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The effects of parity and litter size on bone metabolic activity in pregnant and lactating sows

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Abstract

During gestation and lactation, female mammals often mobilize endogenous nutrient reserves to meet the resource demands of offspring production. These mobilized stores include calcium, phosphorous and other minerals that are resorbed from maternal bone to facilitate rapid mineralization of offspring bones. The extent to which bone mineral is resorbed is governed by the total amount of mineral taken in from the diet, but also by the competing demands of offspring and the minimum level of bone density that a female must sustain to support self-maintenance. The maximum amount of bone that a female may mobilize is undoubtedly dependent a variety of maternal traits, including age and reproductive experience (i.e., parity). We evaluated changes in serum concentrations of biomarkers of metabolic activity (total deoxypyridinoline [tDPD] and osteocalcin [OC]) of maternal bone and its relationship to reproductive output and parity throughout pregnancy and lactation in Yorkshire sows. Litter size did not affect bone metabolism; however, serum concentrations of both tDPD and OC were significantly higher in sows with little or no reproductive experience when compared to sows that had produced at least 3 litters prior to the current reproductive bout. This suggests a shift in ability or physiological strategy to meet offspring mineral demands that is acquired or associated with reproductive experience.

KEYWORDS
bone formation, bone metabolism, bone resorption, parity, reproduction

1 | INTRODUCTION

The reproductive performance of a female is dependent, in part, on a key allocation decision—how much of a particular resource does she retain to maintain her own body condition and how much does she partition to processes that support and improve the condition of her young. In the case of many nutritional resources, the pool of resources from which a female draws may include exogenous sources and a female's somatic reserves (e.g., Jönsson, 1997; Stearns, 1992; Stephens, Boyd, McNamara, & Houston, 2009). Mobilizing somatic nutrients comes at a risk—if too much is mobilized, a female may reduce her ability to use that resource to support future reproductive events and her own survival (Clutton-Brock, 1984; Lack, 1947, 1948; Pontier, Gaillard, & Allaine, 1993; Stearns, 1992; Williams, 1966). Thus, how a female modulates this trade-off between self-maintenance and reproductive effort can play an important role in determining their lifetime reproductive success (Kirkwood & Rose, 1991).

While much of the work evaluating the trade-off between self-maintenance and reproduction has rightfully focused on energy, female vertebrates also trade-off minerals in bone. The production of vertebrate offspring requires a large investment of calcium and phosphorus to support the ossification of the fetal and neonate skeleton, with about 98% of the body's calcium and 80% of the body's phosphorous amassed in bone. Nearly all mammals studied to date mobilize skeletal mineral reserves and subsequently experience some degree of bone loss during reproduction (e.g., Brommage, 1989; Liesegang, Risteli, & Wanner, 2007; Ott, Lipkin, & Newell-Morris, 1999; Peng, Garner, Kusy, & Hirsch, 1988; Schmidt & Hood, 2014). For example, in a study on rats fed a nutritionally complete diet, 19% of the calcium in milk was derived from maternal bone and 96% the calcium that pups ingested from milk was deposited into the offspring skeletal (Brommage, 1989). While the safety factor (ratio of bone failure strain to maximum functional strain) associated with bone is sufficient to resist most conditions an animal experiences (Biewener, 1993), the more mineral that a female mobilizes from bone, the lower the safety factor becomes, and the greater the probability that a bone's capacity to resist strain will be exceeded and fracture.

How females balance the trade-off between maintaining the strength of their own skeleton and mobilizing mineral offspring skeletal development is likely to change in response to variety of intrinsic variables, including reproductive experience and demand. In general, young and/or reproductively inexperienced (e.g., primiparous) females are more likely to abandon their offspring or produce a smaller litter of lower quality young than multiparous females (e.g., Broussard, Dobson, & Murie, 2008) and can be less efficient at meeting the nutritional needs of their offspring (e.g., Kunkele, 2000; Lang, Iverson, & Bowen, 2011).

