UNIVERSIDADE ESTADUAL DO NORTE FLUMINENSE DARCY RIBEIRO

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MODELOS NÃO LINEARES PARA DESCRIÇÃO DO TRÂNSITO DE PARTÍCULAS PELO TRATO DIGESTÓRIO DO RUMINANTE: AVALIAÇÃO DE MODELOS E IMPLICAÇÕES TEÓRICAS

CAMPOS DOS GOYTACAZES
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Dissertação apresentada ao Centro de Ciências e Tecnologias Agropecuárias da Universidade Estadual do Norte Fluminense Darcy Ribeiro, como requisito parcial para obtenção de grau de Mestre em Ciência Animal.

ORIENTADOR: PROF. RICARDO AUGUSTO MENDONÇA VIEIRA

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Dedico esta dissertação à minha família, em especial a minha mãe Neyla, aos meus irmãos e a minha noiva Cléo, que sempre estiveram ao meu lado em todos os momentos .

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“Não possuir algumas das coisas que desejamos é parte indispensável da felicidade”

Bertrand Russel

“Já se disse ser a dúvida
oprincício da sabedoria
Ouvi também dizer
que o temor do Criador o seria
Eterno impasse
entre a religião e filosoia

Certo é
que nada neste mundo
é inacessível ao questionamento
Oportuno instrumento
ao que nos é demasiado obscuro”

André Coeli

BIOGRAFIA

Marcelo Cabral da Silva, Filho de Manuel e Neyla, nascido no Rio de Janeiro, RJ, em 18 de fevereiro de 1983.

Concluiu o ensino médio no Colégio Estadual Olinto da Gama Botelho no Rio de Janeiro – RJ em dezembro de 2002.

Ingressou no Curso de Zootecnia na Universidade Federal Rural do Rio de Janeiro, por meio do Vestibular, em abril de 2007. Concluiu o curso em dezembro de 2011.

Durante a graduação foi bolsista de iniciação científica/FAPERJ de 2009 a 2011. Foi membro do diretório acadêmico do curso de Zootecnia, onde representou os alunos durante a gestão 2009/2010 como diretor de estágios e empregos e na gestão 2010/2011 como presidente. Participou como assessor administrativo da Vital-Jr. Consultoria e Assessoria Zootecnica –empresa Júnior da UFRRJ, de maio de 2010 a dezembro de 2011.

Iniciou o mestrado no curso de Ciência Animal em março de 2012 sob orientação do professor Ricardo Augusto Mendonça Vieira, e em fevereiro de 2014, submeteu-se à defesa de Dissertação para a obtenção do título de mestre em Ciência Animal.

RESUMO

Da Silva, Marcelo Cabral, M. Sc., Universidade Estadual do Norte Fluminense Darcy Ribeiro; fevereiro de 2014; TRÂNSITO DE PARTÍCULAS PELO TRATO DIGESTÓRIO DOS RUMINANTES: AVALIAÇÃO DE MODELOS DE MÚLTIPLOS COMPARTIMENTOS E IMPLICAÇÕES TEÓRICAS. Professor Orientador: Ricardo Augusto Mendonça Vieira.

Perfis fecais dos marcadores de partículas sólidas Cr e La, e do complexo marcador da fase líquida, Co-EDTA, foram obtidos a partir de estudos de cinética de digestão com vacas, novilhos e ovelhas com o objetivo de avaliar modelos matemáticos destinados a interpretar perfis de excreção do marcador nas fezes.Os modelos avaliados foram o modelo multicompartimental (Dhanoa et al.,1985),o modelo Gama descrito como GN (Pond et al., 1988), e o modelo GNG1 (Matis,1972).Os modelos foram ajustados por meio do método dos mínimos quadrados não-lineares ordinários e avaliados com base nos critérios de probabilidade. Apesar das diferenças notáveis em termos de probabilidade, os modelos foram similares em termos de aderência visual aos perfis de tempo observados e apresentaram sobreposição das estimativas, para tempo médio de retenção no compartimento. A maior diferença relativa observada nos modelos foi para a média do tempo de trânsito e a variância até primeiro aparecimento do indicador nas fezes. O modelo com melhor capacidade de imitar os perfis de excreção dos marcadores foi o GN; o modelo GNG1 e o multicompartimental apresentaram estimativas equivalentes em termo de probabilidade de verossimilhança. Portanto, propusemos a derivação matemática do modelo GN para explicar a digestibilidade e o efeito de repleção da digesta ruminoreticular, sempre que o modelo GN for melhor escolha para interpretar estudos de marcadores com base em critérios de probabilidade de verossimilhança.

Palavras chaves: Ruminantes, Trato digestório, Marcadores, Cinética, Modelos matemáticos.

ABSTRACT

Da Silva, Marcelo Cabral, M. Sc.; Universidade Estadual do Norte Fluminense Darcy Ribeiro; Fevereiro 2014; Non linear models to describe the transit of particles through the ruminant digestive tract: evaluation of models and theoretical implications. Advisor: Ricardo Augusto Mendonça Vieira.

Fecal profiles of the particulate markers Cr and La, and of the fluid marker complex Co-EDTA were obtained from digestion kinetic studies with cows, steers, and sheep with the aim of evaluating mathematical models designed to interpret marker excretion profiles in feces. The models evaluated were the multicompartmental model (Dhanoa et al., 1985), the Gamma model described as GN (Pond et al., 1988), and the GNG1 model (Matis, 1972). Models were fitted with ordinary nonlinear least squares and evaluated on the basis of likelihood criteria. Despite remarkable differences in terms of likelihood, models were quite similar in terms of visual adherence to observed time profiles and presented overlapping interval estimates for compartment mean retention times. The major relative numerical discrepancies observed among models were related to the mean and variance of the transit time for the first appearance of the marker in feces. The model with the best performance in mimicking the marker profiles were the GN model; the GNG1 modeland the multicompartmental model were almost equivalent in terms of likelihood. Therefore, we derived a mathematical model to account for digestibility and fill of the ruminoreticular digesta whenever the best model used to interpret marker studies, chosen based on likelihood criteria, is the GN model.

Keywords: Ruminants, Digestive tract, Markers, Kinetics, Mathematical models

Sumário

1. INTRODUÇÃO

O rúmen é um sistema complexo e heterogêneo, formado por digesta líquida e sólida com estratificação deste conteúdo em diferentes camadas, o que torna o processo digestivo nos ruminantes um sistema dinâmico que envolve a entrada e saída de líquidos, de microrganismos e de resíduos não-digeridos (Pereira et al., 2002). A modelagem matemática das funções produtivas, aliada à programação matemática e à avaliação empírica das predições com base nos resultados dos processos digestivos, permite a compreensão deste complexo sistema e a formulação de dietas, visando o melhor desempenho dos animais.

Para tanto, é necessário o empreendimento de esforços na compreensão dos mecanismos que governam o fluxo da digesta e a dinâmica de partículas no trato gastrintestinal (TGI) e como estes mecanismos afetam a eficiência de utilização dos nutrientes pelos animais. A busca por sistemas de produção mais eficientes não é recente (BALCH, 1950; ELLIS e HUSTON, 1968; Ellis et al., 1979; 1994).É possível identificar, na literatura, diversos estudos que buscam predizer o fluxo da digesta, a dinâmica das partículas e o fluxo de nutrientes no TGI dos ruminantes (Balch, 1950; Blaxter, 1956; Campling, 1962; Ellis e Huston, 1968; Úden et al, 1980; Faichney 1989; Vieira, 1997, 2008, 2012).

A taxa de passagem é uma variável fundamental, pois afeta a utilização dos nutrientes e por regular o tempo disponível para que o alimento siga os processos digestório e absortivo (Ehle, 1984). Os métodos de estimação da taxa de passagem da fibra (BALCH, 1950; ELLIS e HUSTON, 1968; ÚDEN et al, 1980) receberam constantes alterações e revisões com o propósito de renderem predições mais exatas e precisas. Estudos de cinética de trânsito das fases sólida e líquida exigem a recuperação de substâncias indigeríveis e facilmente identificáveis, denominadas marcadores. A marcação da fibra foi uma das alterações propostas com o objetivo de aprofundar o conhecimento sobre o comportamento das partículas alimentares no TGI dos ruminantes domésticos (Owens & Hanson, 1992).

A dinâmica de partículas no TGI depende de alguns fatores, tais como a natureza química e dos aspetos físicos e morfológicos, os quais determinam o tempo de degradação no rúmen. A retenção dos alimentos no rúmen-retículo permite uma relação simbiótica entre o animal e os microrganismos ruminais capazes de utilizar esses alimentos ingeridos como substratos para o seu crescimento (Hungate, 1988). Os dados obtidos por meio da dinâmica de partículas e do fluxo da digesta são fundamentais nos modelos de nutrição, que almejem predições acuradas (Offer et al., 2000). Portanto, entender como a digestão e a passagem atuam na remoção da digesta presente no rúmen, estudando como os efeitos combinados desses processos contribuem para maximização do consumo de nutrientes digestíveis, é parte indispensável nos estudos de cinética digestiva. Sendo assim, a análise quantitativa dos efeitos do alimento é, portanto, tarefa necessária para avaliar as relações que ocorrem ao longo do TGI. A modelagem matemática é empregada na descrição das relações dinâmicas ao longo da permanência do alimento no rúmen, de seus efeitos sobre o consumo voluntário e sobre a disponibilidade e o escape ruminal do alimento consumido (Vieira e Fernandes, 2006).

Há na literatura várias técnicas disponíveis para estimar a taxa de passagem (k) ou o tempo médio de retenção (1/k) das partículas pelo TGI dos ruminantes. Nos últimos anos, a estimativa da taxa de passagem tem sido realizada por meio do fornecimento de uma dose pulso do indicador com posterior amostragem das fezes, em intervalos de tempo conhecidos, nos quais são analisadas as concentrações do elemento químico utilizado. A curva de excreção do indicador é, então, ajustada a um modelo matemático para determinar os coeficientes relacionados à passagem das partículas (OLIVEIRA, 1999).

Neste sentido, o estudo da verossimilhança desses modelos matemáticos empregados na descrição do fluxo da digesta e dinâmica de partículas, por conseguinte, na melhoria da eficiência dos animais domésticos, possibilitam um melhor entendimento de como estas variáveis se comportam nos sistemas de produção.

2. OBJETIVO

Avaliar modelos matemáticos desenvolvidos para interpretar perfis de excreção dos marcadores nas fezes, os limites das inferências dos parâmetros e a compatibilidade dos pressupostos matemáticos e biológicos.

3. REVISÃO BIBLIOGRÁFICA

3.1. Evolução do entendimento da dinâmica de partículas no TGI dos ruminantes

Não é recente a preocupação com a compreensão dos processos digestivos. Na literatura, é possível observar uma contínua busca pelo entendimento sobre o comportamento do fluxo da digesta e dinâmica de partículas no TGI dos ruminantes (BALCH, 1950; Blaxter et al., 1956; CAMPLING e FREER, 1962; EVANS et al., 1984; LINDBERG, 1985; Ellis, 1979; WELCH, 1986; Ellis et al. 1979; 1994; 2002; Vieira et al., 2008; Van Bentum e 2012).

Diversos autores empreenderam esforços na compreensão e na descrição dos processos ocorridos no TGI dos ruminantes domésticos (Balch, 1950; Blaxter et al 1956;Castle, 1956 ; Brandt Thacker & 1.958 ; Grovum & Williams , 1973; Ellis et al, 1979; Faichney & Boston, 1983; Faichney , 1984; Dhanoa et al. 1985; France et al. 1985; Vieira et al 1997, 2008).No entanto, devido ao arranjo peculiar do TGI e à heterogeneidade da digesta, estudos sobre cinética de partículassão complexos.

Os primeiros estudos desenvolvidos apresentavam como principal problema a inexatidão das estimativas de fluxo de partículas pelo TGI, pois nos métodos convencionais de marcação da fibra, o marcador se separava do alimento no qual tinha sido fornecido. Marcadores tais como partículas plásticas (Ewing & Smith, 1917, Moore & Winter, 1934), óxido de ferro (Mitchell et al 1928; Moore & Winter, 1934),sementes de milho e sorgo (Warth,1927) eram inadequados. O método descrito por Lenkeit e Habeck (1930) é considerado fisiologicamente mais adequado para estudos de cinética de partículas. Neste método são utilizados o feno ou palha marcados com pigmentos de cor magenta ou fucsina ácida e a recuperação efetuada por contagem de partículas coradas nas amostras de fezes era a base para o estabelecimento da cinética de trânsito (Balch, 1950).

Blaxter et al. (1956) foram os primeiros a empregar uma descrição matemática formal para a excreção do indicador como a soma de dois componentes exponenciais e um tempo de retardo, atraso ou de trânsito no processo de eliminação das partículas alimentares remanescentes do processo digestório no TGI. De acordo com esses autores, a retenção das partículas ocorreria principalmente no rúmen e no abomaso; a constante representaria o tempo de trânsito das partículas nos demais orgãos do trato digestório até o primeiro aparecimento nas fezes.

As partículas dos alimentos que entram no rúmen possuem tamanhos diferentes. A forma da distribuição dessas partículas alimentares é dependente da forma como estas foram fornecidas, da composição química da partícula e atividade de mastigação pelos animais (Pond et al., 1989; Ellis 1968). Partículas maiores que um tamanho mínimo devem ser reduzidas antes que elas possam escapar do rúmen (POPPI et al., 1980). A redução do tamanho de partículas é devido, principalmente, à ruminação, mas a fermentação enfraquece os tecidos e aumenta sua fragilidade, o que contribui para a cominuição das partículas alimentares nas transferências entre os compartimentos do rúmen (Allen e Mertens, 1988).

