ABSTRACT Phosphorus is an essential nutrient involved in most metabolic processes. Most of the interest in Ca metabolism relates to eggshell formation. Although the eggshell is composed of Ca carbonate, metabolism of both Ca and P is closely related such that a deficiency in one can interfere with proper utilization of the other. To understand Ca and P metabolism properly, modeling can be of paramount importance. A new dynamic and mechanistic model of P and Ca metabolism in layers has been developed to simulate diurnal changes in Ca and P and the hourly requirement of the layer for those minerals. The model consists of 8 state variables representing Ca and P pools in the crop, stomachs, plasma, and bone. The flow equations are described by Michaelis-Menten or mass action forms. An experiment that measured Ca and P uptake in layers fed different Ca concentrations during shell-forming days was used for model evaluation. The experiment showed that Ca retained in body and egg decreased from 62.5 to 50.5% of Ca intake when the Ca in diet was increased from 25 to 45 mg/g of feed. The model simulations were in agreement with the trend. Predictions of Ca retention in bone and egg were 63.2, 56.1, and 55.3% for low, medium, and high dietary Ca concentrations. The experimental results showed that P retention in body and egg increased significantly from 11.5% of absorbable P intake at the lowest Ca inclusion concentration to 24.1% at the highest. The model also predicted an increase in P retention in bone and egg from 8.4 to 25.4% of absorbable P intake at the lowest and highest concentration of Ca inclusion, respectively. The advantage of the model is that absorption and utilization can be monitored on an hourly basis and that adjustments can be made accordingly. The model successfully showed how the availability of one mineral affects the utilization of the other and is a useful tool to evaluate feeding strategies aimed at reducing P excretion to the environment in poultry manure.

Key words: phosphorus, calcium, layer, modeling

INTRODUCTION
Phosphorus is an essential nutrient involved not only with bone development, growth, and productivity but also with most metabolic processes of the body. Phosphorus and Ca are the 2 most plentiful minerals in an animal and these elements are closely related so that deficiency or overabundance of one may interfere with the proper utilization of the other (Kebreab and Vitti, 2005). Imbalance in availability of P and Ca can create excess amounts of P to be excreted. Surplus minerals in poultry manure, including P, present an environmental pollution problem for intensive poultry operations.

Excess P from poultry manure contributes to build-up of P in the soil and may be washed from fertilized soil into surface waters causing eutrophication (Sharpley, 1999).

Reduction in P content of feed can mitigate pollution. Such a reduction requires knowledge of mineral absorption and requirements for various purposes in the animal. In layers, P is required for replacement of tissue metabolites such as nucleotides and phospholipids, to maintain skeletal integrity, and for production of the egg. There is a close relationship between P and Ca in layers producing eggs. Calcium is the major structural element in eggshell and large amounts of Ca are required to synthesize the shell. The shell gland is usually active during the dark hours, but Ca stores in the gut may be low at that time because hens have a nocturnal fast (Scanes et al., 1987). Therefore, the layer relies on other Ca sources, particularly from bone. The
Modeling Calcium and Phosphorus Dynamics in Layers

Nutritional requirements of the hen for P are uncertain and vary from 2.0 to 3.5 g of nonphytate or available P (AP) per kilogram of diet during peak lay (Boorman and Gunaratne, 2001). Snow et al. (2004) reported minimum AP requirements of 1.8 g/kg for first-cycle hens and a larger minimum requirement (more than 2.0 g/kg) for second-cycle hens. Uncertainty regarding P requirements is related to, among others, the close relationship between P and Ca dynamics in layers and the wide range in oviposition times, and hence in P and Ca requirements within the day in a flock of layers. Some models have been developed to quantitatively describe mineral flows in hens. Etches (1987) predicted on an hourly basis intestinal Ca content, Ca retention, Ca deposition in eggshell, and flows of Ca into and out of bone reserves, but did not consider P in the model. In studies commissioned by the CVB, Van Krieken (1996) and Tolboom and Kwakkel (1998) modeled Ca and P dynamics in layers partly based on the Etches (1987) model, also on an hourly basis, in which most transactions were linear. However, in describing nutrient dynamics based on the behavior of the system and its underlying components (mechanistic models), differential equations are often used and the mathematically standard way of representing such models is the rate:state formalism (Thornley and France, 2007). The objective of this study is the development and evaluation of a dynamic, mechanistic model of Ca and P dynamics in layers applying the rate:state formalism using linear and nonlinear kinetics, to evaluate various dietary and management strategies for reducing P excretion.

Materials and Methods

Model Overview

A model consisting of 8 state variables representing Ca and P pools in the crop (c), stomachs (proventriculus and gizzard; s), plasma (p), and bone (b) was developed (Figure 1). Phosphorus is defined as absorbable P at the terminal ileum. Zero pools are assigned to Ca and P in the duodenum (d), assuming that duodenal retention time for Ca and P is small. Also, there is little variation in ingesta content of the small intestine during the day or night, whereas large diurnal changes in crop and gizzard contents especially are observed (Scanes et al., 1987). Pool sizes are expressed in milligrams and time in days. State variables (quantities) are denoted by \( Q_i \). Concentration of a state variable \( C_i \) is calculated as pool size divided by BW \( W \) (kg). Differential equations \( \frac{dQ_i}{dt} \) describe the rate of change of state variable \( Q_i \) with time. Rate of utilization of \( i \) in the \( j \) to \( k \) transaction is denoted by \( U_{i,j,k} \) and rate of production of \( i \) in the \( j \) to \( k \) transaction by \( P_{i,j,k} \). The variable \( t' \) (h) is used for diurnal time (time within the day, \( 0 \leq t' \leq 24 \)).

