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LACTATION BIOLOGY SYMPOSIUM: Effects of photoperiod on mammary gland development and lactation¹

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ABSTRACT: Photoperiod, or the daily sequence of light and dark, has dramatic effects on many physiological systems across animal species. Light patterns alter melatonin secretion profiles and, subsequently, the release profiles and circulating concentrations of several hormones that influence a variety of physiological responses. Although the impact of photoperiod on reproductive processes is perhaps the most common example, it is often the seasonal aspects of ovulation and anestrus that are considered. However, in cattle, the final phase of reproduction, that is, lactation, is significantly influenced by photoperiod. In contrast to short days (SDPP; 8 h light:16 h dark), exposure to long days (LDPP) of 16 to 18 h of light and 6 to 8 h of darkness increases milk yield 2 to 3 kg/d, regardless of the stage of lactation. There is evidence that this LDPP effect is due to increased circulating IGF-I, independent of any effect on GH concentrations. Cows that are housed un-

der SDPP during the dry period have increased mammary growth and produce 3 to 4 kg/d more milk in the subsequent lactation compared with cows on LDPP when dry. While cows are on SDPP, circulating prolactin (PRL) diminishes but expression of PRL receptor increases in mammary, liver, and immune cells. Moreover, PRL signaling pathways within those tissues are affected by photoperiod. Further, replacement of PRL to cows on SDPP partially reverses the effects of SDPP on production in the next lactation. Thus, effects on dry cows are mediated through a PRL-dependent pathway. Before maturity, LDPP improve mammary parenchymal accumulation and lean body growth, which lead to greater yields in the first lactation. The accumulated evidence supports the concept that photoperiod manipulation can be harnessed to improve the efficiency of production across the life cycle of the dairy cow.

Key words: insulin-like growth factor I, milk yield, photoperiod, prolactin

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INTRODUCTION

Photoperiod represents the relative duration of light and dark that an organism experiences within a 24-h period. A long-day photoperiod (**LDPP**) is characterized by 16 to 18 h of light and 6 to 8 h of darkness in 24 h, whereas a short-day photoperiod (**SDPP**) is usually 8 h of light and 16 h of darkness. Under natural conditions, the amount of light exposure will wax and wane in a predictable annual pattern. In many species, photoperiod is the predominant environmental cue used to synchronize long-term physiological events related to growth, reproduction, and lactation. Cattle respond to

shifts in photoperiod, and knowledge of that biology can be used to improve the efficiency of milk production, reproduction, and growth.

Photoperiodic responses begin with light perception at photoreceptors in the eye, which transfer the signal to the pineal gland in the brain. Best characterized in rodents, the light stimulus actively inhibits the rate-limiting enzyme of the melatonin synthesis in the pineal gland and, thus, decreases circulating concentrations of melatonin. Evidence that this mechanism is conserved in cattle comes from observation of the vanishingly low concentrations of melatonin under lighted conditions and a robust increase under darkness (Stanisiewski et al., 1988; Buchanan et al., 1992). Across sex and age in cattle, the duration of increased melatonin concentrations then drives shifts in secretion of other hormones, including prolactin (**PRL**), gonadotropins, and IGF-I, all of which increase under LDPP exposure relative to SDPP. Indeed, many of the hormonal changes associated with SDPP in cattle can be driven by providing exogenous melatonin to mimic an extended, increased pattern of secretion. These endocrine changes influence

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the long-term physiological responses in growth, reproduction, and lactation.

PHOTOPERIOD AND REPRODUCTION

Although photoperiod is closely related to reproduction in many species, especially seasonal breeding, the impact on reproduction is more limited in cattle. Heifers exposed to LDPP achieve puberty faster than those on a natural photoperiod (Hansen et al., 1983), and LDPP during the prepubertal period also decreased the time to the first breeding (Rius and Dahl, 2006). Clearly, manipulation of the photoperiod is a promising reproductive management approach during the prepubertal period.

Photoperiodic effects on reproductive performance after puberty are much more subtle in cattle relative to other farmed ungulates. In contrast to sheep, goats, and horses, cattle do not exhibit seasonal cycles of reproduction, except when management constraints dictate they do, such as with many beef herds and grazing dairy production systems. Mature cows will have estrous cycles and become pregnant throughout the year, whereas mature bulls are fertile continuously once puberty is attained. Some seasonal effects on reproduction in cattle do appear to be linked to photoperiod. For example, cows return to estrous cyclicity faster after parturition during the summer compared with those calving in the winter months and natural short days (Hansen, 1985). An endocrine basis for that seasonal difference may lie in the observation that heifers under LDPP show greater LH release in response to estradiol relative to heifers under SDPP (Hansen et al., 1982).