Ellis et al. (1994) avaliaram a digesta e determinaram que as transformações digestivas são determinadas por fatores intrínsecos e por interações destes fatores com os processos cinéticos. Assim, a expressão quantitativa dos processos de digestão e passagem é necessária para estimar precisamente a quantidade e composição dos nutrientes digeridos e sua utilização pelo animal. A saída ruminal ou fluxo de resíduos não digeridos e indigestíveis através do trato digestivo denomina-se taxa de passagem, evento este que atua de forma simultânea e competitiva com a digestão. O fluxo ruminal inclui, além da fibra indigestível, bactérias e outras frações não degradadas do alimento, sendo que a composição e o volume da dieta são variáveis externas que influenciam a digestão, a taxa de digestão e a reciclagem do conteúdo ruminal.

A taxa de passagem é um dos mais importantes parâmetros que influenciam o desaparecimento ruminal da digesta e a ingestão. Mertens e Ely (1982) descreveram que a taxa de passagem dos alimentos ao longo do trato digestivo é influenciada pelos níveis de consumo e forma física da dieta. Os principais fatores determinantes da taxa de passagem são o tamanho e a gravidade específica das partículas (Ellis et al., 2005), pois definem o tempo no qual as partículas do alimento permanecem no rúmen-retículo, bem como distribuição pelas diferentes regiões destes compartimentos. Entender a dinâmica de partículas e o fluxo da digesta permite definir estratégias alimentares e fornece um suporte quantitativo para os estudos de nutrição e, por conseguinte, a melhoria da eficiência de exploração dos animais domésticos (Udén et al., 1982).

3.2 EMPREGO DE MODELOS MATEMÁTICOS NA DESCRIÇÃO DA DINÂMICA DE PARTÍCULAS.

Estudos pioneiros de modelagem por compartimentos foram conduzidos com o objetivo de traduzir a complexidade dos fenômenos naturais de forma que estes possam ser empregados na predição da realidade. Os conceitos estabelecidos nestes primeiros estudos têm sido aplicados com sucesso na nutrição de ruminantes, pois fornecem um referencial teórico sobre as transformações sofridas pela digesta no TGI (Allen and Mertens, 1988; Blaxter et al., 1956; Ellis et al., 1979; France et al., 1985; Matis, 1972; Van Milgen et al., 1991; Waldo et al., 1972).

A quantificação da massa ou conteúdo ruminal é extremamente importante para os estudos relacionados à digestão e cinética de partículas. Diversos métodos podem ser utilizados para quantificar o conteúdo ruminal : determinação direta (abatendo o animal ou esvaziando o órgão) ou indireta, em que são utilizadas substâncias de referência, denominadas marcadores (Cannas et. Al.; 2003).O conceito de "modelagem de sistemas" tem sido frequentemente empregado na exploração pecuária de uma forma geral, com vistas a proporcionar benefícios à exploração dos animais de interesse zootécnico. Os modelos têm como objetivo básico efetuar a representação simplificada da realidade e possibilitam prever o funcionamento do sistema.

Um modelo básico foi proposto por Waldo et al. (1972), para representar a dinâmica de componentes fibrosos no rúmen, assumindo a existência de dois compartimentos ou frações sujeitas às forças que interagem para o desaparecimento da matéria fibrosa ingerida e retida no órgão. Nestes modelos são representadas as forças concorrentes que atuam no desaparecimento dos compostos fibrosos do rúmen e tais forças atuam na digestão de partículas fibrosas e removem de forma gradual a fração potencialmente digerível, e aquelas que propelem as partículas que contém partes digeríveis remanescentes a porção indigerível para os demais compartimentos do TGI. (Figura 1). A matéria fibrosa divide-se, portanto, em frações digeríveis e indigeríveis contidas na partícula alimentar. Cabe enfatizar que o limite entre elas é uma idealização esquemática, pois em sua forma natural, somente é possível visualizar a parte indigerível após exposição da partícula às ações digestoras das enzimas microbianas ruminais por tempo prolongado (Wilson, 1993).

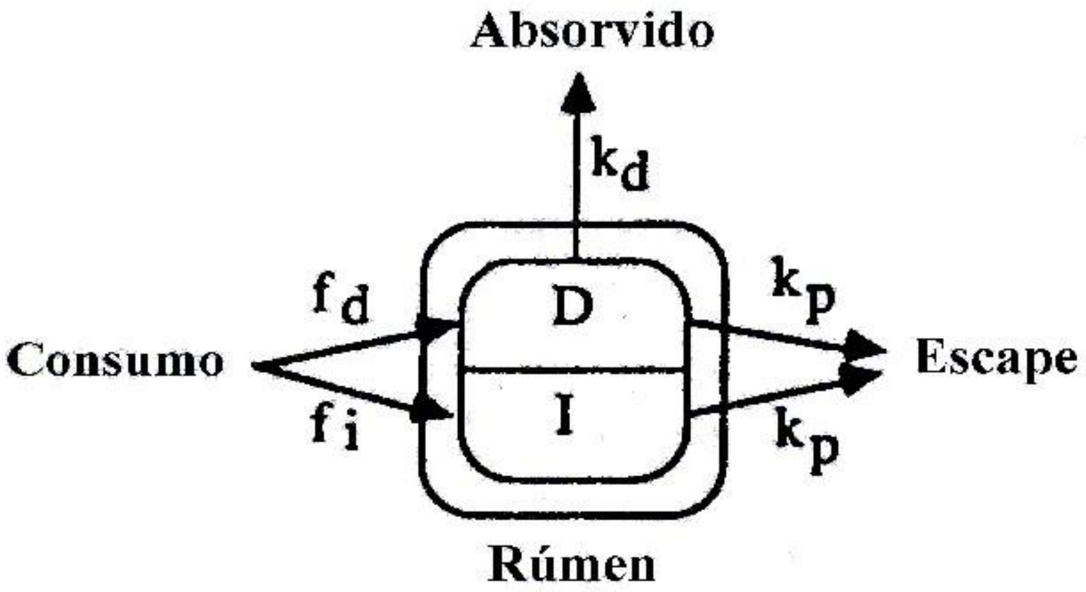

Figura 1: Diagrama de fluxos ilustra a compartimentalização da massa ruminal retida no rúmen e as forças que atuam para o seu ingresso e desaparecimento do órgão. Detalhes no texto. Allen e Mertens (1988).

Na Figura 1, f_d e f_i correspondem às frações digeríveis e indigeríveis da fibra insolúvel consumida (consumo). O montante absorvido é diretamente proporcional à massa ruminal de fibra potencialmente digerível (D). O escape de matéria fibrosa do rúmen depende da quantidade total de fibra presente no rúmen, que equivale à soma das frações digerível (D) e indigerível (I). Ambos os compartimentos são alimentados pela taxa diária de entrada de matéria fibrosa no rúmen (*input*) ou taxa de consumo de fibra (Consumo, Figura 1). Os símbolos k_d e k_p, também ilustrados na Figura 1, denotam as taxas específicas de degradação e passagem e são expressas em unidades recíprocas do tempo $\left(t^{-1}\right)$.

A descrição da taxa de passagem segue uma distribuição gama tempo dependente para a probabilidade de permanência das partículas no sistema (MATIS 1972). A principal diferença entre estes tipos de modelos é que o primeiro assume que a duração da passagem das partículas no rúmen se comporta exponencialmente e o último assume que a duração da passagem de partículas indigestíveis no rúmen tem distribuição gama. O modelo bi exponencial implica que existe probabilidade igual de saída para todas as partículas, independentemente do tamanho ou idade, enquanto que o modelo dependente do tempo implica que a probabilidade de passagem aumenta com o tempo.

Os modelos de distribuição gama com ordem de dependência do tempo são interpretados para explicar os processos físicos, químicos e biológicos que as partículas ingeridas sofrem no TGI, principalmente no rúmen (QUIROZ et al., 1988). O modelo bi exponencial (BLAXTER et al., 1956; GROVUM e WILLIANS, 1973) é uma condição particular do modelo gama tempo dependente (Matis (1972).

Baseado nas observações de Faichney (2005) e Kennedy (2005), Vieira et al (2008) desenvolveram um modelo generalizado de digestão *in vitro* e de cinéticas de partículas marcadas. Este modelo foi contrastado com o modelo de pool-único, comparando as massas observadas e preditas de fibra insolúvel na digesta ruminoreticular.

Vários modelos têm sido propostos na literatura para descrever a cinética de passagem. No entanto, nenhum critério seguro está disponível atualmente para determinar qual modelo seria mais apropriado para descrever os perfis de passagem nas diferentes condições encontradas (QUIROZ et al., 1988; MOORE et al., 1992). O critério sugerido por Vieira et al. (2008) pode ser útil na tomada de decisão acerca da escolha dos melhores modelos para interpretação desses perfis cinéticos. É importante salientar, porém, que a interpretação matemática dos perfis permite extrair informações quantitativas sobre a cinética de partículas no TGI por tanto, é parte essencial do processo de predição do valor nutritivo dos alimentos e do desempenho animal, o que torna a modelagem matemática importante ferramenta da pesquisa no campo da nutrição de ruminantes (Vieira e Fernandes, 2006).

3.3. AVALIAÇÃO DA QUALIDADE DE AJUSTE DOS MODELOS.

A avaliação da adequação do modelo é essencial para o desenvolvimento de estudos em que se pretende determinar a acurácia dos modelos utilizados na nutrição animal. Esta etapa é muito importante, pois dará subsidio para a escolha do melhor modelo. Tedeschi (2006) corrobora o argumento de Forrester (1961) sobre a necessidade de se avaliar a qualidade do ajuste dos modelos matemáticos. A validade de um modelo matemático deve ser julgada pela sua qualidade de ajuste a uma finalidade específica. Sendo assim, é necessário determinar se o modelo é válido para o conjunto de dados utilizados. A determinação do poder preditivo de modelos biomatemáticos pode ser realizada eficientemente combinando-se técnicas estatísticas e uma detalhada averiguação sobre a qualidade dos ajustes do modelo ao propósito para o qual foi construído (Mertens, 1976).

Desta forma, faz-se necessário determinar a concordância entre valores observados e preditos, a precisão, a acurácia e a eficiência do modelo (Tedeschi, 2006). A escolha do modelo que melhor explica a taxa de passagem, bem como a escolha de modelos mais apropriados para cada parâmetro ou variáveis testadas devem ser avaliadas pelo cômputo do critério Akaike ($AICc_h$) Akaike, 1974; Burnham & Anderson, 2004). O $AICc_\eta$ é calculado pela soma dos quadrados do erro (SSE_η), número de parâmetros estimados incluindo a variância residual (Θ_η), e o tamanho da amostra (n_η) para todas as diferentes versões de $N, \forall\eta = 1, 2, \dots, seis$. As diferenças entre os valores do $AICc_\eta$ (Δ_η), a probabilidade de verossimilhança (w_η), e a razão de evidência (ER_η), podem ser computadas por meio das equações empregadas por Vieira et al. (2012) para este mesmo fim.

3.3.1 Critério de informação de Akaike (AIC)

O Critério de Informação de Akaike é um estimador da distância relativa esperada entre dois modelos probabilísticos. Calculado a partir da medida de Kullbac-Leibler (K-L)e permite avaliar com base em sólidos conceitos teóricos sobre a máxima informação e entropia de modelos.Utiliza o princípio da parcimônia na escolha do melhor modelo, ou seja, de acordo com esse critério, nem sempre o modelo mais parametrizado é o melhor (BURNHAM e ANDERSON, 2004). Menores valores de AIC refletem um melhor ajuste (AKAIKE, 1974). Sua expressão é dada por:

$$AIC = -2 \, log \, L(\hat{\theta}) + 2 \, p \tag{1}$$

Em que: p é o número de parâmetros e $L(\hat{\theta})$ o valor do logaritmo da função de verossimilhança obtida considerando as estimativas dos parâmetros.

3.3.2 Critério de informação de Akaike corrigido – AICc

Utilizando critério de Akaike (1974), Sugiura (1978) propôs o critério de informação de Akaike corrigido, derivando uma variante de segunda ordem do AIC.

$$AICc = -2 \log L(\hat{\theta}) + 2\,p(\frac{\mathrm{n}}{\mathrm{n} - \mathrm{p} - 1}) \qquad (2)$$

Em que n representa o número de observações, $logL(\hat{\theta})$ é o logaritmo da verossimilhança (MV ou MVR) e p representa o número total de parâmetros de efeito fixo e aleatório estimado no modelo.

3.3.3 Critério de informação bayesiano (BIC)

O critério de informação bayesiano (BIC), consiste em um critério de avaliação de modelos definido em termos de probabilidade a posteriori. O nome do critério foi estabelecido dessa forma pois o autor utilizou um argumento bayesiano para prová-lo. Assim como o AIC, também leva em conta o grau de parametrização do modelo e, da mesma forma, quanto menor for o valor de BIC (SCHWARZ, 1978), melhor será o ajuste do modelo. Sua expressão é dada por:

$$BIC = -2logL\theta + p\ log(n), \qquad (3)$$

Em que: n é o número de observações utilizadas para ajustar a curva, e p é o número de parâmetros do modelo. No entanto, convém lembrar que Burnham e Anderson demonstraram que, para grandes amostras, os valores de probabilidade de verossimilhança calculados, tanto a partir do BIC como do AIC convergem.

3.3.4 Coeficiente de determinação ajustado (Raj2)

Para evitar dificuldades na interpretação R^2, convém utilizar o R_a^2 (R^2ajustado), definido para uma equação com p+1 coeficientes como:

$$R_{aj}^2 = R^2 - \left(\frac{p-1}{N-p}\right)(1 - R^2) \qquad (4)$$

em que:

$$R^2 = 1 - \frac{SQR}{SQT},$$

$$SQR = \sum_{i=1}^{n}\left(Y_i - \widehat{Y}_i\right)^2$$

é a soma de quadrados do resíduo,

$\widehat{Y}_i = f(x_i, \hat{\theta})$,

$SQT = \sum_{i=1}^{n}(Y_i - \overline{Y}_i)^2$é a soma de quadrados total,

n é o número de observações utilizadas para ajustar a curva e p é o número de parâmetros na função, incluindo o intercepto.