The model was written in the Advanced Continuous Simulation Language, ACSLXtreme (Aegis Group, Huntsville, AL). Euler’s method of integration, with a step size of 0.6 min, was used and the model was run for 5 d. Usually, within 3 d, quasi-steady state is achieved, and the results are taken for the last day of simulation (d 5).

Model Components

Ca and P in the Crop. There is 1 input to each crop pool from the feed:

\[
P_{\text{Ca,Caf}} = I_f C_{\text{Caf}} \quad [1]
\]

\[
P_{\text{P,Caf}} = I_f C_{\text{Pf}} \quad [2]
\]

where \( I_f \) is feed intake (g/d) and \( C_{\text{Caf}} \) and \( C_{\text{Pf}} \) are the concentration (mg/g) of Ca and P, respectively, in the feed (Table 1). A layer is assumed to lay an egg at \( L = 1, 2, \ldots, \) or 7 h after light is switched on; alternatively, on rest days, the layer will not produce an egg. Hens generally consume considerably less food on days when either an ovulation or oviposition is missed than on other days (Scanes et al., 1987). Assuming a rate of lay of 95 eggs every 100 d (Table 1) and the day before the rest day (assumed to occur when \( L = 7 \) h) occurs 5 times every 100 d, the driving variable \( I_f \) was set to

![Figure 1. Diagrammatic representation of the Ca and P model. Boxes enclosed by solid lines indicate state variables; boxes enclosed by dashed lines indicate zero pools; arrows indicate flows. Subscripts C, S, D, P, and B denote crop, stomachs, duodenum, plasma, and bone, respectively.](https://example.com/figure1.png)
101% of averaged intake when \( L = 1, 2, \ldots, 6 \) h and 90% of averaged intake on the rest day and the day before rest day (Etches, 1987). Feed intake is assumed continuous during the photoperiod. The photoperiod is set at 16 h/d, and light is switched on at \( t' = 0 \) h.

Outflows of Ca and P to the stomachs (proventriculus and gizzard) are:

\[
U_{\text{Cac}, \text{CacCas}} = k_{\text{CacCas}} Q_{\text{Cac}}, \quad [3]
\]

\[
U_{\text{Pc}, \text{PcPs}} = k_{\text{PcPs}} Q_{\text{Pc}}, \quad [4]
\]

where \( k_{\text{CacCas}} (/d) \) and \( k_{\text{PcPs}} (/d) \) are fractional outflow rates of Ca and P, with values based on data reported by Van der Klis et al. (1990; Table 1). Rates of change of pool size in the crop are:

\[
dQ_{\text{Cac}}/dt = P_{\text{Cac}, \text{CafCac}} - U_{\text{Cac}, \text{CacCas}}; \quad [5]
\]

\[
dQ_{\text{Pc}}/dt = P_{\text{Pc}, \text{PfPc}} - U_{\text{Pc}, \text{PcPs}}; \quad [6]
\]

**Ca and P in the Stomachs.** There is 1 input to each of the 2 stomach pools from the crop:

\[
P_{\text{Cac}, \text{CacCas}} = U_{\text{Cac}, \text{CacCas}}; \quad [7]
\]

\[
P_{\text{Pc}, \text{PcPs}} = U_{\text{Pc}, \text{PcPs}}; \quad [8]
\]

**Outflows are to the duodenum:**

\[
U_{\text{Cac}, \text{CasCad}} = k_{\text{CasCad}} Q_{\text{Cas}}, \quad [9]
\]

\[
U_{\text{Pc}, \text{PsPd}} = k_{\text{PsPd}} Q_{\text{Ps}}, \quad [10]
\]

where \( k_{\text{CasCad}} (/d) \) and \( k_{\text{PsPd}} (/d) \) are fractional rates of outflow of Ca and P, respectively, to the duodenum (Van der Klis et al., 1990; Table 1). Rates of change of pool size in the stomachs are:

\[
dQ_{\text{Cac}}/dt = P_{\text{Cac}, \text{CacCas}} - U_{\text{Cac}, \text{CacCad}}; \quad [11]
\]

\[
dQ_{\text{Ps}}/dt = P_{\text{Ps}, \text{PsPd}} - U_{\text{Ps}, \text{PsPd}}. \quad [12]
\]

**Ca and P in the Duodenum.** Calcium and P in the duodenum are represented as zero pools, where input equals output without quantification of pool size. Inflow to the duodenum (mg/d) equals outflow from the stomachs:

\[
P_{\text{Cac}, \text{CasCad}} = U_{\text{Cac}, \text{CasCad}}; \quad [13]
\]

\[
P_{\text{Ps}, \text{PsPd}} = U_{\text{Ps}, \text{PsPd}}. \quad [14]
\]

The upper part of the small intestine is the most active in absorbing Ca and P (Hurwitz and Bar, 1965).