It follows that bone metabolic activity could also be impacted by maternal reproductive experience (Allali et al., 2007; Giesemann, Lewis, Miller, & Akhter, 1998). In both sheep and goats, bone loss during a female's second reproductive bout is less substantial than during the first, even though milk production is also greater in these experienced females (Liesegang et al., 2007). Women that produce and nurse twins or triplets lose more bone than those that have one child (Laskey et al., 1998), and female rats that produced large litters experienced greater bone loss than those that produced fewer offspring (Peng et al., 1988). Yet in another study, no difference in the bone mineral density of female rats that nursed either two or six pups has also been observed (Sengupta, Arshad, Sharma, Dubey, & Singh, 2005).

It has been shown that loss of bone mass and strength during reproduction is lower in fifth parity sows relative to primiparous sows despite the fact that primiparous sows have smaller, weaker and less mineralized bones than older more experienced sows (Giesemann et al., 1998). There is also some evidence that bone loss increases with litter size and parity, and that sows are likely trading-off skeletal condition for reproduction. Sows that produce larger litters (11–12 young) exhibit reduced metacarpal strength compared to those that produce smaller litters (6–7 young), as well as a decrease in rib and vertebra bone ash and femur thickness from first to second parity (Maxson & Mahan, 1986).

For sows that produce statistically similar litter sizes (ca. 13 young), primiparous sows generally exhibit higher bone deposition activity and lower bone resorptive activity over a reproductive bout than multiparous sows (2–11 prior reproductive events; van Riet et al., 2016). However, as with other mammals, primiparous and early parity sows tend to produce less offspring per birth (Edwards, 2002; Hughes, 1998; Smith, Stalder, Serenius, Baas, & Mabry, 2008).

Thus, when considering changes in reproductive output relative to reproductive experience within the context of bone mobilization and mineral allocation, it is feasible that efficiency of these functions may increase with parity in sows. As such, greater reproductive output should be associated with elevated bone metabolic activity, and reproductive experience (i.e., parity) should influence how sows accommodate mineral demands of developing offspring.

With this investigation, we predicted that bone mineral mobilization will be lowest in inexperienced sows. We also expected that females that produce larger litters will mobilize more mineral from bone to meet the demands of their growing offspring, but this will be less pronounced in both inexperienced and possibly older females because of greater constraints placed on females in each of these groups.

2 | MATERIALS AND METHODS

We collected serum samples from 15 Yorkshire sows bred and maintained at the Auburn University Swine Teaching and Research Facility (Auburn, AL, USA). Sow age ranged from 10.5 to 50 months, and parity ranged from 0 to 6 prior births. All husbandry and feeding practices described below were performed by staff at the facility following their standard protocols. All sows were bred with the same male within 3 days of each other (9–11 October, 2009). Sows were placed on restricted feed throughout gestation, and as sows consumed all available food, there was no difference between individuals with regard to food intake. During gestation, sows were fed a diet contained 13% protein, 4.5% fat, 0.72% calcium, 0.6% phosphorous, and provided approximately 3,230 kcal/kg metabolizable energy. During lactation, sows were provided food ad libitum, and feed a diet with 19% protein, 8.3% fat, 0.75% calcium, 0.63% phosphorus, and provided about 3,470 kcal/kg metabolizable energy. Food intake during lactation was recorded from parturition to weaning for each sow. Sows were weighed prior to breeding and after giving birth, and number and mass of live-born young was recorded at birth. Sows frequently produce stillborn young, and as mineral demands of lactation generally outweigh mineral transferred in utero, we only excluded data from sows that produced litters that contained less than 80% live-born young.