É importante ressaltar que o R_{aj}^2 não deve ser utilizado para avaliação de modelos não lineares pois, segundo Segundo Ratkoswsky (1990), o R_{aj}^2 não tem significado lógico para modelos não lineares.

3.3.5 Análise de Resíduos

Draper e Smith (1966) sugeriram que a análise de resíduos é um procedimento válido e usual para diagnosticar a qualidade de ajuste tanto de modelos lineares como não lineares. Endreyni (1976) enfatizou que a avaliação por meio dos resíduos é um critério sensível para avaliar a adequação de modelos de cinética digestiva. Assim, quanto maior o número de corridas de sinal dos desvios padronizados em um perfil (Draper & Smith, 1966), melhor será o ajuste do modelo (Vieira et al., 1997b).

O sucesso de qualquer método de ajuste de curvas pode ser julgado pela habilidade do modelo em descrever os dados, sem super ou subestimar, sistematicamente, alguma seção do perfil de passagem de partículas, o que resulta na obtenção de estimativas mais acuradas dos parâmetros (Dhanoa et al., 1985; Vieira et al., 1997b).

3.4 Modelos de cinética de trânsito

Dhanoa et al. (1985), propuseram a existência de mais de dois compartimentos de retenção e mistura de partículas no TGI ao assumirem que o fluxo da digesta representava um processo exponencial multicompartimental, ou seja, baseavam-se na pressuposição de que o fluxo através desses múltiplos compartimentos apresentava probabilidade de escape exponencialmente distribuída, tempo-independente.O modelo é descrito pela equação:

$$C_t = S\exp(-k_1 t)\exp(-(N-2)\exp(-(k_1 - k_2)t)) + e_t, \qquad (5)$$

Em que: Ct é a concentração do indicador (mg/kg) de partícula nas fezes no tempo t(h), e_t é o erro aleatório, k_1 é a taxa fracionária de escape do rúmen-retículo, é a taxa fracionária de escape atribuída ao pós rúmen, N representa o número de compartimentose S é o parâmetro escalar em função de k_1, k_2 e N

Pond et al. (1988) e Matis (1972) supondo dois compartimentos e um tempo de retardo da excreção fecal, introduziram elementos estocásticos no modelos proposto por Blaxter et al. (1956). A função geral assume que o tempo de retenção (R_i) é uma, com um tempo de atraso fixo (τ) do compartimento terminal até o exterior do sistema e um tempo total de permanência da partícula no sistema (T). A probabilidade de se encontrar uma partícula no i-ésimo compartimento introduzida no sistema no tempo zero é:$\left(p_i(t)\right)$

A equação abaixo descreve o modelo GN

$$\dot{p}_0(t) = (\lambda t)^{N-1}\lambda \exp(-\lambda t)/(N-1)! \qquad (6)$$

Em que $\dot{p}_0(t)$ é a função densidade de probabilidade associada a T, λ é o valor assintótico da taxa de passagem fracionária tempo dependente para N > 1, N é um inteiro positivo, cujos valores são válidos para N≥2. N eq. (6) a média e o desvios são dados pelas expressões: $\mu_T = N/\lambda$ e $\sigma_T^2 = N/\lambda^2$.

Observando que os processos de mistura e redução das partículas recém-ingeridas alteram sua probabilidade de escape por meio do orifício retículo-omasal, Matis (1972) e Matis et al., (1989) propuseram uma série de modelos estocásticos (GNG1)para interpretar excreção fecal de marcadores de partículas. A formulação geral para o modelo é baseada no tempo de rentenção(tempo de permanência R_i) como variável aleatória, com um tempo fixo de atraso(τ) do compartimento terminal até o exterior do sistema, e um tempo total (T) de permanência da partícula no sistema. No último compartimento tem um caso especial de distribuição Gamma$\left(\Gamma(N,\lambda,t)\right)$: a distribuição exponencial $\Gamma(N,\lambda,t) = E(k,t)$ para $N = 1$. A probabilidade de encontrar uma partícula aleatória no tempo zero, no primeiro compartimento é $p_1(t) = \exp(-\lambda t)\sum_{i=0}^{N-1}(\lambda t)^i/i!$, e no segundo compartimentoé $p_2(t) = \delta^N \exp(-kt) - \exp(-\lambda t)\sum_{i=0}^{N-1}\delta^i(\lambda t)^{N-i}/(N-i)!$.

Em que: δ é uma simplificação obtida por meio da expressão: $\delta = \lambda/(\lambda - k)$,$k$ taxa fracionária de passagem de uma partícula aleatória, e λ esta associada ao primeiro compartimento como no modelos GN.

Os momentos do modelo bicompartimental são:

$$\mu_T^{'} = N/\lambda + 1/k; \tag{7}$$

$$\sigma_T^2 = N/\lambda^2 + 1/k^2 \tag{8}$$

Matis et al (1989) definiu o ponto final para este modelo como:$\dot{p}_0(t) = kp_2(t)$e , recomendou a substituição de $\dot{p}_0(t^*)$, nas equações $\dot{p}_0(t) = (\lambda t)^{N-1}\lambda \exp(-\lambda t)/(N-1)!$ e $\dot{p}_0(t) = kp_2(t)$ para obtenção de estimativas válidas para trânsito de partículas com elementos estocásticos. A equação abaixo descreve a série de modelos GNG1.

$$C_t = \begin{cases} e_t \text{for } t < \tau \ (t^* < 0); \\ C_0\dot{p}_0(t^*) + e_t \text{for } \ t \geq \tau \ (t^* \geq 0). \end{cases} \tag{9}$$

Em que C_t apresentam o mesmo significado da eq. 5 , $t^* = t - \tau, C_0$ e τ são derivadas conforme sugerido por Vieira et al. (2008). Os momentos T obtido pelo da eq. (9)com a expressão $\dot{p}_0(t) = kp_2(t)$no lugar de $\dot{p}_0(t^*)$, são $\mu_T = \tau + N/\lambda + 1/k$ e eq. (8)como variância, enquanto $\mu_T = N/\lambda)$ e $\sigma_T^2 = N/\lambda^2$são os momentos de T ajustados pela eq. (9)com eq. 6substituindo $\dot{p}_0(t^*)$.

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CAPÍTULO 1

O capítulo a seguir corresponde a um artigo integrante desta dissertação submetido como manuscrito ao periódico JournalofTheoreticalBiology (ISSN: 0377-8401) e, como tal, sua redação e edição foram preparadas segundo às normas deste periódico, normas essas constantes na página do mesmo na rede mundial de computadores conforme o endereço a seguir:

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Nonlinear models to describe the transit of particles through the ruminant digestive tract: evaluation of models and theoretical implications

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Abstract. Fecal profiles of the particulate markers Cr and La, and of the fluid marker complex Co-EDTA were obtained from digestion kinetic studies with cows, steers, and sheep with the aim of evaluating mathematical models designed to interpret marker excretion profiles in feces. The models evaluated were the multicompartmental model (Dhanoa et al., 1985), the Gamma model described as GN (Pond et al., 1988), and the GNG1 model (Matis, 1972). Models were fitted by ordinary nonlinear least squares and evaluated on the basis of likelihood criteria. Despite remarkable differences in terms of likelihood, models were quite similar in terms of visual adherence to observed time profiles and presented overlapping interval estimates for compartment mean retention times. The major relative numerical discrepancies observed among models were related to the mean and variance of the transit time for the first appearance of the marker in feces. The model with the best performance in mimicking the marker profiles were the GN model; the GNG1 model and the multicompartmental model were almost equivalent in terms of likelihood. Therefore, we derived a mathematical model to account for digestibility and fill of the ruminoreticular digesta whenever the best model used to interpret marker studies, chosen based on likelihood criteria, is the GN model.

Keywords: Ruminants, Digestive tract, Markers, Kinetics, Mathematical models

1. Introduction

The fecal excretion profiles of a marker are characterized by a time delay followed by a sharp increase in the concentration of the marker that peaks and decrease smoothly and asymptotically to zero, particularly in ruminant species (Uden et al., 1982). This pattern is actually the first derivative of the accumulated fecal recovery of a marker fed as a pulse dose to an animal (Balch, 1950; Blaxter et al., 1956). Several markers have been used to trace both solid and particulate phases of the digesta in the ruminant gastrointestinal tract. There is no ideal marker (Owens and Hanson, 1992), but chromium (Cr), lanthanides, and soluble complexes of Cr and cobalt (Co) have been extensively used in studies regarding digestion kinetics (Ellis and Huston, 1968; Ellis and Beever, 1984; Hartnell and Satter, 1979a; Hartnell and Satter, 1979b; Udén et al., 1980). The marker concentration in the feces of ruminants have been described by nonlinear mathematical models in which parameters have theoretical meanings applicable to the field of ruminant nutrition (France, 1998), and some of the most used models in the literature were evaluated in the present study.

Compartmental models of one (Matis et al., 1989; Pond et al., 1988), two (Blaxter et al., 1956; Matis, 1972; Matis and Hartley, 1971), or multiple (Dhanoa et al., 1985) compartments have been used to describe the transit of markers through the gastrointestinal tract of ruminants (Offer and Dixon, 2000). Some researchers have compared these models based on their quality of fit to fecal excretion profiles of the markers (Beauchemin and Buchanan-Smith, 1989; Susmel et al., 1996). However, the basic problem regarding the application of these models is the biological interpretation of the rate constants (Huhtanen et al., 1995; Susmel et al., 1996; Van Soest, 1994; Vieira et al., 2008a), and not necessarily differences regarding the adherence of the fitted models to the marker profiles. Each one of these models was built on both biological and mathematical assumptions; the assumptions are mathematical constraints, so that results obtained by the operation of the model do not become impossible, absurd, or undetermined. Biological assumptions regard definitions about pools, compartments, flow-rates, and order and direction of reactions among pools and outflow to the system exterior. Therefore, the incitements to perform this study were the understanding of how such nonlinear models operate, the limits of the inferences taken from its estimated parameters, the compatibility of mathematical and theoretical assumptions among models and with the real world, and corollaries resulting from the use of these models in the interpretation of marker excretion profiles.

2. Material and Methods

Fecal profiles of particulate markers chromium (Cr; 52 profiles) and lanthanum (La; 30 profiles), and fluid phase marker cobalt–ethylenediaminetetraacetic acid (Co-EDTA; 57 profiles) were gathered from studies performed on digestion kinetics by Vieira et al. (1997), Pádua (2009), Favoreto et al. (2008), Santos (2011), and A. M. Fernandes (unpublished results). Domestic ruminant species used in these studies were cattle and sheep: steers (12 Cr and 11 Co-EDTA profiles), and dry (six Cr profiles) and lactating dairy cows (28 Cr and 18 Co-EDTA profiles) formed the cattle group, whereas mature weathers (six Cr, 30 La, and 28 Co profiles) formed the sheep group.

2.1. Particulate markers Cr and La

In the referred studies, the forage fiber particles were prepared according to the methodologies presented by Ellis and Beever (1984) and Úden et al. (1982). The Cr-mordant particles were prepared from samples of the forage fed treated with neutral detergent solution and soaked with a solution of potassium dichromate. The tetravalent chromium was reduced by ascorbic acid to yield Cr^{3+} in order to form strong covalent bonds with the negatively charged fibrous particles. Forage particles marked were from elephant grass (*Pennisetum purpureum* Schum.) assessments at different cutting heights (Vieira et al., 1997), Stargrass (*Cynodon nlemfuensis* Vanderyst (Bogdan)), and Mombasa grass (*Megathyrsus maximus* (Jacq.) B. K. Simon & S. W. L. Jacobs) grazed by the experimental animals (Favoreto et al., 2008; Santos, 2011), sugar cane (*Saccharum* sp.) (Pádua, 2009), and corn (*Zea mays* L.) (A. M. Fernandes, unpublished results) silage. The elephant grass was fed chopped to dry dairy cows; lactating dairy cows grazed on paddocks of Mombasa grass or Stargrass; steers were fed on sugar cane silage; and wethers were fed on corn silage. Pulse-doses of Cr-mordant fibers were mixed to 250 g of ground corn and offered to lactating dairy cows and steers; the dry cows received the pulse-doses of Cr-mordant directly through rumen cannulas.

La was the particulate marker for concentrate feed (mainly soybean meal and ground corn mixtures; unpublished results from A. M. Fernandes). The Fiber from concentrates was prepared according to Ellis and Beever (1984). Samples taken from the offered concentrates were treated with neutral detergent and soaked in a pH-controlled $LaCl_3$ solution so that the negatively charged fiber particles of concentrates adsorbed the La^{3+} cations. Pulse-doses were offered to the wethers mixed with 100 g of ground corn.

2.2. Fluid phase marker Co-EDTA

The Co-EDTA complex was prepared according to the technique presented by Úden et al. (1982). In the experiments reported here, the dry powder of Co-EDTA was solubilized in water and then orally administered to lactating cows (Favoreto et al., 2008; Santos, 2011), steers (Pádua, 2009), and wethers (A. M. Fernandes, unpublished results).

2.3. Fecal collection schemes and chemical analysis of Cr, La, and Co

All profiles gathered from the referred studies are time-series of marker concentrations (mg/kg) in the fecal dry matter. Feces were taken as grab samples directly from the rectum of the steers, dry dairy cows, lactating dairy cows, and wethers at predetermined times after markers were pulse-dosed to the animals. A sample was taken prior to the administration of the marker pulse-dose to represent zero-time; afterwards, grab samples were taken to form a sequence per animal, including the zero-time, of 21, 23, 24, 28, and 29 time points according to the study. The time for fecal collections lasted from zero to 148 h (Vieira et al., 1997), 144 h (A. M. Fernandes, unpublished), 192 hours (Favoreto et al., 2008; Santos, 2011), and 216 hours (Pádua, 2009).