---

**Table 1.** Layer reference and model parameter values

<table>
<thead>
<tr>
<th>Item</th>
<th>Amount or flow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feed 110 g/d</td>
<td>110 g/d</td>
</tr>
<tr>
<td>Ca concentration in feed 40 mg of Ca/g of feed</td>
<td>40 mg of Ca/g of feed</td>
</tr>
<tr>
<td>P concentration in feed 2.8 mg of P/g of feed</td>
<td>2.8 mg of P/g of feed</td>
</tr>
<tr>
<td>Live weight 1.7 kg</td>
<td>1.7 kg</td>
</tr>
<tr>
<td>Eggs per 100 d 95 eggs</td>
<td>95 eggs</td>
</tr>
<tr>
<td>Egg weight 59 g</td>
<td>59 g</td>
</tr>
<tr>
<td>P in yolk 0.31 g of yolk/g of egg</td>
<td>5.70 mg of P/g of yolk</td>
</tr>
<tr>
<td>Ca in yolk 1.40 mg of Ca/g of yolk</td>
<td>0.59 g of white/g of egg</td>
</tr>
<tr>
<td>Egg white 0.14 mg of P/g of white</td>
<td>0.11 mg of Ca/g of white</td>
</tr>
<tr>
<td>P in white 0.10 g of shell/g of egg</td>
<td>1.30 mg of P/g of shell</td>
</tr>
<tr>
<td>Ca in shell 372.88 mg of Ca/g of shell</td>
<td>372.88 mg of Ca/g of shell</td>
</tr>
</tbody>
</table>

**Model parameter**

<table>
<thead>
<tr>
<th>Item</th>
<th>Parameter value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ratio of Ca to P in bone (( f_{\text{Ca}, \text{P}} ))</td>
<td>2.2 mg of Ca/mg of P</td>
</tr>
<tr>
<td>Inhibition constant of Ca mobilization (( J_{\text{CaCal}} ))</td>
<td>5 mg of Ca/kg of live weight</td>
</tr>
<tr>
<td>Inhibition constant of P mobilization (( J_{\text{PbPp}} ))</td>
<td>5 mg of P/kg of live weight</td>
</tr>
<tr>
<td>Fractional outflow rate of Ca from the crop (( k_{\text{CacCas}} ))</td>
<td>10.6/d</td>
</tr>
<tr>
<td>Fractional outflow rate of P from the crop (( k_{\text{PcPs}} ))</td>
<td>10.6/d</td>
</tr>
<tr>
<td>Fractional outflow rate of Ca from the stomachs (( k_{\text{CacCad}} ))</td>
<td>21.6/d</td>
</tr>
<tr>
<td>Fractional outflow rate of P from the stomachs (( k_{\text{PpPd}} ))</td>
<td>21.6/d</td>
</tr>
<tr>
<td>Fractional absorption of Ca from the duodenum (( k_{\text{CasCad}} ))</td>
<td>0.7 if eggshell is being formed; 0.4 if no eggshell is being formed</td>
</tr>
<tr>
<td>Affinity constant of Ca deposition (( M_{\text{CaP}} ))</td>
<td>5 mg of Ca/kg of live weight</td>
</tr>
<tr>
<td>Affinity constant of P deposition (( M_{\text{Pb}} ))</td>
<td>5 mg of P/kg of live weight</td>
</tr>
<tr>
<td>Maintenance Ca requirement per unit live weight (( R_{\text{CapCam}} ))</td>
<td>55 mg of Ca/kg of live weight per day</td>
</tr>
<tr>
<td>Maintenance P requirement per unit live weight (( R_{\text{PpPm}} ))</td>
<td>14 mg of P/kg of live weight per day</td>
</tr>
<tr>
<td>Maximal rate of Ca deposition in bone (( V_{\text{CapCab}} ))</td>
<td>4,500 mg of Ca/kg of live weight per day</td>
</tr>
<tr>
<td>Maximal rate of bone Ca mobilization (( V_{\text{CabCa}} ))</td>
<td>4,500 mg of Ca/kg of live weight per day</td>
</tr>
</tbody>
</table>
Absorption from the duodenum into blood plasma (mg/d) is represented as:

\[ U_{\text{Cad,CadCap}} = k_{\text{CadCap}} P_{\text{Cad,CasCad}} \]  
\[ U_{\text{Pd,PdPp}} = k_{\text{PdPp}} P_{\text{Pd,PdPp}} \]

where \( k_{\text{CadCap}} \) and \( k_{\text{PdPp}} \) are fractional absorption of Ca and P, respectively, from the duodenum. As P is defined in the model as absorbable P at the terminal ileum, \( k_{\text{PdPp}} \) is set at 1. Calcium retention on shell-forming days is greater than on days in which no shell formation occurs (Clunies et al., 1992), presumably because during times of high Ca demand, 1,25-dihydroxycholecalciferol concentrations are increased, stimulating Ca absorption from gut into blood. Parameter \( k_{\text{CadCap}} \) is taken as 0.7 during eggshell formation, when Ca requirements are high and 0.4 when there is no eggshell formation (Hurwitz and Bar, 1969). Nonabsorbed Ca is excreted in feces.