PHOTOPERIOD AND GROWTH

A portion of the acceleration of puberty may be related to the increase in lean body growth observed in heifers grown under LDPP compared with SDPP. That is, calves on LDPP schedule gain more BW, achieve greater withers height, and have more lean tissue than those on a SDPP, and that growth is achieved at the same DMI (Petitclerc et al., 1984; Rius et al., 2005). The effects of LDPP on growth are consistent with the greater concentrations of IGF-I relative to SDPP treatment (Kendall et al., 2003; Spicer et al., 2007). Further evidence that growth is driven by photoperiodic effects on the calves physiology come from a study by Petitclerc et al. (1983), wherein LDPP exposure improved growth across 2 different levels of nutrient intake. Thus, the effect of lighting is not on feeding behavior, that is, more intake because the lights are on, but rather on the metabolism of ingested nutrients by the animals.

Beyond the effects on overall lean tissue accretion, LDPP photoperiod manipulation during the prepubertal growth phase increases mammary parenchyma growth relative to SDPP (Petitclerc et al., 1984, 1985). A recent study followed heifers raised under LDPP in the prepubertal period until the first lactation, where

they ultimately produced more milk than contemporary herdmates raised under SDPP, indicating that the mammary growth effects persist into the initial lactation (Rius and Dahl, 2006). Relative to SDPP, however, the LDPP heifers were heavier and taller at parturition, which is also associated with increased production (Rius and Dahl, 2006).

Limited investigation of preweaning growth indicates that LDPP may improve growth of young calves in a manner similar to older animals. A recent study of Osborne et al. (2007) compared LDPP and SDPP effects on performance of neonatal calves from birth until 8 wk of age. Relative to SDPP, calves under LDPP had greater starter intake and ADG before weaning, and LDPP calves generated more ruminal VFA than SDPP, with most of the photoperiodic effects observed after 4 wk of age. Although body composition was not quantified, these data support the conclusion that LDPP during the neonatal period enhances overall body growth, possibly through an acceleration of rumen development, compared with calves under SDPP.

In summary, exposure of calves to LDPP during the growth phase yields larger, leaner animals at maturity, with greater mammary parenchymal growth, and these effects are associated with greater yield after calving. The underlying mechanism of these progrowth effects by LDPP is consistent with the observed effects of LDPP on IGF-I and PRL, and the positive effect of those endocrine factors on mammary and lean tissue growth.

PHOTOPERIOD AND LACTATION

As discussed previously, a primary impact of photoperiod is on reproduction, particularly preovulatory events that result in the initiation of estrous cyclicity in seasonal breeders (Karsch et al., 1988). That coordination of ovulation, and thus parturition, with environmental and resource conditions most conducive to neonatal survival has proven a successful strategy to many mammals (Gwinner, 1986). It is perhaps not surprising then that the coordination extends to the final phase of mammalian reproduction, that is, lactation. In cattle, Peters et al. (1978) made the initial report of a galactopoietic effect of LDPP relative to a natural day length, and that observation has been subsequently verified across the lactation cycle, at a range of production levels, and in other ruminant species (Dahl et al., 2000; Dahl and Petitclerc, 2003).

During lactation, the response to LDPP becomes significant relative to SDPP after 3- to 4-wk exposure to the extended lighting schedule, and cows respond to LDPP during any stage of lactation with 3 kg/d more milk compared with their counterparts under SDPP (Dahl and Petitclerc, 2003). Of interest, there is no carryover effect after the treatment terminates and the production of cows previously on LDPP decreases to that of SDPP animals after all cows return to the same photoperiod (Dahl et al., 2000). There is evidence that

the galactopoietic effect of LDPP during the lactation period is mediated by increases in circulating IGF-I and that increase in IGF-I is not associated with any change in circulating GH or GH receptor (Dahl et al., 1997; Kendall et al., 2003). Additional evidence supports the concept of LDPP inducing a GH-independent stimulation of IGF-I that drives greater yield. The administration of both recombinant bovine (b) ST and LDPP during the lactation period exerts additive effects on milk production, which means the photoperiod and GH may exert their galactopoietic effects by different mechanisms and can be applied together to increase lactation persistency (Miller et al., 1999). Further, Collier et al. (2008) observed that cows treated with recombinant bST had variable IGF-I responses dependent on the season of treatment, with greater IGF-I associated with the longer days of the summer and lesser values during the short days of winter.

