of pregnancy to a peak of 606 pg/ml at Week 48 of pregnancy. In this study, a similar pattern for oestradiol-17 β concentrations occurred although the basal concentrations were lower, 10–46 pg/ml, during the majority of pregnancy before reaching a peak of 196 ± 10 pg/ml during the final third of pregnancy.

In camels, follicular development during early pregnancy has been reported by Elwishy *et al.* (1981) to occur in spite of the presence of the corpus luteum. High concentrations of oestrogen in allantoic fluid on the day of parturition have also been demonstrated, suggesting the placenta as a probable source of oestrogen (Elias *et al.*, 1984a). The rising concentrations of oestrogen during pregnancy in the llama may, therefore, be from either a follicular or placental origin.

Plasma triiodothyronine concentrations in the llama were relatively unchanged during the periparturient period, while thyroxine concentration decreased before parturition, and then increased to preparturient levels in the immediate post-partum period. The triiodothyronine concentrations were similar to those previously reported for pregnant llamas (Smith *et al.*, 1989), and thyroxine concentrations in this study (58.1 ± 0.9 ng/ml) were in the lower end of the range previously reported for pregnant llamas (Smith *et al.*, 1989). These concentrations are similar to those reported for the goat (Riis & Madsen, 1985). In the dromedary camel, triiodothyronine and thyroxine concentrations increased throughout pregnancy (Heshmat *et al.*, 1984), while thyroxine concentrations in the goat decreased 1–2 days before parturition (Riis & Madsen, 1985) perhaps as a result of nutrient redistribution to the mammary gland in preparation for lactation (Riis & Madsen, 1985). A similar explanation for the changes in thyroxine concentrations in the llama may be applicable.

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