**Ca and P in the Plasma.** There are 2 inputs each to the Ca and P pools, absorption from the duodenum (\( P_{\text{Cap,CadCap}} \) and \( P_{\text{Pp,PdPp}} \)) and mobilization from bone (\( P_{\text{Cap,CabCap}} \) and \( P_{\text{Pp,PbPp}} \)) (all mg/d):

\[ P_{\text{Cap,CadCap}} = U_{\text{Cad,CadCap}} \]  
\[ P_{\text{Pp,PdPp}} = U_{\text{Pd,PdPp}} \]  
\[ P_{\text{Cap,CabCap}} = U_{\text{Cab,CabCap}} \]  
\[ P_{\text{Pp,PbPp}} = U_{\text{Pb,PbPp}} \]

Three outputs each from the plasma Ca and P pools are represented (i.e., utilization for egg synthesis, deposition in bone, and excretion in urine).

Calcium and P for egg synthesis (\( U_{\text{Cap,CapCae}} \) and \( U_{\text{Pp,PpPe}} \), mg/d) are the sum of utilization for yolk, white (albumen), and shell formation:

\[ U_{\text{Cap,CapCae}} = U_{\text{Cap,CapCayolk}} + U_{\text{Cap,CapCawhite}} + U_{\text{Cap,CapCashell}} \]  
\[ U_{\text{Pp,PpPe}} = U_{\text{Pp,PpPyolk}} + U_{\text{Pp,PpPwhite}} + U_{\text{Pp,PpPshell}} \]

The shell is assumed to be formed in the 20 h before oviposition (Etches, 1987) and to follow a logistic pattern (Thornley and France, 2007):

\[ y = a/[1 + e^{-b(x - c)}] - d \]

where \( y \) (g/g) is fraction of shell formed, \( x \) (h) is time from start of shell formation, and parameters \( a, b, c \), and \( d \) have values of 1.11, 0.308, 8.5, and 0.08, respectively (Figure 2a). Parameter \( d \) was added to the logistic equation because, unlike the use of sigmoidal functions for the analysis of growth (Lopez et al., 2000), the amount of shell at 0 h has to be zero. The parameters of the curve were estimated by Van Krieken (1996) based on data collected from literature and reported by Etches (1987). Differentiating gives the fractional rate of eggshell formation (Figure 2b):

\[ \frac{dy}{dx} = \frac{abe^{-b(x - c)}}{[1 + e^{-b(x - c)}]^2}. \]

As oviposition occurs at \( x = 20 \) (i.e., when \( t' = L \)), instantaneous fractional rate of eggshell formation, \( k_E \) (/d), is expressed in the model as:

\[ k_E = 0, \quad L < t' < L + 4, \]  
\[ = \frac{abe^{-b(x - c)}}{[1 + e^{-b(x - c)}]^2}, \quad t' > L + 4. \]

There are 2 exceptions to this calculation of \( k_E \). First, when \( L = 7 \) h, it is assumed that there is no ovulation on that day and, consequently, the next day will be a rest day; hence, \( k_E \) is 0/d when \( t' \geq 7 \) h. Second, on a
rest day, there is no oviposition but the layer is preparing for an egg at \( L = 1 \) h on the next day. Hence, on a rest day, \( k_E \) is 0/d if \( t' < 5 \) h. The above equation for \( k_E \) applies at all other times.

Egg white formation is taken to occur at the same time and rate as shell formation. This simplification was made to facilitate model development and has a minor effect on Ca and P requirements because amounts of Ca and P in egg white are only 0.2 and 4.2% of total Ca and P, respectively, and plasma Ca for bone synthesis based on availability of the egg and by egg weight, and multiplied by the fraction of that component in the egg and by egg weight, and multiplied by the fractional rate of laying in a 100-d period (all from Table 1).

Depositions of Ca and P in bone are represented as saturable processes:

\[
U_{\text{Cap,Cap,Cab}} = V_{\text{Cap,Cab}} W/(1 + M_{\text{Cap,Cab}}/C_{\text{Cap},P}),
\]

\[
U_{\text{Pp,Pp,Pb},P} = V_{\text{Cap,Cab}} W/[f_{\text{Ca},P} (1 + M_{\text{Pp,Pb}}/C_{\text{Pp}})],
\]

\[
U_{\text{Cap,Cap,Cab},P} = U_{\text{Pp,Pp,Pb},P} f_{\text{Ca},P},
\]

\[
U_{\text{Pp,Pp,Pb},P} = U_{\text{Cap,Cap,Cab},P} f_{\text{Ca},P},
\]