The chemical analyzes used in the reported studies were based on spectrometric methods of Atomic Absorption (Favoreto et al., 2008; Pádua, 2009; Vieira, 1997) and

Inductively Coupled Plasma (Santos, 2011; A. M. Fernandes, unpublished results) to quantify the metal elements recovered in the fecal matter (Moore et al., 1992; Hartnell and Satter, 1991). In all studies, grab fecal samples were dried in a forced air oven (55 °C for 48 h and grounded to pass through a 1 mm screen) and then either ashed or acid digested to oxidize the organic matter. Nitric acid was used either to solubilize fecal ashes or to digest fecal organic matter in conjunction with perchloric acid according to method 975.03 (AOAC, 1998). Corrections were used to remove systematic, biased absorbance readings when no marker presence was expected in the profile, e.g., by taking as reference for correction the zero-time readings or when the marker elimination phase had already stabilized indicating the complete elimination of the marker, particularly in the terminal portion of the marker excretion profile.

2.4. Nonlinear mathematical models

The transit of a marker through the gastrointestinal tract of ruminants have been described as a flow-path formed by several marker retention compartments connected in a sequence of irreversible flows (Blaxter et al., 1956; Dhanoa et al., 1985; Matis, 1972; Matis and Hartley, 1971). The escape of a marker administered as a pulse dose is assumed to follow first-order kinetics in all compartments. Each compartment has a first-order fractional rate of escape and due to the connecting sequential nature of the $1, 2, \cdots, n$ discrete compartments, it is also assumed that the fractional escape rates, namely k_i (1/h) $\forall i = 1, 2, \cdots, n-1$, are subjected to the constraint $k_1 < k_2 < \cdots < k_{n-1}$. A possible solution to this system is based on the approximation used by Dhanoa et al. (1985) that yielded:

$$C_t = S \exp(-k_1 t) \exp(-(n-2) \exp(-(k_1 - k_2)t)) + e_t, \qquad (1)$$

in which C_t is the marker concentration in feces at a given time t (h), and e_t is the random error term assumed to be normal, independent, and identically distributed with mean zero and variance σ^2. The scale parameter S is a function of k_1, k_2, and n. The parameter S also depend on the ratio (or concentration) of marker in the first compartment mass (mg/kg) at time zero. The slowest rate (k_1) is ascribed to the fractional escape rate of the marker from the ruminoreticulum, which is assumed to be the compartment with the largest and slowest turnover time $(1/k_1)$. According to Grovum and Williams (1973a), the compartment in second place in terms of turnover time $(1/k_2)$ is assumed to be located post-ruminally, and its passage rate (k_2) have been ascribed to the passage of the marker through the caecum and proximal colon. The deterministic solution to compute the total mean retention time (h) in the gastrointestinal tract $(TMRT)$ of the ruminant is provided as follows (Dhanoa et al., 1985; France, 1998):

$$TMRT = 1/k_1 + 1/k_2 + \sum_{i=3}^{n-1} 1/\big(k_2 + (i-2)(k_2 - k_1)\big). \tag{2}$$

The time (h) for the first appearance of the marker in feces is the transit time, namely $\tau = \sum_{i=3}^{n-1} 1/\big(k_2 + (i-2)(k_2 - k_1)\big)$.

In addition to the common error, Matis and Hartley (1971) and Matis (1972) introduced another stochastic element in the mechanistic formulation deduced by Blaxter et al. (1956) about the transit of feed residues through the gastrointestinal tract of sheep. The general gamma function was used to model one-compartment and double-compartment systems with non exponential retention times of homogeneous particles within compartments (Matis et al., 1989; Pond et al., 1988). The general formulation is based on the retention time (also called sojourn time, R_i) as a random variable, a fixed time delay (τ) from the terminal compartment to the system exterior, and a total residence time (T) of a random particle in the system. Stochastically, there is a probability $\big(p_i(t)\big)$ of finding in the i-th compartment a given particle introduced into compartment one at time zero. There is also the probability of finding the random particle within the system at a given time (t) that represents the survivorship function

$(p_T(t))$, and the probability that a given random particle can be found in the system exterior (output, o) at time t $(p_o(t) = 1 - p_T(t))$, which is the cumulative distribution function for T. Therefore, the probability density function associated to T is $f_T(t) = dp_o(t)/dt = \dot{p}_o(t)$, which represents a model with Erlang residence times in a single compartment as follows:

$$\dot{p}_o(t) = (\lambda t)^{N-1}\lambda \exp(-\lambda t)/(N-1)!, \qquad (3)$$

in which λ (1/h) is the asymptotic value of the age-dependent fractional rate of passage, $\forall N \in \mathbb{Z}^+ \wedge N \geq 2$. To mimic the time profiles, whenever $t < \tau, \dot{p}_o(t) = 0$, otherwise Eq. (3) operates. For Eq. (3), the mean (μ_T, h) and variance (σ_T^2, h^2) of T are given by

$$\mu_T = N/\lambda, \text{ and} \qquad (4)$$

$$\sigma_T^2 = N/\lambda^2. \qquad (5)$$

The model described by Eq. (3) has been used to interpret marker excretion profiles and is usually referred to as a class of GN models; the acronym GN is used to represent the gamma distribution with parameter N (Ellis et al., 2002; Matis et al., 1989; Pond et al., 1988).

Matis and Hartley (1971) and Matis (1972) extended this preceding derivation for a double compartment system in which lifetimes or retention times of particles in the first compartment are gamma distributed, and lifetimes of particles in the second compartment are exponentially distributed. In fact, particles in the second compartment have a special case of the gamma distribution $(\Gamma(N, \lambda, t))$: the exponential distribution, i.e., $E(k, t) = \Gamma(N, \lambda, t)$, for $N = 1$. Therefore, the probability of finding a given marked random particle dosed at time zero in the first compartment is $p_1(t) = \exp(-\lambda t)\sum_{i=0}^{N-1}(\lambda t)^i/i!$, and in the second compartment is

$$p_2(t) = \delta^N \exp(-kt) - \exp(-\lambda t)\sum_{i=0}^{N-1}\delta^i(\lambda t)^{N-i}/(N-i)!. \qquad (6)$$

In Eq. (6), $\delta = \lambda/(\lambda - k)$, k is the fractional rate of escape of the random particle from the second pool represented by fluid diluted particles (turnover pool) below the raft in the ruminoreticular compartment, and λ has the same meaning as previously ascribed and is associated to the transference of the particle from the first compartment or raft to the turnover pool (Vieira et al., 2008a). The mean and variance of the double-compartment model are specified as follows:

$$\mu_T' = N/\lambda + 1/k, \text{ and} \tag{7}$$

$$\sigma_T^2 = N/\lambda^2 + 1/k^2. \tag{8}$$

Matis et al. (1989) defined the endpoint model for this double-compartment system as

$$\dot{p}_o(t) = kp_2(t), \tag{9}$$

and the model have been called as GNG1 class of models because of the gamma distribution with parameter N associated to the raft pool and the exponential distribution associated to the turnover pool (Ellis et al., 1994; Matis et al., 1989; Pond et al., 1988; Wylie et al., 2000).

In order to obtain valid parameter estimates regarding the transit of particles with stochastic elements, one can fit the following segmented model after replacing $\dot{p}_o(t^*)$ by Eq. (3) or Eq. (9) accordingly (Matis et al., 1989):

$$C_t = \begin{cases} e_t & \text{for } t < \tau \ (t^* < 0); \\ C_0\dot{p}_o(t^*) + e_t & \text{for } t \geq \tau \ (t^* \geq 0). \end{cases}$$

(10)

In Eq, (10), C_t and e_t have the same meanings as described for Eq. (1); $t^* = t - \tau$, and C_0 and τ, following the derivation suggested by Vieira et al. (2008a), are the concentration of the marker in the first compartment at time zero and the transit time (h) for a given marked particle that passed through the reticulo-omasal orifice to be recovered in the fecal matter, respectively. The mean and variance for T in the ruminoreticulum estimated by fitting Eq. (10) with Eq. (9) in place of $\dot{p}_o(t^*)$ are Eqns. (7)–(8), respectively, whereas Eqns. (4)–(5) are the mean and variance for T by fitting Eq. (10) with Eq. (3) in place of $\dot{p}_o(t^*)$. The total mean retention time in the gastrointestinal tract ($TMRT$) estimated for Eq. (10) with Eq. (9) in place of $\dot{p}_o(t^*)$ was $\mu_T = \tau + N/\lambda + 1/k$, and the variance estimator given by Eq. (8).

2.5. Model fitting and evaluation of the quality of fit

The nonlinear models described by Eq. (1), and Eqns. (3) or (9) in place of $\dot{p}_o(t^*)$ in Eq. (10) were fitted by means of the PROC NLIN of SAS (v.9, SAS Systems Inc., Cary, NC, USA). The algorithm for minimization of the sum of squares of errors (SSE) was the Newton method. However, when correlations between parameters were greater than 0.9 the Marquardt algorithm was preferred. The quality of fit of the models was assessed by computing likelihood criteria (Akaike, 1974; Burnham and Anderson, 2004; Sugiura, 1978). The models were ranked based on the corrected Akaike information criterion $AICc_h$, the differences $\Delta_h = AICc_h - \text{minimum}\, AICc_h$, the likelihood probability $w_h = \exp(-\Delta_h/2)/\sum_{h=1}^{H}\exp(-\Delta_h/2)$, and the evidence ratio as $ER_h = (\text{maximum}\, w_h)/w_h$, for each one of the *h*-th models in the set, according to the recommendations described by Burnham and Anderson (2004) and Vieira et al. (2012).

3. Results

3.1. *Model fitting*

The number of fits with $\Delta_h = 0$ revealed the superiority of the GN model in mimicking the time profiles of particulate markers Cr and La (Table 1). We expected that GN would best mimic Co-EDTA profiles too, but surprisingly the GNG1 model was unequivocally superior in terms of likelihood support, i.e., the number of profiles with $0 \leq \Delta_h \leq 2.0$ was higher for GNG1 for mimicking Co-EDTA profiles. All models with $\Delta_h > 2.0$ were considered to have much less or even no support in terms of likelihood. The model proposed by Dhanoa et al. (1985) described by Eq. (1) performed equally likely to the GNG1 model for Cr and La if considered only the best fits, i.e., for $\Delta_h = 0$.

Nonetheless, the GNG1 model yielded 43 and 20 fits for Cr and La, respectively, and 163 fits to Co-EDTA profiles with sufficient likelihood because $0 \leq \Delta_h \leq 2.0$. In general, the GNG1 model presented more likelihood support for describing the transit of the fluid phase marker Co-EDTA, whereas the GN model presented more likelihood for describing the passage of Cr and La. Because N for GN models varied from two to six, and N for GNG1 models varied from one to six, the number of models or equivalent hypotheses evaluated in the multimodel selection process was 12 for each one of the Cr, La, and Co-EDTA excretion profiles.

Some additional criteria for evaluating the quality of fit of the models could only be established after estimating the nonlinear parameters. Estimates that were biologically relevant according to the principles that guided the model development process were accounted for in the judgment of the quality of fit. For example, for both GN and GNG1 models, because estimates for parameters τ and N were inversely related, i.e., as N increased the estimates of τ decreased or even became zero, the model chosen was the one with $0 \leq \Delta_h \leq 2.0$ that yielded estimates considered plausible whenever $\tau > 7$ h. Because τ do not figure in Eq. (1) and is implicitly estimated by the sum in Eq. (2), this aspect was irrelevant to the fitting of Eq. (1). Therefore, the model that best suited the Cr excretion profiles summarized in Table 2 was the GN model, seconded by GNG1, and then by Eq. (1). In the case of La, the GN model was considered the best choice, followed by Eq. (1), and lately by the GNG1 model. The GNG1 model best mimicked the Co-EDTA excretion profiles in first place, followed respectively in terms of number of well-mimicked profiles by GN and Eq. (1). The case of the Co-EDTA and Cr-mordant excretion profiles are worthy of note, because for some cases estimates of parameter λ were much greater than estimates of parameter k; as much as 80 times greater. In those cases, the SSE were insensitive to increases in N, but this did not mean that the model was not capable to mimic the time profiles and even of being considered the best choice. This problem was not applicable to Eq. (1) because n is an estimable parameter in that equation.

3.2. *Scale and dispersion estimates of the mean retention time*

The Akaike criterion and the derived measures were sensitive to differences in the fitted time trends (Figs. 1 and 2). Sometimes, the evidence ratio (ER_h) reached very high values and this is an indicative that the model would be a poorer choice for mimicking the time trend of the marker excretion. An example to illustrate this situation is shown on panel (c) of Fig. 1. Despite the G1G1 model (Eq. (10) for $N = 1$) had likelihood support, i.e. $\mathit{\Delta}_h = 0.0$ and $w_h = 0.891$, and Eq. (1) had no likelihood support ($\mathit{\Delta}_h = 14.7$ and $w_h = 0.001$), the predicted trend lines were very close to each other so that its practical difference was nil. In that case, $\hat{\mu}_T = \hat{\tau} + 1/\hat{\lambda} + 1/\hat{k} = 34.8$ h and $\hat{\sigma}_T = 17.3$ h for G1G1, and for Eq. (1) $\hat{\mu}_T = 35.9$ h and $\hat{\sigma}_T = 18.7$ h, so that, for practical reasons, μ_T can be predicted by both models despite the likelihood differences. Therefore, for many cases likelihood differences were remarkable (e.g., Fig. 1, panels e and f), and yet mean retention times were estimated with very likely overlapping intervals. For instance, in Fig. 1e, the fit of G2 resulted in $\hat{\mu}_T = 61.6$ and $\hat{\sigma}_T = 35.7$ h, respectively, whereas for Eq. (1) the estimates of the mean and variance were $\hat{\mu}_T = 73.8$ and $\hat{\sigma}_T = 52.3$ h, respectively. In other example presented, the estimates of the total mean retention time overlapped too for Eq. (1) and G3, even the former model representing a poorer choice than the latter (Fig. 2, panel d). The estimates for G3 were $\hat{\mu}_T = 60.2$ and $\hat{\sigma}_T = 35.2$ h, whereas the estimates for Eq. (1) were $\hat{\mu}_T = 72.8$ and $\hat{\sigma}_T = 52.4$ h. In resume, differences among estimates about mean residence times for particles in the system based on the three models fitted to the same profiles were not likely to have occurred.