The effect of LDPP on PRL has also been implicated as an endocrine mechanism whereby LDPP increase milk yield, but the observations are conflicting. For example, direct supplementation of PRL to mature cows around the peak of lactation has no effect on milk yield in an established lactation (Plaut et al., 1987). In contrast, supplementation of melatonin to late-lactation cows decreased PRL and reduced milk yield (Auldust et al., 2007). Of interest, melatonin treatment had no effect on IGF-I in those late-lactation cows. One possibility is that LDPP affects the milking induced surge of PRL and slows the decline in that response as lactation advances (Koprowski and Tucker, 1973). Such an effect would be consistent with the lack of overall impact of PRL injection because it is specific to the milking-induced rise. The effect of melatonin would be expected to reduce both basal and milking-induced increases in PRL, although that remains to be confirmed experimentally. In a recent study, quinagolide, a PRL-release inhibitor, was administered to lactating cows for approximately 8 wk to examine the effect of decreased PRL on milk yield (Lacasse et al., 2011). After 4 wk, quinagolide-treated cows produced less milk compared with controls that received vehicle. However, only the milking-induced PRL surge was decreased in quinagolide-treated cows but not basal PRL. That outcome indicates that depression of the milking-induced PRL surge can alter yield even in the absence of effects on basal PRL. A reduction in PRL may affect mammary cell number via altered IGFBP signaling. Specifically, Accorsi et al. (2002) observed an increase in IGFBP-5 expression in cultured mammary explants in the absence of PRL relative to explants supplemented with PRL. Because IGFBP-5 promotes apoptosis, those *in vitro* data indicate that the increased PRL under LDPP could lead to slower losses of mammary cells relative to ambient photoperiod and, thus, slower declines in milk yield. The preceding discussion provides a theoretical framework whereby LDPP may influence milk yield via effects on PRL, yet further study is needed to confirm or refute that hypothesis.

The effect of photoperiod during the dry period is dramatically different from that in lactation, in that SDPP exposure leads to subsequent yields consistently greater than those of cows on LDPP when dry. Specifically, cows on SDPP when dry for 60 d achieve yields of 3 to 4 kg/d more in the subsequent lactation than those on LDPP when dry (Miller et al., 2000; Auchtung et al., 2005). There is evidence that sheep (Mikolayunas et al., 2008) and goats (Mabjeesh et al., 2007) respond to SDPP when dry in a similar manner to cows; that is, SDPP results in greater yield of milk in the next lactation. The effect in cattle is dependent on the duration of treatment because cows that were exposed to SDPP for only the final 21 d of the dry period did not exhibit the improvement in milk yield in the subsequent lactation (Reid et al., 2004). However, Velasco et al. (2008) reported that treatment with SDPP during a shortened dry period of about 42 d did result in greater milk yield relative to cows on LDPP. Indeed, the SDPP cows in the study of Velasco et al. (2008) averaged 35 d dry despite the target of 6 wk dry. Thus, SDPP during the dry period improve milk yield in the next lactation in ruminants, and that effect takes between 35 and 60 d to be fully expressed.

The enhanced milk output is due to increased mammary gland development during the dry period under SDPP (Wall et al., 2005a). Relative to LDPP, SDPP during the dry period increases mammary cell proliferation and decreases cell apoptosis (Wall et al., 2005a). This enhanced mammary growth by SDPP during the dry period increases the number of functional mammary secretory cells at parturition and, in turn, increases the lactation performance. The SDPP effect on the mammary gland during the dry period is mediated by enhanced PRL signaling. In response to SDPP, circulating concentrations of PRL decline and there is a concomitant increase in expression of PRL receptor (PRL-r) in many tissues, including the liver, mammary gland, and lymphocytes (Auchtung et al., 2003, 2005). Although PRL-r signaling influences several intracellular systems, one specific pathway altered by SDPP is the expression of suppressors of cytokine signaling (SOCS). A decrease in SOCS expression would be expected to enhance mammary growth because expression of the SOCS family of genes is generally associated with feedback inhibition of PRL signaling (Wall et al., 2005b).