where \( U_{\text{Cap,Cap,Cab}} \) and \( U_{\text{Cap,Cap,Cab},P} \) are utilization of plasma Ca for bone synthesis based on availability of plasma Ca and P, respectively, and \( U_{\text{Pp,Pp,Pb},P} \) and \( U_{\text{Pp,Pp,Pb},P} \) are utilization of plasma P for bone synthesis based on availability of plasma P and plasma Ca, respectively (all in mg/d). In addition, \( V_{\text{Cap,Cab}} \) [mg/(kg of BW) per d] is maximal rate of Ca deposition in bone, \( M_{\text{Cap,Cab}} \) and \( M_{\text{Pp,Pb}} \) [mg/(kg of BW)] are affinity constants, \( C_{\text{Cap}} \) and \( C_{\text{Pp}} \) [mg/kg of BW] are concentrations of Ca and P in plasma, and \( f_{\text{Ca},P} \) is the ratio of Ca to P in bone, assumed fixed (Table 1). The maximal rate of Ca deposition was assumed to be equal to that of Ca mobilization from bone. Actual deposition of Ca (\( U_{\text{Cap,Cap,Cab}} \), mg/d) and P (\( U_{\text{Pp,Pp,Pb},P} \), mg/d) are therefore the minima:

\[
U_{\text{Cap,Cap,Cab}} = \text{MIN}(U_{\text{Cap,Cap,Cab},Ca}, U_{\text{Cap,Cap,Cab},P}),
\]

\[
U_{\text{Pp,Pp,Pb},P} = \text{MIN}(U_{\text{Pp,Pp,Pb},P}, U_{\text{Pp,Pp,Pb},Ca}).
\]

Utilization (mg/d) of Ca and P for maintenance is:

\[
U_{\text{Cap,Cap,Cam}} = R_{\text{Cap,Cam}} W,
\]

\[
U_{\text{Pp,Pp,Pm}} = R_{\text{Pp,Pm}} W,
\]

where \( R_{\text{Cap,Cam}} \) and \( R_{\text{Pp,Pm}} \) [both mg/(kg of BW) per d] are Ca and P maintenance requirements per unit of BW (Table 1) based on recommendations of WPSA (1984) and CVB (1994).

Calcium and P excreted in urine are the sum of (i) basal requirement for Ca and P (maintenance requirement), plus (ii) amount of Ca or P in plasma that cannot be used for bone synthesis because the other mineral (P and Ca, respectively) is lacking, plus (iii) amount of Ca or P released from bone because P or Ca is required for egg synthesis, respectively:

\[
U_{\text{Cap,Cap,Cam}} = U_{\text{Cap,Cap,Cam}} + \text{MAX}(0, U_{\text{Cap,Cap,Cab},Ca} - U_{\text{Cap,Cap,Cab},P}) + \text{MAX}(0, U_{\text{Cap,Cap,Cab},P} - U_{\text{Pp,Pp,Pb},P}),
\]

\[
U_{\text{Pp,Pp,Pm}} = U_{\text{Pp,Pp,Pm}} + \text{MAX}(0, U_{\text{Pp,Pp,Pb},P} - U_{\text{Pp,Pp,Pb},P}) + \text{MAX}(0, U_{\text{Pp,Pp,Pb},P} - U_{\text{Pp,Pp,Pb},P}),
\]

where \( U_{\text{Cap,Cap,Cab},P} \) and \( U_{\text{Cap,Cap,Cab},Ca} \) are mobilization of bone Ca based on P and Ca needs, respectively, and \( U_{\text{Pp,Pp,Pb},P} \) and \( U_{\text{Pp,Pp,Pb},P} \) are mobilization of bone P based on P and Ca needs, respectively (all in mg/d). This representation of P mobilization as a function of (among others) Ca requirements is in line with observations that plasma P concentration is an indication of bone mobilization to provide Ca for shell formation (Boorman and Gunaratne, 2001). In these equations, it is assumed that any mineral not used for bone synthesis because availability of the other mineral is not enough to support that synthesis is excreted in urine. Equally, any mineral that has been mobilized because of necessary mobilization of the other mineral is excreted in urine. Thus, it is assumed that temporary storage of one of the minerals that is in excess does not occur.

Rates of change of pool size in the plasma are:

\[
dQ_{\text{Cap},d} = P_{\text{Cap,Cap,Cap}} + P_{\text{Cap,Cap,Cab}} - U_{\text{Cap,Cap,Cam}} - U_{\text{Cap,Cap,Cab}},
\]

\[
dQ_{\text{Pp},d} = P_{\text{Pp,Pp,Pp}} + P_{\text{Pp,Pp,Pb}} - U_{\text{Pp,Pp,Pm}} - U_{\text{Pp,Pp,Pb}},
\]

**Ca and P in the Bone.** There is 1 input to each bone pool from plasma:

\[
P_{\text{Cap,Cap,Cab}} = U_{\text{Cap,Cap,Cab}},
\]

\[
P_{\text{Pp,Pp,Pb}} = U_{\text{Pp,Pp,Pb}}.
\]