3.3. *Patterns exhibited by the marker profiles*

The patterns exhibited by markers in fecal profiles shared some characteristics. The excretion of the fluid-phase marker Co-EDTA always presented after the time delay a sharp increase in its fecal concentration, no matter the species under study and raising condition. Lactating cows grazing Mombasa grass and Stargrass presented this pattern (Fig. 2, panels a and b) and sheep fed corn silage at different planes of nutrition also exhibited this pattern (Fig. 1, panels g and h) for Co-EDTA. The particulate marker La used for concentrate feeds to generate the profiles evaluated in the present study also exhibited a trend similar to Co-EDTA in sheep (Fig. 1, panels a, b, and c). The G1G1 fit to the La excretion profile (Fig. 1c) yielded $\hat{\mu}_T = 34.8$ and $\hat{\sigma}_T = 17.3$ h, whereas the estimates from the fit of G3G1 for Co-EDTA (Fig. 1g) were $\hat{\mu}_T = 41.9$ and $\hat{\sigma}_T = 25.1$ h, thus evidencing that the interval estimates for passage of Co-EDTA and La marked particles probably overlapped. The profiles of the roughage marker Cr presented areas under the curves that appeared larger than La and Co-EDTA ones, as it is possible to appraise visually on Figs. 1 and 2. The estimates for Cr retention times of Fig. 1e were $\hat{\mu}_T = 61.6$ and $\hat{\sigma}_T = 35.7$ h, and those related to Fig. 1f were $\hat{\mu}_T = 55.1$ and $\hat{\sigma}_T = 28.5$ h.

Some fitted examples are shown in Tables 3, 4, and 5 to illustrate important properties about marker profiles that can be inferred from parameter estimates and of mean retention times of markers. Estimates obtained for parameter k of GNG1 and for parameter k_1 of Eq. (1) were about the same order of magnitude (10^{-2}); the same can be said about point estimates of parameters λ and k_2 (10^{-1} order), although direct comparisons between N values of GN and GNG1 and n of Eq. (1) are not applicable (Tables 3, 4, and 5). Direct comparisons among λ and k of GNG1, k_1 and k_2 of Eq. (1), and λ of GN are useless too; for that one should have to take the reciprocals $1/\mu_T^{'}$ of GN and GNG1 and compare to k_1 of Eq. (1) estimates, because they represent ruminoreticular passage, a common assumption for all three models. Despite our estimates had originated from marker profiles of different animals and diets, they rounded about the same order of magnitude (10^{-2}) for the range of estimates of k_1 (0.02 to 0.09/h), whereas the estimated ranges for $1/\mu_T^{'}$ of GN and GNG1 were 0.02 to 0.07 and 0.01 to 0.06/h, respectively (Tables 3, 4, and 5). Nonetheless, these values should be looked with caution, because the lower the estimate of the fractional rate the larger the estimate of the mean retention time. As an example, a hypothetical $\widehat{1/\mu_T^{'}} = 0.01/\text{h}$ for GNG1 corresponds to a $\widehat{\mu_T^{'}} = 100$ h two times greater than $1/\hat{k}_1 = 50$ h for $\hat{k}_1 = 0.02/\text{h}$ in the ruminoreticulum.

3.4. *Variations about estimates of the transit time*

There were large variations in the scale ($\hat{\tau}$) and dispersion ($\hat{\sigma}_\tau$) estimates of the transit time of the particulate (Cr and La) and fluid (Co-EDTA) markers. The estimates of the transit time ($\hat{\tau} \pm \hat{\sigma}_\tau$) of Cr in cows were 11.4 ± 4.5 (17 profiles), 14.6 ± 2.4 (10 profiles), and 12.2 ± 4.7 h (seven profiles) for GN, GNG1, and Eq. (1), respectively. For steers, 1.7 ± 2.4 (two profiles), 6.3 ± 1.1 (three profiles), and 15.6 ± 0.2 h (seven profiles), respectively, for transit time estimates of Cr with GN, GNG1, and Eq. (1), whereas for sheep, the transit times of Cr were solely estimated with GNG1 as 15.6 ± 0.2 h (six profiles). The transit times for Co in cows were 5.8 (one profile), 7.5 ± 1.5 (15 profiles), and 8.6 ± 2.0 h (two profiles), in steers were 11.0 (one profile), 11.5 ± 3.4 (eight profiles), and 13.0 ± 1.4 h (two profiles), and in sheep were 11.5 ± 2.3 (nine profiles), 11.3 ± 2.4 (17 profiles), and 7.8 ± 0.0 h (two profiles) estimated with GN, GNG1, and Eq. (1). For La in sheep, the respective estimates of the transit time with GN (21 profiles), GNG1 (three profiles), and Eq. (1) (six profiles) were 12.5 ± 4.4, 12.8 ± 1.8, and 11.6 ± 3.5 h.

4. Discussion

The retention of particles in the ruminant gastrointestinal tract has been investigated in ruminants to assess the amount of substrates digested in the ruminoreticulum and in the rest of the gastrointestinal tract (Allen and Mertens, 1988;

Ellis, 1978; Orskov and McDonald, 1979; Sniffen et al., 1992; Van Soest et al., 1992; Waldo et al., 1972). With that information, the amounts of metabolizable energy and protein available for maintenance and productive processes can be predicted from digested protein, carbohydrate, and lipid fractions; upon ruminal availability of non-protein nitrogen, true protein, carbohydrates, microbial yield and ultimately animal performance are predictable outputs (AFRC, 1993; Fox et al., 1992; Russell et al., 1992; Sniffen et al., 1992). The digestible amounts are the net result of the competing digestive and propelling forces over feed residues throughout the gastrointestinal tract (Blaxter et al., 1956; Van Soest et al., 1992; Waldo et al., 1972). Many studies were performed to update concepts by using recently developed statistical procedures and meta-analyses to obtain better ways to relate empirically passage rates with animal and dietary characteristics in new versions of the nutritional systems (Offner and Sauvant, 2004; Regadas Filho et al., 2014; Tedeschi et al., 2010; Tedeschi et al., 2012; Tylutki et al., 2008). Nonetheless, there are misconceptions in the biological interpretation of the fractional rates in the model equations studied here (Susmel et al., 1996) that have been employed in such nutritional systems (Vieira et al., 2008a). Such misconceptions started with Blaxter et al. (1956). Although well aware of the work of Balch (1950), who estimated that 80% of the mean retention time of particles was attributable to the retention process in the ruminoreticulum, Blaxter and coworkers ascribed two physical compartments of retention in the ruminant gastrointestinal tract, namely the ruminoreticulum and abomasum. Statistically, Matis and Hartley (1971) and Matis (1972) generalized the mathematical description of the transit process by assigning probability density functions to the first (Gamma) and second (Exponential) physical compartments of retention in the Blaxter's model. The view of a ruminoreticular retention followed by a post-rumen retention was strengthened by the series of papers published by Grovum and coworkers (Grovum and Williams, 1973a; Grovum and

Williams, 1973b; Grovum and Williams, 1973c; Grovum and Williams, 1973d; Grovum and Phillips, 1973; Grovum and Hecker, 1973; Grovum and Williams, 1977). These researchers used the Blaxter's model, which in its turn is a particular case of the Matis's model GNG1 for $N = 1$. This kinetic interpretation influenced many studies about digestibility in ruminants so that only the fractional passage rate associated to the descending phase of the marker excretion profile in feces was used to estimate ruminal degradability (Bartocci et al., 1997; Pereira et al., 1998; Udén et al., 1980; Vieira, 1997). A critic to the Grovum and coworkers' approach relies on the fact that a tubular segment cannot be treated as a retention compartment. If one pools and then samples the digesta of a tubular segment the sample taken is not representative of the digesta in a retention compartment or stagnant segment. A tubular segment has a transit time with a possible laminar flow-type or even an erratic but caudally directional flow-type of digesta particles, whereas a retention or stagnant compartment has a residence (turnover) time for particles therein, and to which can be ascribed a probability density function such as Eqns. (3) and (9) (Ellis et al., 1991; Ellis et al., 1994; France et al., 1985; Matis, 1987; Matis et al., 1989). The erratic or random flow type causes some delays and might contribute to the shape exhibited by the marker excretion profile in feces (Ellis et al., 1994).

The ruminoreticular digesta stratifies for ruminants that consume diets with adequate amounts of forage fiber (Welch, 1982). The stratification allows the identification of at least three distinct phases within the ruminoreticulum: (1) the gaseous phase in the dorsal sac; (2) the raft (lag-rumination, non-mixing) pool formed by buoyant particles; and (3) the fluid phase with less buoyant, small particles dispersed within the liquid as a ruminal escape or turnover (mixing) pool (Ellis et al., 1991; Ellis et al., 1994; Ellis et al., 1999). The concept of a raft or lag-rumination and an escape or turnover pools was based on the theoretical considerations proposed by R. E. Hungate

(1966) and T. M. Sutherland (1989). This two-pools system cause the wave of retention of particles that succeeds the linear delay or transit time (τ) typically exhibited by marker excretion profiles in the feces of ruminants. This means that marked particles leaving the rumen through the reticulo-omasal orifice hypothetically follows a tubular flow through the rest of the gastrointestinal tract. This view was originally presented by Ellis et al. (1979) and have been corroborated (Allen and Mertens, 1988; Huhtanen and Kukkonen, 1995; Huhtanen et al., 1995; Poppi, 2001; Vieira et al., 2008a; Wylie et al., 2000) and put into practice (Caetano et al., 2014; de Oliveira et al., 2011; Tedeschi et al., 2012). The basic critics to this view is whether the unknown effects of the possible retention in the abomasum and large bowel cause enough disturbances in the ascending phase of the fecal profile (Susmel et al., 1996; Van Soest, 1994), so that a strict association of both ascending/descending phases (reflects of N, λ and k) to the respective lag and escape pools is dubious. In addition, some researchers had observed that the G2 and the G1G1 models presented poor fits (Grovum and Williams, 1973b; Susmel et al., 1996; Uden et al., 1982), but this problem is easily solved by increasing the order of time dependency in GN and GNG1 models (Ellis et al., 1979). However, there is a negative effect of time dependency (N) over transit time (τ) estimates, so that an increase in N can cause a substantial reduction in τ (Ellis et al., 1979; Pereira et al., 2005; Vieira et al., 2008a). This fact was observed in the present study too, even with an adequate programming of the model fitting process in the NLIN procedure by using the "if…then….else" sentence to fit segmented models such as Eq. (10).

Despite its greater likelihood, the GN model appeared to yield systematically lower estimates of τ than the GNG1 model and Eq. (1). There is a confounding effect of the retention of particles in segments caudal to the ruminoreticulum that might alters the ascending phase of the marker excretion profile (Susmel et al., 1996; Van Soest, 1994). Another influence is marker migration from the particulate phase to other solutes of the digesta not intended to trace, a non-ideal characteristic of the lanthanides (Beauchemin and Buchanan-Smith, 1989; Hartnell and Satter, 1979a; Owens and Hanson, 1992). Nonetheless, the migration occurs mostly post-ruminally and because digesta particles more likely flow concurrently with the liquid phase in tubular segments lessens the problem of particle migration (Ellis et al., 2005; Ellis et al., 1994) and might be of little influence on estimates of τ and λ. According to the particle size theory, particles leaving the rumen do not suffer further comminution in the rest of the gastrointestinal tract and have the same particle size distribution profile encountered in the fecal matter (Poppi et al., 1980). However, it is possible that marker migration may disturb the ascending phase of the marker excretion profile so that a biphasic model that accounts for the migration process may yield more accurate estimates of the passage rates (Richter and Schlecht, 2006). Although the selective retention of particles apart from liquid in the abomasum might occur and the abomasum cannot be strictly considered a tubular segment like the small intestine (Grovum and Williams, 1973d), the mean retention time of a particulate marker from the proximal duodenum to feces and from the mouth to feces differ basically with reference to τ (Ellis et al., 1994). Therefore, the accurate estimation of the transit time and a correct biological interpretation of the parameters are critical to avoid biases over estimates of other passage rate parameters and inferences taken from those estimates.