A pivotal study to test the hypothesis that PRL mediates the effects of SDPP in dry cows involves replacement of PRL to cows on SDPP and observation of the production and other responses relative to those on SDPP or LDPP only. Crawford et al. (2005) placed cows on LDPP or SDPP at dry off and confirmed that exposure to LDPP increased circulating PRL approximately 2-fold relative to SDPP. Circulating PRL was increased after constant subcutaneous infusion of PRL for the last 6 wk of the dry period, and the SDPP+PRL cows had circulating concentrations of PRL of 7.8 ± 1.4 ng/mL, intermediate to the concentrations observed in

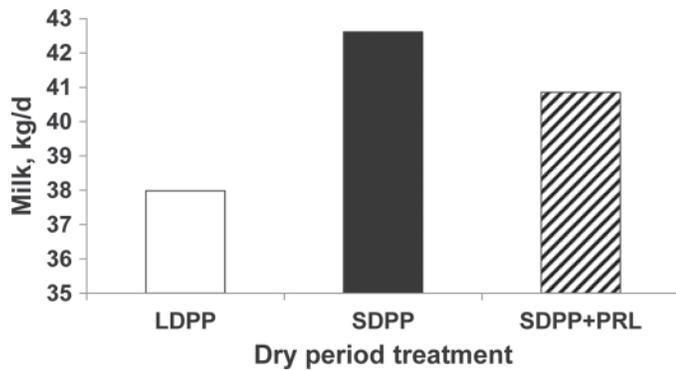


Figure 1. Effect of photoperiod and prolactin (PRL) treatments during the dry period on subsequent milk production (Crawford et al., 2005). Long-day photoperiod (LDPP; □), short-day photoperiod (SDPP; ■), and SDPP+PRL (hatched bars). The SDPP cows produced more milk than LDPP cows ($P = 0.02$), and SDPP+PRL cows tended to produce more milk than LDPP cows ($P = 0.14$). SED = 2.50 kg/d.

LDPP (10.8 ± 2.5 ng/mL) and SDPP (4.2 ± 1.0 ng/mL) cows. After calving, milk production followed a similar pattern to that of PRL, with SDPP+PRL yields intermediate to those of SDPP and LDPP cows (Figure

1). These data support the concept that decreases in circulating PRL during the dry period associated with exposure to SDPP result in greater yields in the subsequent lactation.

PHOTOPERIODIC EFFECTS ON IMMUNE FUNCTION

In addition to the effects on mammary gland and other reproductive tissues, PRL influences immune function. Therefore, it is not surprising that photoperiod affects cattle immune function via shifts in PRL secretion. Steer calves under SDPP had increased peripheral blood mononuclear cell (PBMC) proliferation in response to mitogens in vitro and enhanced neutrophil chemotaxis to IL-8 in vitro compared with LDPP-treated calves (Auchtung and Dahl, 2004). Similar PBMC responses were observed in cows exposed to SDPP when dry (Auchtung et al., 2004). These data indicate that SDPP cows would have improved immune status at calving relative to those on LDPP. Indeed, cows under SDPP had reductions in somatic cell counts during the dry period in contrast to cows under LDPP