Outputs from bone are to plasma:

\[
U_{\text{Cap,Cap,Cam}} = \text{MAX}(U_{\text{Cap,Cap,Cab},P}, U_{\text{Cap,Cap,Cab},Ca}),
\]

\[
U_{\text{Pp,Pp,Pm}} = \text{MAX}(U_{\text{Pp,Pp,Pb},P}, U_{\text{Pp,Pp,Pb},P}),
\]
where $U_{\text{Cab,CabCap;P}}$ and $U_{\text{Cab,CabCap;Ca}}$ (mg/d) are rates of Ca utilization for bone synthesis based on availability of P or of Ca in plasma, respectively. Similarly, $U_{\text{Pb,Pp,Pp;P}}$ and $U_{\text{Pb,Pp,Pp;Ca}}$ (mg/d) are corresponding rates of P utilization. Mobilization of Ca and P from bone is assumed inhibited by plasma availability of these minerals (Boorman and Gunaratne, 2001): 

$$U_{\text{Cab,CabCap;Ca}} = V_{\text{CabCap}} \frac{W}{1 + C_{\text{CabCap}}/J_{\text{CabCap}}}, \quad [43]$$

$$U_{\text{Pb,Pp,Pp;P}} = V_{\text{CabCap}} \frac{W}{f_{\text{Ca;P}}(1 + C_{\text{Pp}}/J_{\text{Pp,Pp}})}, \quad [44]$$

$$U_{\text{Cab,CabCap;P}} = U_{\text{Pb,Pp,Pp;P}} f_{\text{Ca;P}}, \quad [45]$$

$$U_{\text{Pb,Pp,Pp;Ca}} = U_{\text{Cab,CabCap;Ca}}/f_{\text{Ca;P}}, \quad [46]$$

where $V_{\text{CabCap}}$ [mg/(kg of BW) per d] is maximal rate of bone Ca mobilization and $J_{\text{CabCap}}$ and $J_{\text{Pp,Pp}}$ [mg/(kg of BW)] are inhibition constants (Table 1). Maximal rate of bone Ca mobilization was set at such a rate as to sustain maximal rates of Ca utilization for egg synthesis when other Ca sources are not available. Rates of change of pool size in bone are:

$$\frac{dQ_{\text{Cab}}}{dt} = P_{\text{Cab,CabCap;Cab}} - U_{\text{Cab,CabCap;Ca}} \quad [47]$$

$$\frac{dQ_{\text{Pp}}}{dt} = P_{\text{Pb,Pp,Pp;P}} - U_{\text{Pb,Pp,Pp;P}} \quad [48]$$

**RESULTS AND DISCUSSION**

**Model Results in Default Simulation**

Diurnal changes in Ca and P for a layer laying an egg when $L = 1$ h are presented in Figure 3. An overview of hourly and daily P dynamics in such a layer is presented in Table 2.

In the default situation, the photoperiod is 16 h/d. From the moment light is switched on (at 0 h), feed intake commences and, consequently, Ca and P absorption increase. After 16 h, feed intake ceases and, therefore, Ca and P absorption decline because the amounts of Ca and P present in crop and stomach quickly decrease because their fractional outflow rates are high and no new Ca or P enters the crop. In the present simulations, a continuous intake is assumed. However, depending on the light scheme used, ad libitum feed intake may vary during the day. In a continuous lighting scheme, feed intake was reduced in the 2-h period before oviposition, whereas immediately after oviposition, feed intake was increased (Savory, 1978). A somewhat greater feed intake in the second half of the light period has also been observed. Keshavarz (1998), for example, found that hens consumed 40% of daily feed intake during the first 8 h after light was switched on and 60% during the 8-h period before light was switched off, in a 16-h light scheme. Such patterns of feed intake can easily be incorporated in the model because feed intake is an independent driving variable. If the feed intake is greater during the second phase of the photoperiod, the simulated rate of Ca absorption from the gut will show a more gradual increase toward a maximum value around the start of the dark period, and a slower decrease in Ca absorption in the dark period than the absorption patterns shown in Figure 3a.

Fractional rates of passage of Ca and P from the crop and stomachs are assumed not to vary within the day. Data on diurnal changes in transit times are scarce. Scanes et al. (1987) observed a gradual decrease in crop and gizzard contents during the dark period. However, crop and gizzard remained virtually empty during the first half of the photophase, when feed intake has already commenced. Such a pattern suggests much smaller retention times in the first half of the photoperiod than at other times of the day. Fractional rate of passage of Ca from the stomachs ($k_{\text{Cab,Cab}}$) will be greatly affected by source and particle size of Ca, with larger particles having a lower rate of solubilization and presumably a lower rate of passage from the
stomachs and limestone showing higher rates of solubilization than oyster shell (Rao and Roland, 1989). Storage of particulate material in the gizzard releases the Ca more slowly overnight when the bird does not feed. Indeed, in the model, assuming a lower fractional rate of passage of Ca from the stomachs resulted in a less rapid approach to maximal Ca absorption and a slower rate of decline of Ca absorption during the dark period (simulation results not shown).

From the moment of oviposition (h 1), Ca requirements are small until h 5, when formation of a new eggshell starts. Phosphorus requirements are more equal during the day than Ca requirements because unlike Ca the majority of P is required for synthesis of egg yolk, assumed to be a continuous process. In the first hour, P absorption is smaller than P requirements, and therefore P and Ca mobilization from bone occurs. In this hour, all mobilized P is utilized for maintenance and egg production, and P excretion in urine is merely related to maintenance. In contrast, mobilized Ca cannot be utilized or stored and is therefore excreted in urine.