The mathematical models used in the present study did not present, at least visually, differences in terms of their adherence to the marker excretion profiles (see section 3), although likelihood differences among models and variability of estimates for τ were remarkable. Nonetheless, the attributes of the profiles, particularly the mean retention time, computed as France et al. (1985) and Matis et al. (1989) stretched out, presented probable overlapping intervals, but the basic difference among the models GN, GNG1, and Eq. (1) is conceptual. An important constraint associated to Eq. (1) is

$k_1 < k_2 < \cdots < k_{N-1}$. This means that the first physical compartment is the one with the largest mean retention time, seconded by another physical compartment that also promotes retention but assumed to be located post-ruminally (Dhanoa et al., 1989; Dhanoa et al., 1985; France et al., 1985). Consequently, following this reasoning, k_1 is necessarily associated to the first stagnant compartment of the system, i.e., the ruminoreticulum and the mean residence time therein is estimated as $1/k_1$. This interpretation differ from the hypothesis ascribed to the GN and GNG1 models because as conceptually stated by Ellis et al. (1979) “the animal body can be viewed as composed of an assortment of pools or compartments containing characteristic molecules enclosed to some extent by anatomical boundaries”. In this latter view, the first and the second compartments are within the ruminoreticulum as a poor mixing, lag-rumination pool or raft, and a turnover pool or escapable pool of fluid dispersed particles; to the raft is ascribed the asymptotic rate λ, and k to the turnover or escape pool of particles eligible to leave the ruminoreticulum through the reticulo-omasal orifice (Ellis et al., 1991; Ellis et al., 1994; Ellis et al., 1999). For an effective modeling of this approach, however, it is important to assume that $k < \lambda$ (Vieira et al., 2008a); this does not necessarily imply that $N/\lambda < 1/k$, but rather $\forall\, N/\lambda \wedge 1/k$. By accommodating a reversible process between the raft and the escapable pool that accounts explicitly for entrapment of smaller particles by the raft, Poppi (2001) found a mean retention time for the raft larger than the reciprocal of output rate of particles from the rumen, which means turnover in the escapable pool. As an exercise, we tried to estimate the GNG1 model without constraining $k < \lambda$ and estimates of k in the range 10^1 to 10^2/h of magnitude figured as possible outputs; although such estimates seem unlikely in the real world, even so the model mimicked the marker excretion profiles with likelihood probability.

The fact that replacing $\dot{p}_o(t)$ of Eq. (10) with Eq. (3) resulted in a model (GN) that best mimicked the passage profiles of the particulate markers Cr and La in the present study implied that the assumption of a single pool in the rumen with nonexponential residence times for particles was more likely among all other assumptions studied. Nonetheless, the gamma time dependency introduced by Matis (1972) in the Blaxter's compartmental analysis of the digestion process of the sheep as a generalizing animal model (Blaxter et al., 1956) is an evidence of the poor mixing nature of the stagnant segments where retention of particles occurs, and many of the different approaches reported in the literature (Dhanoa et al., 1985; Ellis et al., 1979; Ellis et al., 1994; Poppi, 2001; Vieira et al., 2008a; Walz et al., 2004) arose to deal with this problem of poor mixing (Van Bentum and Nelson, 2011). Nonetheless, the modelling of the transit process of forage particles in the ruminant gastrointestinal tract needs to be balanced by parsimony. If many of the physiological aspects assumed to have some influence on the overall retention process in the ruminoreticulum are considered, the model would be overparameterized, and thus, useless. Therefore, no more than four parameters can be efficiently estimated from marker excretion profiles (Dhanoa et al., 1989; France et al., 1985).

4.1. Theoretical implications by choosing model GN

The nonexponential residence times of the particles within the ruminoreticulum may be the result of a retention process in that organ where predominates two partially commingled pools: a pool where occurs a poor mixing of particles named raft or "mat" that borders a second pool of fluid diluted particles with an exponential residence time. This model can be used to estimate the digestion and rumen fill of fibrous particles in the organ (Vieira et al., 2008a). Following that derivation, the one compartment system with nonexponential retention times can be abstracted as a sequence of sequential pools with exponentially distributed transference rates, as depicted in Figure 3. In fact, this representation is only an abstraction and a convenient mathematical artifice (Matis, 1987); actually, the entering particle has a probability to be found in the system defined by Eq. (3), i.e., the gamma function

$$\Gamma(N,\lambda,t) = (\lambda t)^{N-1}\lambda \exp(-\lambda t)/\Gamma(N), \tag{11}$$

in which $\Gamma(N) = (N-1)!, \forall N \in \mathbb{Z}^{+}$ (Mood et al., 1974), and other parameters have the same meanings as previously described. The system represents the process of progressive transfer of a particle out of the ruminoreticulum (Ellis et al., 1991; Huhtanen and Kukkonen, 1995; Huhtanen et al., 1995; Hungate, 1966; Sutherland, 1989). As resumed by Vieira et al. (2008a), hydration of the recently ingested forage particles well masticated during ingestion, and the colonization of particles by microbes are events that have to occur prior to digestion itself; as digestion and fermentation by microbes takes place, the consumption of readily available substrates firstly enhances the natural buoyancy of particles. The progress of degradation of particles weakens the cell wall matrix and the physical breakdown (comminution) of particles by rumination occur. This series of progressive and simultaneous events provoke delays in the clearance of particles from the raft downwards the fluid phase of the ruminal ventral sac. Nevertheless, as particles become more processed, buoyancy reduces, particles gain density while still comminute to a size that can leave the organ through the reticulo-omasal orifice forced by liquid currents formed by ruminoreticular and omasal contractions, and gain the rest of the gastrointestinal tract toward feces (Figure 3). Mathematically, a possible steady-state solution to this dynamic system arises by solving the following differential equations that abstracts the previously described mechanisms of particle digestion and flow:

$$(dA/dt)_1 = f_A\, dF/dt - (\lambda + k_d)(A)_1, \tag{12}$$

$$(dA/dt)_2 = \lambda(A)_1 - (\lambda + k_d)(A)_2, \tag{13}$$

$$\vdots \qquad \vdots$$

$$(dA/dt)_N = \lambda(A)_{N-1} - (\lambda + k_d)(A)_N, \tag{14}$$

$$(dU/dt)_1 = f_U\, dF/dt - \lambda(U)_1, \tag{15}$$

$$(dU/dt)_2 = \lambda(U)_1 - \lambda(U)_2, \tag{16}$$

$$\vdots \qquad \vdots$$

and $(dU/dt)_N = \lambda(U)_{N-1} - \lambda(U)_N$. (17)

The pools of available (PA) and unavailable (PU) substrates are given by assuming steady-state conditions so that feed intake rate is averaged, i.e., $dF/dt \xrightarrow{steady\ -state} \bar{F}$, $(dA/dt)_1 = \cdots = (dA/dt)_N = 0$, and $(dU/dt)_1 = \cdots = (dU/dt)_N = 0$. For $N \geq 2$ abstract sub-pools of A (available) and U (unavailable) fractions of the same particle, we have:

$PA = (A)_1 + \cdots + (A)_N = (f_A\bar{F}/(\lambda + k_d)) \sum_{i=1}^{N}(\lambda/(\lambda + k_d))^{i-1}$, and (18)

$$PU = (U)_1 + \cdots + (U)_N = f_U\bar{F}N/\lambda. \tag{19}$$

The fractions of available and unavailable substrates in the feed (or diet) are f_A and f_U, which can be estimated by in vitro, in situ, or in vivo procedures (Huhtanen et al., 2008; Nocek, 1988; Vieira et al., 2008b). The amount of available substrate digested in the ruminoreticulum can also be assessed by assuming steady-state conditions, which imply an averaged $dDigested/dt \xrightarrow{steady\ -state} \bar{D}$ (mass units/unit of time), and a coefficient of digestibility (D, dimensionless) that can be calculated as follows:

$\bar{D} = k_d \sum_{i=1}^{N}(A)_i = (f_A\bar{F}k_d/(\lambda + k_d)) \sum_{i=1}^{N}(\lambda/(\lambda + k_d))^{i-1}$, so that (20)

$$D = \bar{D}/(f_A\bar{F}) = (k_d/(\lambda + k_d)) \sum_{i=1}^{N}(\lambda/(\lambda + k_d))^{i-1}. \tag{21}$$

Finally, the average amount of substrate present in the ruminoreticulum (rumen fill, mass units) is the sum of the sizes of the pools PA and PU, calculated as

$$Q = PA + PU = (f_A\bar{F}/(\lambda + k_d)) \sum_{i=1}^{N}(\lambda/(\lambda + k_d))^{i-1} + f_U\bar{F}N/\lambda. \tag{22}$$

This alternative modelling may be useful whenever the fit of the GN model to fecal excretion profiles of particulate markers present better likelihood than models GNG1 and Eq. (1). As additional constraints we have for $N = 0, \sum_{i=1}^{N}(\lambda/(\lambda + k_d))^{i-1} = 1$, and for $N = 1, \sum_{i=1}^{1}(\lambda/(\lambda + k_d))^{0} = 1$.

The preceding derivation does not preclude the use of Eq. (1) to compute the digestibility by assuming the ruminoreticulum as the sole stagnant segment of the gastrointestinal tract. Following the derivation suggested by Ellis et al. (1994), by ignoring the conceptual problem associated to the k_1 and k_2 rate constants of Eq. (1), one can assume an average rate obtained as

$$\bar{k}_p = k_1 k_2/(k_1 + k_2) \qquad (23)$$

to be used in the models deduced by Waldo et al. (1972), Ellis (1978), and Van Soest et al. (1992). These models are based on a particular case of the derivation presented by Vieira et al. (2008a). This derivation has empirical evidence because $\bar{k}_p$ yields estimates close to the estimates obtained by rumen evacuation. Although rumen evacuation is based on pooling the stagnant digesta of the ruminoreticulum and demand the use of rumen cannulated animals or slaughtered animals, it provides solutions close to Eqns. (20)–(22). Some authors have demonstrated that the rumen evacuation technique by slaughtering or cannulating animals yields estimates more reliable to estimate rumen kinetics (Cannas et al., 2003; Ellis et al., 1994; Huhtanen and Sveinbjörnsson, 2006; Huhtanen et al., 2007; Huhtanen et al., 2008).

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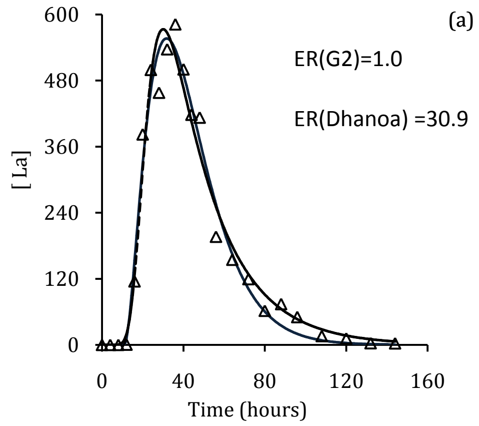
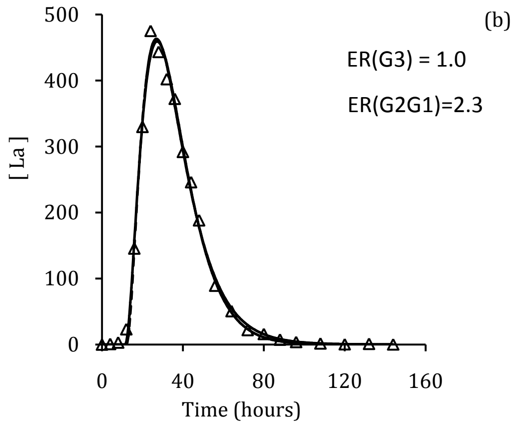
5. CONCLUSÕES

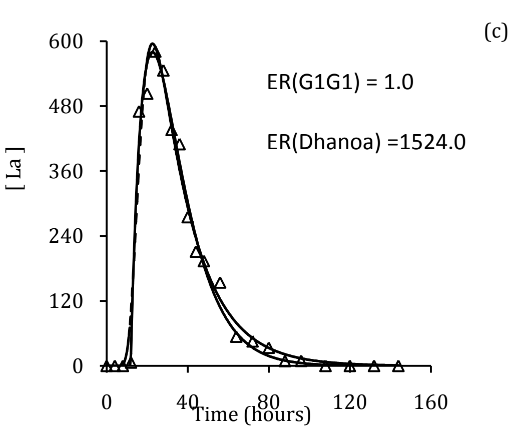
O modelo com a melhor capacidade de ajuste aos perfis dos marcador foi o modelo de GN; o modelo de GNG1 e o modelo multicompartmental foram praticamente equivalentes em termos de probabilidade.

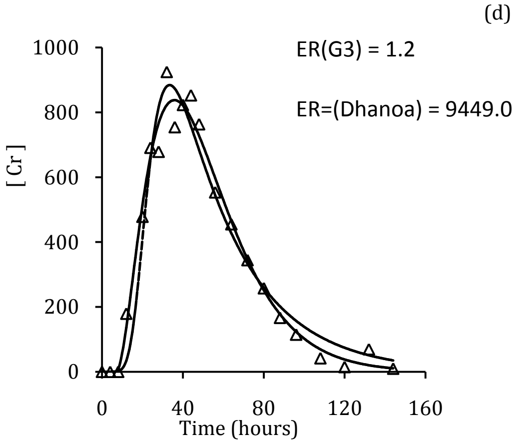
Os modelos foram muitos semelhantes em termos de aderência visual, apesar de notáveis diferenças em termos de probabilidade. Fica circunscrito que as diferenças entre os três modelos estudados são conceituais. Devido a este fato, foi proposta uma modelagem alternativa, para os casos em que o modelo GN for melhor ajuste que os modelos GNG1 e eq. (1). A solução matemática proposta no presente estudo é inédita na literatura.