We drew approximately 1.0 mL of blood from a marginal ear vein, using a 22-gauge needle and a 3-mL syringe, and immediately transferred it to 4 mL glass serum collection tubes. Within 1 h of collection, we centrifuged blood for 10 minutes at 500 *g*, drew serum off of the sample and stored it at −80°C until analysis. We collected samples eight times over the course of one reproductive bout: one day prior to breeding (day 1), day 42, 84 and 98 of gestation (each ±5 days), the day of parturition, days 14 and 21 of lactation, and 3 days after weaning. We collected samples at approximately the same time of day (12:00–14:30) to control for diurnal fluctuations in the concentration of bone markers (Allen, 2003; Ladlow, Hoffmann, Breur, Richardson, & Allen, 2002). All procedures performed in this study were approved by the Auburn University Institutional Animal Care and Use Committee (protocol number: 2009-1595).

We measured serum concentrations in duplicate of two products of bone metabolism—total deoxypyridinoline (tDPD), a marker of bone resorption, and osteocalcin (OC), a marker of bone deposition. Concentrations of serum tDPD and OC were measured for each individual using commercially available ELISA kits (MicroVue Osteocalcin and MicroVue Total DPD, Quidel Corp., Santa Clara, CA, USA) following manufacturer's instructions.

For statistical analyses, we classified sows based on parity and live-born litter size. We categorized sows that had 0-2 previous reproductive events as "inexperienced" ($n = 5$), 3–4 as "intermediate" ($n = 5$) and 5–6 as "experienced" ($n = 5$). We categorized litters containing 2–10 live-born offspring as "small" ($n = 7$) and 11–16 as "large" ($n = 8$). There was also a positive correlation between live-born litter size and live-born litter mass at birth ($F_{1,11} = 49.97$, $p < 0.0001$); thus, only litter size was included in the models.

We measured the effect of sow parity and live-born litter size on serum concentrations of bone resorption and deposition markers over time, using a mixed model (PROC MIXED), with individual sow designated as a random effect, day as the repeated variable and using an autoregressive (AR1) covariance structure, which was selected based on AICC values and number of parameters included in the model. We tested the effects of litter size and parity on total food consumed per individual during lactation in an ANOVA (PROC GLM), and we used general linear models (PROC GLM) to assess if parity or sow mass influenced litter size, and if litter size influenced mass of individual offspring at birth. All analyses were conducted in SAS 9.1 (SAS Institute; Cary, NC, USA).

3 | RESULTS

Live-born litter size ranged from 2 to 16 piglets (10 ± 1 *SE*). Three sows produced litters that comprised of 33–58% live-born young; therefore, data for these females were excluded from analysis. The other 12 sows produced 92% ± 2 *SE* live-born young in their litters. Of those females included in this study, maternal age and parity were strongly correlated ($F_{1,61} = 266.26$, $R^2 = 0.816$, $p < 0.0001$). Neither parity nor maternal mass prior to breeding had an effect on number of live-born offspring produced ($F_{2,11} = 1.16$, $p = 0.356$; $F_{1,11} = 1.18$, $p = 0.301$ respectively). Neither parity nor litter size affected food intake during lactation ($F_{2,13} = 0.09$, $p = 0.915$; $F_{1,13} = 1.64$, $p = 0.236$, respectively), nor did they interact ($F_{2,13} = 1.02$, $p = 0.402$). The size of the litter at birth (excluding stillborns) did not affect the mass of individual young of that litter ($F_{1,11} = 0.18$, $p = 0.678$).

Osteocalcin concentrations changed significantly over the course of the reproductive bout ($F_{7,49} = 7.68$, $p < 0.0001$) while tDPD levels remained constant ($F_{7,47} = 0.85$, $p = 0.555$). Parity significantly affected OC and tDPD concentrations ($F_{2,49} = 20.61$, $p < 0.0001$; $F_{2,47} = 10.99$, $p = 0.0001$, respectively); inexperienced sows exhibited greater OC and tDPD concentrations than did intermediate and experienced sows (Figure 1). There was no significant interaction between day and parity or litter size for either OC or tDPD ($p \geq 0.062$ in all cases).

4 | DISCUSSION

Our results suggest that patterns of bone metabolism during gestation and lactation are impacted by maternal reproductive experience. Specifically, sows with less reproductive experience (0–2 prior reproductive events) display higher rates of bone deposition and resorption, thus higher rates bone turnover, than more experienced sows (3–6 prior reproductive events).