After shell formation starts (h 5), Ca requirements increase and decrease in a pattern related to that of shell formation. Simulated Ca requirements are greatest some 11 to 17 h after previous oviposition, which is qualitatively in line with the most rapid rates of shell secretion occurring during 12 to 18 h postoviposition observed by Clunies and Leeson (1995). The simulated Ca and P absorption is sufficient to meet Ca and P requirements until h 18 and 20, respectively. However, the surplus of P absorbed cannot always be utilized for bone synthesis because Ca may be lacking to support this synthesis. That is the case from approximately h 11 to 18. Hence, a part of absorbed P is not utilized in these hours and is excreted in urine. From h 18 until the end of the dark period, Ca has to be mobilized to support requirements, and consequently, P is mobilized as well. A large part of this mobilized P is not required for maintenance or egg synthesis and consequently is excreted in urine. Note that there are 2 reasons why P is unutilized and excreted in the urine. From h 11 to 18, P absorption from blood is too high relative to Ca availability to support high bone synthesis rates. From h 18 to 24, unutilized P largely originates from bone mobilization because of Ca requirements. The simulated large amounts of P excreted during the process of shell formation are qualitatively in line with data of Hurwitz and Bar (1965).

The simulations for a layer at oviposition 1 h after light is switched on indicate that 8% of AP intake is utilized for maintenance, 36% of AP intake is deposited in the egg, and 22% of AP intake is deposited in bone. Therefore, approximately one-third of AP intake (viz. 107.9 out of 311.1 mg/d) is not utilized because of instantaneous deficits of Ca. Total net P deposition in bone is 67.8 mg/d. This would indicate that dietary AP can be reduced by 22%. However, evaluation of feeding strategies requires simulations at all possible hours of oviposition and assumptions on the frequency distribution of those hours within a flock of layers, described later.

When oviposition occurs at later times after light is switched on, relatively more of the shell-forming pro-

<table>
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<th>Maintenance</th>
<th>Not utilized</th>
<th>Into bone</th>
<th>Into urine</th>
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<tr>
<td>Total (mg/d)</td>
<td>311.1</td>
<td>111.6</td>
<td>23.8</td>
<td>107.9</td>
<td>67.8</td>
<td>131.7</td>
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cess occurs during the night. Hence, Ca requirements occur especially at hours during the dark period when Ca supply from the gut is small. This is illustrated in Figure 4 for oviposition at $L = 5$ h. From h 16 until h 2 of the following day, simulated Ca requirement is much greater than Ca absorption due to high shell synthesis rate and declining rate of Ca absorption, giving rise to bone mobilization. Consequently, large amounts of P are mobilized as well and are excreted in urine. During h 2 until 15, bone synthesis is limited because P is limiting and the Ca surplus will be excreted. The amount of P not utilized (328.2 mg/d) is even greater than the amount of AP from the feed (311.1 mg/d; Table 3). Over a whole day, there is net P mobilization of bone (152.5 mg/d). In this case, dietary absorbable P cannot be reduced because of bone depletion that has already occurred.

On a rest day, there is no oviposition, but Ca demands are high to form the shell for the next day. Given the lower Ca intake concentration on a rest day, there is bone mobilization during peak shell synthesis rates as well as during most of the dark hours (Figure 5). The amount of P not utilized is therefore greater than on a day with oviposition at h 1 (123.5 and 107.9 mg/d, respectively).

To calculate total Ca and P flows during a longer period, assumptions about the frequency distribution of hours of oviposition within a flock of layers have to be made. Based on observations on frequency of laying times reported by Van Krieken (1996) and a rate of lay of 95 eggs per 100 d, average P flows in a layer are presented in Table 3. Such a frequency distribution of laying times may depend on the strain of laying hens and calculations can easily be adapted to analyze different frequency distributions. Over a period of 100 d, the simulations indicate that, on average, 221.2 mg of P/d is not utilized because of Ca shortage and is excreted with urine. The P mobilization from bone is on average 48.3 mg/d, which corresponds to mobilization of Ca of 106.3 mg/d. Given such a level of bone mobilization, osteoporosis problems may occur. This negative Ca balance is more pronounced than the Ca balances reported by Clunies et al. (1992) of −107, −22, and 163 mg/d for dietary Ca concentrations of 25, 35, or 45 mg/g of feed, respectively. However, the hens in their study had a lower rate of lay (some 90 eggs per 100 d), therefore demanding less Ca and giving more opportunity for bone repair. Also, dietary AP concentration was 4.5 mg/g, whereas in the present simulations, a concentration of 2.8 mg/g was adopted. A greater supply of P will increase bone deposition rate at those hours when P, and not Ca, is limiting.

Model simulations indicate several options to reduce this level of bone depletion. Because there are hours

**Figure 4.** Simulated diurnal dynamics of Ca (a) and P (b) in a layer at oviposition 5 h after light is switched on. An arrow denotes time of oviposition. Ca or P absorption is absorption from the duodenum, Ca or P requirement is requirement for maintenance and egg production (shell, yolk, and white), and Ca or P deposition is bone synthesis (positive values) or bone mobilization (negative values).