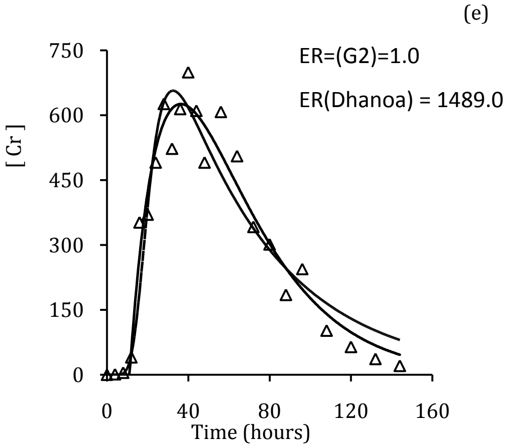
APÊNDICE

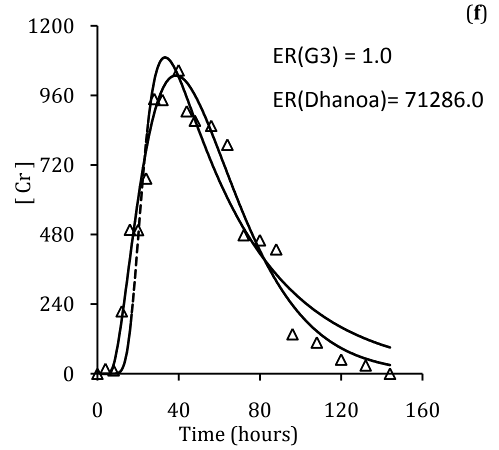

(a)
ER(G2)=1.0
ER(Dhanoa) =30.9
[La]
600
480
360
240
120
0
0
40
80
120
160
Time (hours)

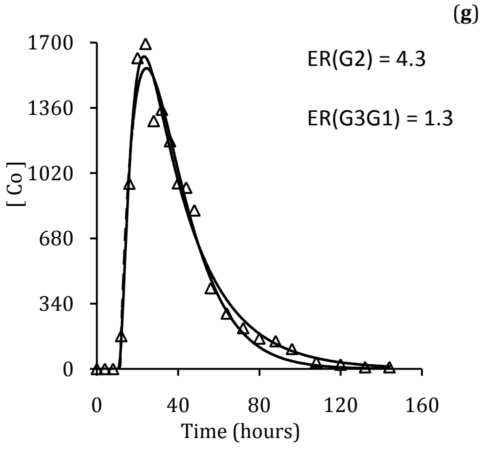

(b)
ER(G3) = 1.0
ER(G2G1)=2.3
[La]
500
400
300
200
100
0
0
40
80
120
160
Time (hours)


(c)
ER(G1G1) = 1.0
ER(Dhanoa) =1524.0
[La]
600
480
360
240
120
0
0
40
80
120
160
Time (hours)


(d)
ER(G3) = 1.2
ER=(Dhanoa) = 9449.0
[Cr]
1000
800
600
400
200
0
0
40
80
120
160
Time (hours)


(e)
ER=(G2)=1.0
ER(Dhanoa) = 1489.0
[Cr]
750
600
450
300
150
0
0
40
80
120
160
Time (hours)


(f)
ER(G3) = 1.0
ER(Dhanoa)= 71286.0
[Cr]
1200
960
720
480
240
0
0
40
80
120
160
Time (hours)


(g)
ER(G2) = 4.3
ER(G3G1) = 1.3
[Co]
1700
1360
1020
680
340
0
0
40
80
120
160
Time (hours)

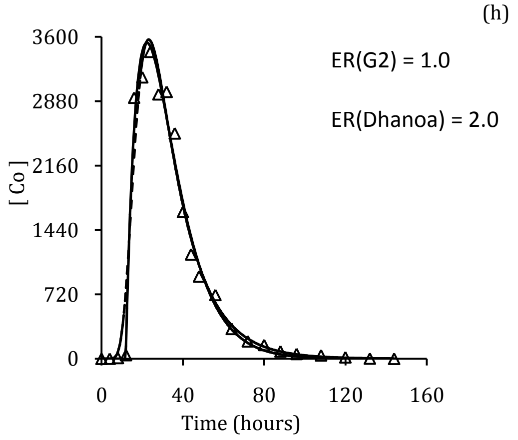
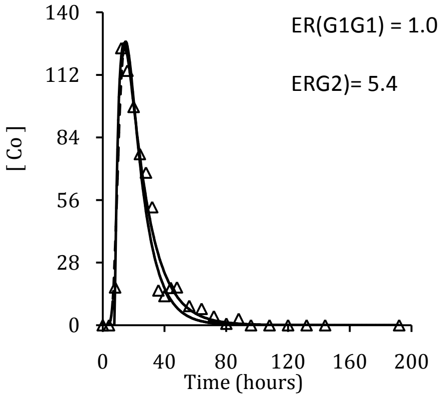
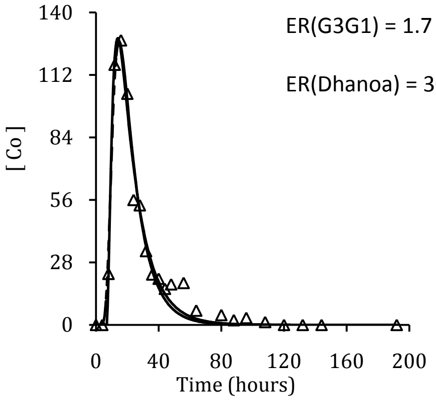

(h)
ER(G2) = 1.0
ER(Dhanoa) = 2.0
[Co]
3600
2880
2160
1440
720
0
0
40
80
120
160
Time (hours)

Figure 1. Observed concentration of markers in the feces of sheep (△), predicted concentration (solid lines) by the best model with good evidence ratios (values closest to one are better), and predicted concentration (dashed lines) by a model with poorer evidence ratios (larger ER values). Panels depict the concentrations (mg/kg of fecal dry matter) of La ([La], mg/kg), Cr ([Cr]), and Co ([Co]) as functions time; as well as the evidence ratios of models GN, GNG1, and Dhanoa, namely ER(GN), ER(GNG1), and ER(Dhanoa), respectively.

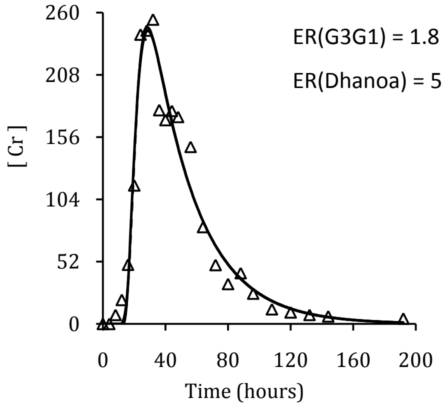
(a)


ER(G1G1) = 1.0
ERG2)= 5.4
[Co]
140
112
84
56
28
0
0
40
80
120
160
200
Time (hours)

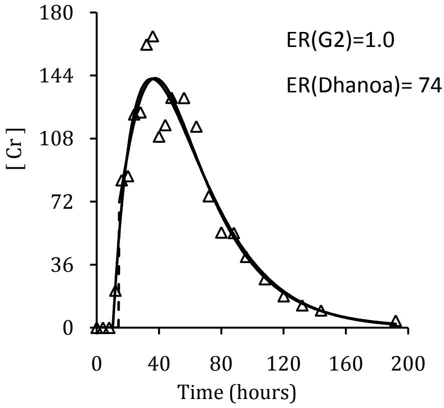
(**b**)


ER(G3G1) = 1.7
ER(Dhanoa) = 30.4
[Co]
140
112
84
56
28
0
0
40
80
120
160
200
Time (hours)

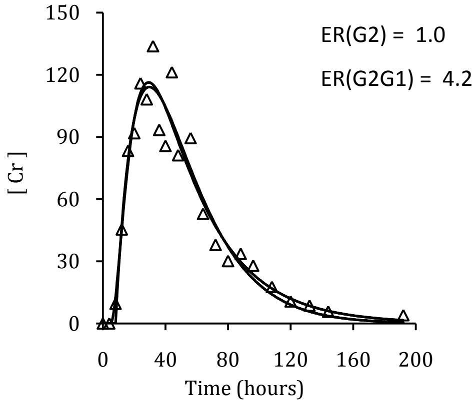
(c)


ER(G3G1) = 1.8
ER(Dhanoa) = 5.6
[Cr]
260
208
156
104
52
0
0
40
80
120
160
200
Time (hours)

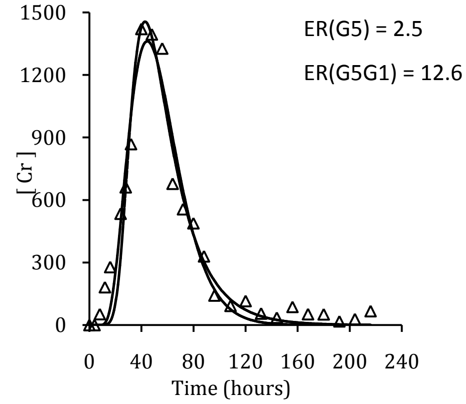
(d)


ER(G2)=1.0
ER(Dhanoa)= 74.0
[Cr]
180
144
108
72
36
0
0
40
80
120
160
200
Time (hours)

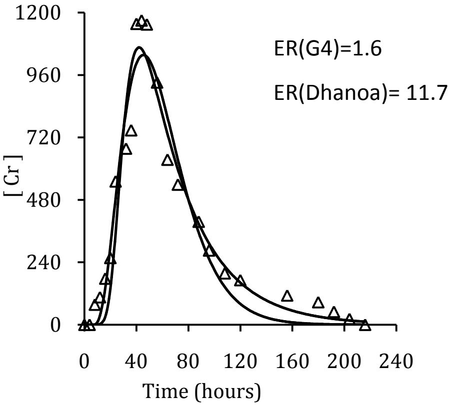
(**e**)


ER(G2) = 1.0
ER(G2G1) = 4.2
[Cr]
150
120
90
60
30
0
0
40
80
120
160
200
Time (hours)

(**f**)


ER(G5) = 2.5
ER(G5G1) = 12.6
[Cr]
1500
1200
900
600
300
0
0
40
80
120
160
200
240
Time (hours)

(**g**)


ER(G4)=1.6
ER(Dhanoa)= 11.7
[Cr]
1200
960
720
480
240
0
0
40
80
120
160
200
240
Time (hours)

(**h**)

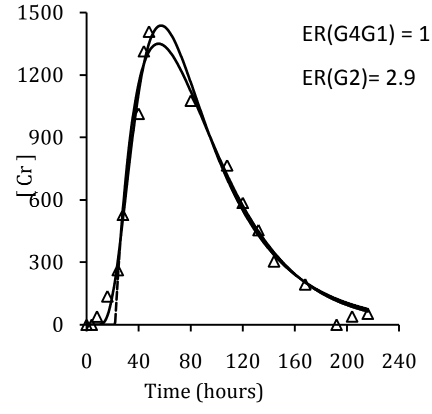
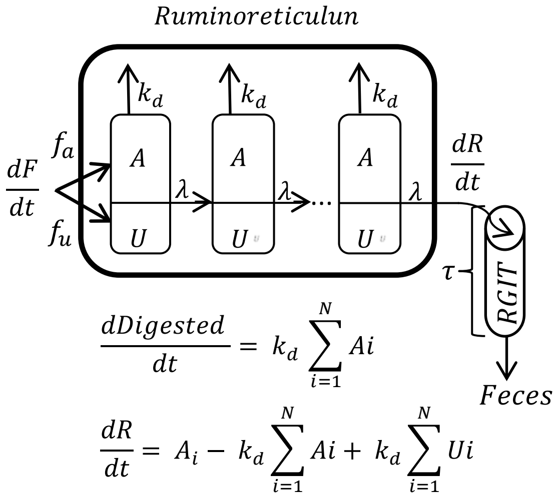

ER(G4G1) = 1.7
ER(G2)= 2.9
[Cr]
1500
1200
900
600
300
0
0
40
80
120
160
200
240
Time (hours)

Figure 2. Observed fecal marker concentrations (△, mg/kg of dry matter), predicted concentration by the best model (solid lines) with good evidence ratios (values closest to one are better), and predicted concentration (dashed lines) by a model with poorer evidence ratios (larger ER values). Panels depict the concentrations (mg/kg of fecal dry matter) of La ([La], mg/kg), Cr ([Cr]), and Co ([Co]) as functions of time; as well as the evidence ratios of models GN, GNG1, and Dhanoa, namely ER(GN), ER(GNG1), and ER(Dhanoa), respectively. On panels (a) and (b) are shown Co concentration ([Co]) and on panels (c), (d), and (e) are shown Cr concentration ([Cr]) for grazing, lactating dairy cows. On panels (f), (g), and (h) are [Cr] × time profiles obtained from confined steers fed sugarcane as roughage.



$$\frac{dDigested}{dt} = k_d \sum_{i=1}^{N} Ai$$

$$\frac{dR}{dt} = A_i - k_d \sum_{i=1}^{N} Ai + k_d \sum_{i=1}^{N} Ui$$

Figure 3. Schematic representation of the digestion and flow path of particles through the ruminoreticulum and throughout the rest of the gastrointestinal tract (RGIT) until their first appearance in feces. The meanings of parameters are listed in Table 1.

Table 1. Number of fits with difference values of the Akaike criterion (Δ_h) obtained for fitting the compartmental models to the particulate markers (Cr and La) and fluid-phase marker (Co).

Marker/Model[a]	$\Delta_h = 0$	$0 < \Delta_h \leq 2.0$	$\Delta_h > 2.0$
Cr			
Dhanoa et al.	14	4	35
GN	25	41	42
GNG1	13	30	236
La			
Dhanoa et al.	6	2	22
GN	21	0	28
GNG1	3	17	157
Co			
Dhanoa et al.	6	1	43
GN	11	1	273
GNG1	40	123	156

[a] Model by Dhanoa et al. (1985); model GN Pond et al. (1988); and Model GNG1 by Matis (1972).

Table 2. Number of marker excretion profiles best mimicked by a specific model.

Marker/Species	Dhanoa et al.[a]	GN[a]	GNG1[a]	Subtotals
Cr				
Cow	7	17	10	34
Steer	7	3	2	12
Sheep	0	6	0	6
Co				
Cow	2	1	15	18
Steer	2	1	8	11
Sheep	2	9	17	28
La				
Sheep	6	21	3	30
Subtotals	25	59	55	139

[a] Model by Dhanoa et al. (1985);model GN Pond et al. (1988); and Model GNG1 by Matis (1972).