Food utilization efficiency has been shown to vary with parity and with age of first mating in sows (Brooks & Smith, 1980; Yang, Eastham, Phillips, & Whittemore, 1989); as there was no variation in food intake between sows in our study, our findings indicate that parity may also affect the ability to and/or efficiency of mobilizing and transferring mineral to their young to support skeletal development. As there was no difference in offspring number or size relative to parity, it appears that sufficient resources are being allocated to offspring regardless of differences in bone metabolic activity.

It is important to note that parity and age are typically strongly correlated, as was true in this study. Although the literature focuses primarily on reproductive experience with regard to reproductive output and allocation, it is not possible to uncouple the effects of these individual variables on bone metabolic activity during a reproductive bout. However, age and parity both represent a degree of physiological maturity that could feasibly be associated with a capacity to allocate nutrients to their offspring. For example, both young and reproductively inexperienced sows may have had insufficient time or physiological stimulation, respectively, to accumulate sufficient bone mineral reserves prior to conception. Further study is necessary to determine the effects of these two maternal attributes.

On the day of parturition, bone deposition activity (OC concentration) was lower than it had been during gestation, and bone resorption (tDPD concentration) was at its highest point for the entire course of the reproductive bout (Figure 1), suggesting a physiological shift in how mineral is mobilized from the maternal skeleton that parallels the shift from placental calcium transfer during pregnancy to the production of calcium-rich milk during lactation. Like most mammals, sows rapidly deposit calcium into their young during late gestation (Hansard, Itoh, Glenn, & Thrasher, 1966). Calcium content is about 10.4 ± 1.3 g/offspring and 131 ± 12 g/litter at parturition, with about 50% of accumulation occurring during last 2 weeks of gestation (Mahan, Watts, & St-Pierre, 2009). This is similar for humans, where about 80% of the approximately 30 g of calcium