**Table 3.** Simulated daily P flows (mg/d) in layers at various laying times ($L$) after light is switched on and averaged P flow in a 100-d period

<table>
<thead>
<tr>
<th>$L$ (h)</th>
<th>Days/100 d</th>
<th>Absorbed</th>
<th>Into egg</th>
<th>Maintenance</th>
<th>Not utilized</th>
<th>Into bone</th>
<th>Into urine</th>
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</thead>
<tbody>
<tr>
<td>1</td>
<td>15</td>
<td>311.1</td>
<td>111.6</td>
<td>23.8</td>
<td>107.9</td>
<td>67.8</td>
<td>131.7</td>
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<td>2</td>
<td>16</td>
<td>311.1</td>
<td>111.6</td>
<td>23.8</td>
<td>167.3</td>
<td>8.4</td>
<td>191.1</td>
</tr>
<tr>
<td>3</td>
<td>20</td>
<td>311.1</td>
<td>111.6</td>
<td>23.8</td>
<td>224.2</td>
<td>−48.5</td>
<td>248.0</td>
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<tr>
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<td>17</td>
<td>311.1</td>
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<td>23.8</td>
<td>278.1</td>
<td>−102.4</td>
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</tr>
<tr>
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<td>7</td>
<td>5</td>
<td>277.2</td>
<td>101.4</td>
<td>23.8</td>
<td>62.9</td>
<td>89.1</td>
<td>86.7</td>
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<tr>
<td>Rest day</td>
<td>5</td>
<td>277.2</td>
<td>111.3</td>
<td>23.8</td>
<td>123.5</td>
<td>18.6</td>
<td>147.3</td>
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<tr>
<td>Weighted average</td>
<td>307.7</td>
<td>111.1</td>
<td>23.8</td>
<td>221.2</td>
<td>−48.3</td>
<td>245.0</td>
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during the day when Ca is in short supply and hence P cannot be utilized properly, supplying more Ca with the diet or ensuring a pattern of Ca absorption that better matches average instantaneous Ca requirements will reduce this mobilization and reduce P excretion to the environment. Equally, an increase in P supply may help to resynthesize bone at times when Ca supply is sufficient (normally during non-shell-forming hours), but this option will increase P excretion with urine to the environment as well. Increases in dietary P and Ca concentrations may affect apparent digestion of these nutrients. Elevated dietary Ca concentrations increase pH in the gut and as a result P absorption is decreased. High plasma P concentrations decrease Ca absorption from the gut (Keshavarz and Austic, 1990). The present model has AP as a driving variable and absorption of Ca is either 40 or 70%. Therefore, if such interactions between dietary Ca and P concentrations are expected to occur, the Ca absorption values or concentrations of dietary AP should be changed. The model developed here is a promising tool in evaluating such alternative feeding strategies for effects on bone depletion or synthesis and P excretion in urine and augments the number of mechanistic models in animal nutrition that address concerns about environmental sustainability (Dumas et al., 2008).

**Model Evaluation**

There is a paucity of recent experiments conducted that measured the inputs required to run the model. Particularly, experiments that compared Ca and P metabolism in hens offered feed at different oviposition times and measured Ca and P concentrations in medullary bones are lacking. Therefore, evaluation of the model is limited to assessment of its accuracy of prediction when details of feed and excretion are available. Clunies (1989) conducted an experiment that measured Ca and P uptake in layers fed different Ca concentrations during shell-forming days. A total of twenty-seven 42-wk-old Single Comb White Leghorn hens were offered 1 of 3 feeds differing in Ca concentration: 25, 35, and 45 mg/g. All diets were formulated to the same concentration of AP (4.5 mg/g). The experiment showed that the percentage of Ca retained in body and egg was 62.5, 51.4, and 50.5% of feed Ca intake for low, medium, and high Ca concentrations in diet, respectively. Experimental data were used as an input to the model and simulations were run for each concentration of Ca in the diet. The model predictions were 63.2, 56.1, and 55.3% for low, medium, and high Ca concentrations in the diet, which is close to observed values. The experimental results showed that P retention in body and egg (expressed as percentage of AP intake) increased significantly from 11.5% at the lowest Ca inclusion concentration to 23.8% at the medium Ca intake concentration. However, there was no significant difference between the medium and highest Ca inclusion concentrations in P retention. The model simulations show that P retention increased from 8.4% in the lowest Ca inclusion concentration to 24.7% at medium and 25.4% at the highest concentration of Ca inclusion. A full model evaluation analysis using tools such as MS prediction error or Lin's concordance correlation coefficient cannot be made because only mean values are available. However, the trend of predictions is consistent with observations. Further experiments are required to test the model comprehensively and adjust the parameters if justified by the results.

The model developed is a tool to quantify Ca and P dynamics within a 24-h period based on understanding of the processes involved and to evaluate Ca and P dynamics for a wide range of oviposition times. This will help to evaluate feeding strategies aimed at reducing P excretion to the environment in poultry manure.

![Figure 5](image) Simulated diurnal dynamics of Ca (a) and P (b) in a layer on a rest day (no oviposition). Ca or P absorption is absorption from the duodenum, Ca or P requirement is requirement for maintenance and egg production (shell, yolk, and white), and Ca or P deposition is bone synthesis (positive values) or bone mobilization (negative values).
ACKNOWLEDGMENTS

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REFERENCES