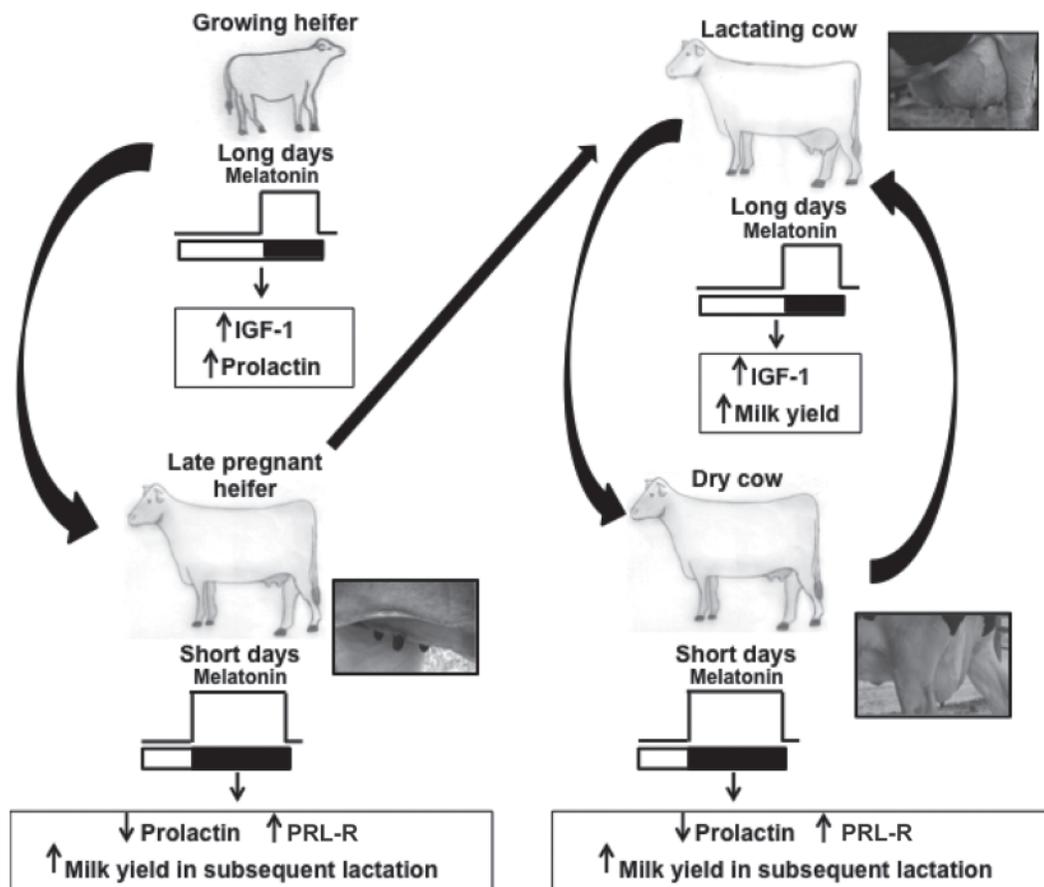


Figure 2. Summary model of the physiological effects and management outcomes of photoperiod management of dairy cattle. Exposure to long days promotes lean body and mammary growth and accelerates puberty in growing heifers relative to short days. These effects are associated with increases in circulating IGF-I and prolactin, which are both associated with altered melatonin profiles in cattle. During the latter stages of pregnancy in both pregnant heifers and dry cows, exposure to short days is recommended to reduce circulating prolactin and increase the expression of prolactin receptor at mammary, immune, and hepatic tissues. Cows and heifers exposed to short days during pregnancy subsequently produce more milk than those on long days when dry. Lactating cows should be exposed to long days because there is an increase in circulating IGF-I and prolactin and an increase in milk yield during established lactation. PRL-R = prolactin receptor. Adapted from Dahl and Thompson (2012) with permission from the publisher, John Wiley and Sons Inc. (Ames, IA).

(Auchtung et al., 2004), supporting the concept of a more robust immune response in SDPP cows. Because cows are at significant risk of new intramammary infection during the dry period, photoperiod manipulation may offer a management intervention to improve health and productivity.

The question of fidelity of mRNA and protein expression arises with regard to assessment of the biological impact of the inverse relationship of PRL and PRL-r under variable photoperiods. At least 2 lines of evidence support the use of PRL-r mRNA as an indicator of receptor function. First, the observed direct inverse relationship between circulating PRL and PRL-r expression is consistent with a physiological negative feedback loop. In addition, there is direct evidence that relative to LDPP, lymphocytes collected from cattle on SDPP have a more robust response to PRL (Auchtung and Dahl, 2004). Lymphocytes were harvested from steers after exposure to LDPP or SDPP, and then cultured in vitro with or without PRL and challenged with mitogens. In contrast to LDPP, lymphocytes from SDPP steers responded at reduced concentrations of PRL, which serves as a functional indicator of greater PRL-r expression.

Examination of PRL-r expression under SDPP and LDPP also offers an opportunity to further isolate the effects of photoperiod that result from shifts in circulating PRL. Using a bromocriptine treatment on LDPP calves to suppress PRL secretion, we observed that the reduced PRL stimulated an increase in PRL-r expression and PBMC responses relative to LDPP alone (Auchtung et al., 2003). Further, replacement of PRL to calves under SDPP such that circulating PRL concentrations matched contemporary LDPP calves resulted in PRL-r and PBMC responses similar to LDPP (Auchtung et al., 2003). Because the responses followed PRL concentrations regardless of photoperiod, these data strongly support the conclusion that PRL is the endocrine mediator of the photoperiodic effects.

SUMMARY AND CONCLUSIONS

From the preceding discussion, it is clear that photoperiod has substantial effects on reproduction, growth, lactation, and health across the life cycle. Figure 2 presents the recommended manipulation of light patterns to optimize the physiological responses from birth to parturition and through the dry period. In the growing calf, LDPP stimulates lean growth mammary development and hastens puberty. As the first calving approaches, and during the dry period, SDPP improves mammary development and immune status and yield in the subsequent lactation. Finally, during lactation, LDPP increases milk production and the efficiency of lactation. Photoperiod manipulation offers an excellent example of how understanding of the basic biology of responses to the environment can be harnessed to improve animal performance and health.

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