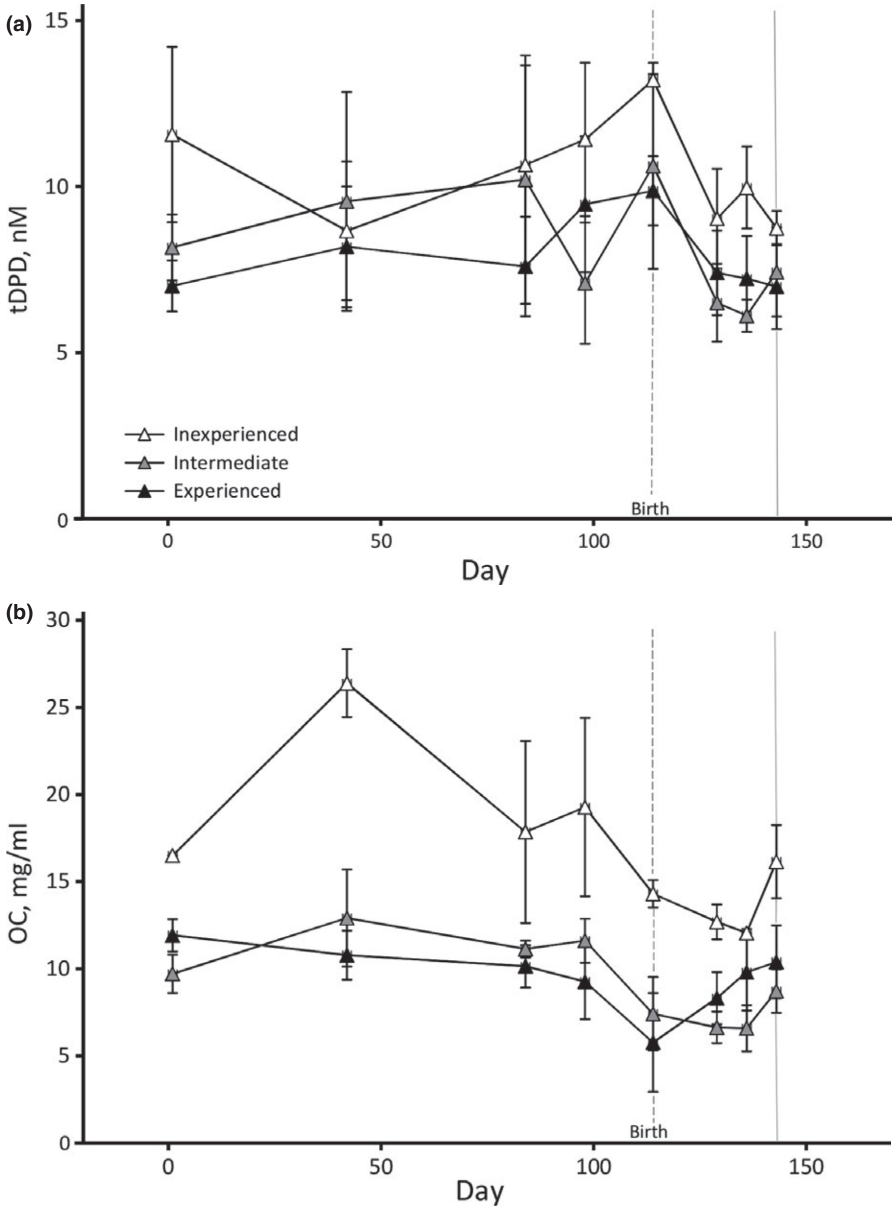

FIGURE 1 Serum concentrations of (a) total deoxypyridinoline (tDPD), a bone resorption marker, and (b) osteocalcin (OC), a bone deposition marker, from day of breeding (day 1 of gestation) to 3 days after the litter was weaned (solid line), for sows that had previously produced 0–2 litters (inexperienced; white), 3–4 litters (intermediate; gray) and 5–6 litters (experienced; black). Parturition (day 114) is indicated with a dotted line

deposited into human fetal skeleton is accreted during the last trimester. However, in most mammalian species that have been studied, calcium transferred to young during lactation greatly exceeds gestation. For example, the mean daily calcium deposition in the fetal skeletal averages 260 mg per day during the last trimester in humans, while up to 400 mg of calcium is lost daily during lactation (Kovacs, 2005). This dramatic change is supported by a shift in bone metabolism (Kovacs, 2005) and may be reflected in our observed change in bone marker concentrations around the time of parturition.

Limited exogenous resource availability can result in a reduction in litter size or offspring mass (e.g., Geffen et al., 1996; Tannerfeldt & Angerbjorn, 1998); yet, studies that manipulate dietary intake cannot address the effects of offspring production on maternal condition. When resources are abundant, such as in our study, we can begin to tease apart the influence that litter size and mass can have on maternal endogenous resource utilization. Sows have been artificially selected for production, and generally are slaughtered before they could incur costs associated with reproduction and old age; it follows that, in a sense, they have been selected to prioritize investment in offspring over self-maintenance. Indeed, symptoms such as lameness, which may be indicative of skeletal pathologies, are common by the age of 3 in breeding sows (Anil, Anil, & Deen, 2009). Also, in our study, the mass of individual offspring did not decline with increasing litter size, suggesting that mothers invested the same amount of resources into individual young regardless of the number produced. However, sows that produce large litters do not consume more feed during lactation than those producing smaller litters (Eissen, Apeldoorn, Kanis, Verstegen, & de Greef, 2003; Eklou-Kalonji et al., 1999), and there was no relationship between litter size and bone metabolism or food intake in our study.

This apparent paradox suggests that variation in bone metabolic activity during reproduction is driven by how available mineral is used, rather that the quantity of mineral that is available. This idea is supported by our results that indicate that only parity (and, potentially, age) influenced patterns of bone metabolism during gestation and lactation, and that this capacity changes with maternal experience. Further investigation into bone metabolic activity of reproductively inexperienced sows of different ages will aid in clarifying the relationship between parity and bone metabolism.

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