Table 3. Some examples of parameter estimates of Eq. (1) with calculated Akaike difference within parentheses ($\mathit{\Delta}_h$) obtained for Cr, Co, and La in cows, steers, and sheep.

Markers	Parameters of Eq. (1) or model of Dhanoa et al. (1985) andderivedmeasures								
	N^a	k_1 $^{\mathrm{b}}$	k_2 $^{\mathrm{c}}$	τ^{d}	$1/k_2$	$\mu_T'^{d}$	μ_T^d	$\sigma_T^{2\,\mathrm{f}}$	σ_T $^{\mathrm{f}}$
Cr									
Cow($\mathit{\Delta}_h = 0.0$)	30	0.0192	0.1945	16.6	5.1	52.1	73.8	2741.5	52.4
Steer($\mathit{\Delta}_h = 0.0$)	30	0.0295	0.1282	28.3	7.8	33.9	70.0	1209.0	34.8
Co									
Cow($\mathit{\Delta}_h = 0.0$)	30	0.0837	0.4757	7.2	2.1	11.9	21.3	147.2	12.1
Steer($\mathit{\Delta}_h = 0.0$)	30	0.0625	0.2947	12.1	3.4	16.0	31.5	267.3	16.3
Sheep($\mathit{\Delta}_h = 0.0$)	39	0.0873	0.3593	11.2	2.8	11.5	25.4	138.9	11.8
La									
Sheep($\mathit{\Delta}_h = 0.0$)	39	0.0488	0.1480	29.9	6.8	20.5	57.1	464.9	21.6

[a] Number of compartments.

[b] Fractional passage rate in the ruminoreticulum (1/h).

[c] Post-ruminal fractional passage rate in a given compartment of retention (1/h).

[d] Transit time (h) of a particle from the reticulo-omasal orifice to reach the feces (see Eq. (2)).

[e] Mean retention time in the rumen ($\mu_T' = 1/k_1$, h)and total tract ($\mu_T = \tau + 1/k_1 + 1/k_2$, h).

[f] Variance of the mean retention time in the rumen ($\sigma_T^2 = 1/k_1^2 + 1/k_2^2$, h^2) and its square root (σ_T, h).

Table 4. Some parameter estimates of the GN model obtained with marker profiles of Cr, Co, and La for cows, steers, and sheep.

Marker	Parameters						
	N[a]	λ[b]	τ[c]	$\mu_T^{'}$[d]	μ_T[d]	σ_T^2[e]	σ_T[e]
Cr							
Cow ($\Delta_h = 0.0$)	2	0.0401	10.4	49.8	60.2	1240.9	35.2
Steer ($\Delta_h = 1.2$)	4	0.0775	6.7	51.6	58.3	665.9	25.8
Sheep ($\Delta_h = 0.0$)	2	0.0396	11.1	50.5	61.6	1273.4	35.7
Co							
Cow ($\Delta_h = 0.0$)	2	0.1486	5.8	13.5	19.3	90.5	9.5
Steer ($\Delta_h = 1.0$)	2	0.1249	11.1	16.0	27.1	128.1	11.3
Sheep ($\Delta_h = 0.0$)	2	0.0956	11.8	20.9	32.8	218.0	14.8
La							
Sheep ($\Delta_h = 0.0$)	3	0.1266	11.5	23.7	35.1	187.1	13.7

[a] Order of time dependency (dimensionless).

[b] Asymptotic rate (1/h) of transference of particles from rumen.

[c] Transit time (h) of a particle from the reticulo-omasal orifice to reach the feces.

[d] Mean retention time in the rumen ($\mu_T^{'} = N/\lambda$, h) and total tract ($\mu_T = \tau + N/\lambda$, h).

[e] Variance of the mean retention time in the rumen (σ_T^2, h^2) and its square root (σ_T, h).

Table 5. Some examples of parameter estimates of the GNG1 model with calculated Akaike difference within parentheses (Δ_h) obtained for Cr, Co, and La in cows, steers, and sheep.

Marker	Parameters of GNG1 model obtained by replacing Eq. (9) in Eq. (10)									
	N[a]	λ[b]	k[c]	τ[d]	N/λ[b]	$1/k$[c]	μ_T'[e]	μ_T[e]	σ_T^2[f]	σ_T[f]
Cr										
Cow ($\Delta_h = 1.2$)	3	0.3306	0.0343	12.7	9.1	29.1	38.2	51.4	875.1	29.6
Steer ($\Delta_h = 1.1$)	4	0.1181	0.0207	7.8	33.9	48.2	82.1	89.9	2611.8	51.1
Co										
Cow ($\Delta_h = 0.0$)	1	0.3092	0.0746	7.7	3.2	13.4	16.6	24.3	190.0	13.8
Steer ($\Delta_h = 1.3$)	2	0.6212	0.0720	10.9	3.2	13.9	17.1	28.0	198.2	14.1
Sheep ($\Delta_h = 1.3$)	4	0.2889	0.0420	10.6	6.9	23.8	30.7	41.3	590.0	24.4
La										
Sheep ($\Delta_h = 0.0$)	1	0.1424	0.0631	11.9	7.0	15.8	22.9	34.8	300.2	17.3

[a] Order of time dependency (dimensionless).
[b] Asymptotic rate (1/h) of transference of particles from the raft pool to the poll of fluid diluted particles.
[c] Fractional rate of passage (1/h) of particles out of the pool of fluid diluted particles.
[d] Transit time (h) of a particle from the reticulo-omasal orifice to reach the feces.
[e] Mean retention time in the rumen ($\mu_T' = N/\lambda + 1/k$, h) and total tract ($\mu_T = \tau + N/\lambda + 1/k$, h).
[f] Variance of the mean retention time in the rumen (σ_T^2, h^2) and its square root(σ_T, h).

/Arquivo de dados*/

Cromo

```
data marcelo;
  title 'cinética de passagem de partículas: Vieira et al. (1997)';
  input time     a1 a2 a3 a4 a5 a6;
  y = a1 - a6;
  n = 21;

  datalines;
  0   0.0   0.0   4.5   0.0   0.0   0.0
  8   0.0   0.0   0.0   0.0   0.0   0.0
  16  0.0   0.0   17.9  11.7  0.0   7.3
  24  7.4   8.1   40.5  40.6  24.2  29.5
  28  20.9  14.4  47.1  43.0  38.7  54.5
  32  34.4  34.5  62.9  63.0  85.6  0.0
  36  30.4  34.0  73.7  68.8  80.6  67.5
  40  35.4  36.6  85.8  74.7  105.0 82.0
  44  28.4  28.4  82.6  75.9  89.8  59.1
  48  35.6  38.0  0.0   0.0   64.3  73.2
  52  27.7  40.4  55.7  52.2  72.4  71.8
  56  27.6  31.1  65.1  50.0  61.3  66.8
  60  0.0   0.0   55.4  45.6  75.4  69.3
  64  14.7  21.1  45.0  44.2  63.9  52.4
  72  14.3  18.0  39.4  32.7  56.8  39.3
  80  8.0   15.0  34.2  20.3  39.8  29.1
  88  7.9   7.9   30.0  23.4  36.4  36.2
  100 0.0   0.0   0.0   0.0   27.2  30.3
  112 0.0   0.0   0.0   0.0   21.0  0.0
  124 0.0   0.0   7.7   4.7   15.0  20.5
  148 0.0   0.0   8.0   0.0   0.0   7.8
```

```
data marcelo;
 title 'cinética de passagem de partículas:Pádua (2009)';
 input time     a1 a2 a3 a4 a5 a6 a7 a8 a9 a10 a11 a12;
 y = a1 - a12;
 n = 29;

 datalines;
 0   0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0
 4   0.0     0.0     0.0     0.0     113.6   0.0     0.0     0.0     0.0     0.0     0.0     0.0
 8   0.0     0.0     0.0     86.7    0.0     69.1    42.5    52.9    77.2    52.8    39.0    56.8
 12  47.4    0.0     0.0     242.1   0.0     78.8    127.5   181.9   105.9   100.9   0.0     139.9
 16  89.2    67.8    146.8   345.6   242.7   0.0     175.5   278.5   177.7   136.6   136.4   204.5
 20  294.5   163.9   199.8   453.0   296.3   218.5   0.0     0.0     256.9   242.5   0.0     307.6
 24  273.8   310.6   299.1   0.0     348.9   367.3   322.0   534.5   550.9   286.2   262.6   413.7
 28  278.6   565.5   618.3   753.7   502.0   0.0     408.9   661.1   0.0     460.3   527.9   0.0
 32  600.0   450.2   831.0   0.0     629.4   692.0   0.0     868.4   677.2   0.0     0.0     741.7
 36  843.9   574.0   1134.5  958.6   996.6   0.0     1169.5  0.0     747.7   594.6   0.0     0.0
 40  881.9   851.8   1527.8  0.0     1358.6  1147.0  1771.6  1420.7  1156.8  1574.6  1013.4  1529.6
 44  1017.1  1214.9  2161.8  1173.4  1442.1  1424.4  0.0     0.0     1169.5  1256.2  1314.2  1481.0
 48  715.1   1156.0  1761.3  1271.6  1483.3  1427.8  2239.3  1394.5  1154.4  0.0     1408.2  1434.0
 56  699.7   1153.4  1525.3  859.01  196.1   1122.8  1727.2  1326.9  931.0   1077.5  0.0     1172.2
 64  342.1   615.1   709.9   597.6   820.8   899.0   1252.6  677.9   634.6   860.3   0.0     0.0
 72  302.0   835.6   624.3   539.6   628.3   840.5   1118.3  555.9   538.8   682.1   0.0     743.5
 80  275.5   710.6   412.8   391.9   518.8   666.8   850.2   488.6   0.0     548.7   1076.9  608.7
 88  194.9   592.5   406.2   0.0     408.8   0.0     547.4   329.8   396.2   345.6   0.0     438.3
 96  0.0     477.7   200.6   156.5   285.7   364.3   276.5   142.0   285.7   0.0     0.0     286.0
 108 65.4    387.0   0.0     83.0    218.6   255.0   266.1   92.3    197.7   168.7   765.8   185.9
 120 55.8    354.2   93.0    80.3    120.8   233.0   165.8   115.6   171.7   127.5   585.5   143.9
 132 18.2    288.1   0.0     56.3    81.8    138.0   129.2   55.4    0.0     93.9    454.6   105.0
 144 77.3    25.7    24.6    42.2    81.3    97.1    0.0     36.0    0.0     70.0    304.9   81.9
 156 91.3    176.7   103.8   48.7    74.1    104.4   86.1    87.4    112.7   0.0     0.0     85.6
 168 50.1    149.6   51.9    60.1    0.0     108.8   0.0     52.4    0.0     91.9    194.2   62.2
 180 56.9    142.1   47.8    79.6    0.0     87.6    55.2    51.8    87.0    76.0    0.0     0.0
 192 57.9    55.9    102.5   52.7    46.2    30.8    0.0     18.3    49.8    0.0     46.3    19.4
 204 16.9    58.5    16.9    19.4    16.9    21.9    23.3    28.6    22.2    0.0     40.2    27.2
 216 73.9    31.1    95.2    21.8    24.7    23.5    26.9    67.2    0.0     68.1    52.8    27.2
 ;
```

```
data marcelo;
 title 'cinética de passagem de partículas: Favoreto et al. (2008)';
 input time     a1 a2 a3 a4 a5 a6 a7 a8;
 y = a1 - a8;
 n = 24;

 datalines;
 0    0.0    0.0   0.0   0.0   0.0   0.0   0.0   0.0
 4    0.0    0.0   0.0   0.0   0.0   0.0   0.0   0.0
 8    7.5    4.2   9.5   0.0   5.9   9.0   2.5   4.9
 12   20.0   18.6  45.4  21.2  12.6  28.4  11.6  18.1
 16   49.4   34.1  83.3  84.2  41.5  53.2  24.4  115.7
 20   115.7  66.7  91.8  86.6  125.2 112.0 90.0  157.9
 24   241.7  109.5 115.9 121.8 177.5 132.9 124.3 222.4
 28   245.1  134.8 108.2 123.0 178.6 177.3 144.6 229.9
 32   254.3  149.7 133.8 161.7 139.1 112.0 137.5 205.7
 36   178.6  139.2 93.4  166.5 131.1 119.6 0.0   117.7
 40   170.3  110.2 85.6  109.2 107.2 104.7 0.0   143.6
 44   178.0  113.6 121.3 115.7 122.6 121.3 99.7  168.4
 48   172.9  114.2 81.2  131.3 154.7 146.8 90.5  165.6
 56   147.9  125.7 89.5  131.2 127.3 106.7 0.0   139.2
 64   80.9   102.2 52.9  114.9 94.3  70.4  77.0  97.6
 72   49.2   69.1  37.9  75.1  47.1  48.7  68.8  72.5
 80   33.3   78.1  30.1  54.4  49.1  40.4  66.5  59.2
 88   42.4   63.6  33.6  54.1  51.4  43.9  0.0   63.8
 96   25.3   50.1  27.9  40.5  34.5  31.5  0.0   60.7
 108  12.2   35.2  17.7  27.7  .     183.3 0.0   33.7
 120  9.6    19.8  10.6  18.0  27.8  11.3  0.0   27.7
 132  7.5    18.1  8.6   12.8  31.4  6.9   37.9  14.9
 144  6.2    9.9   5.6   9.9   25.6  5.7   33.6  10.0
 192  4.4    6.5   4.0   4.0   6.5   13.2  8.2   5.6
 ;
```

```
data marcelo;
 title 'cinética de passagem de partículas:Santos (2011)';
 input time    a1 a2 a3 a4 a5 a6 a7 a8 a9 a10 a11 a12 a13 a14 a15 a16 a17 a18 a19 a20;
 y = a1 - a20;
 n = 24;

 datalines;
 0      0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
 1      0.00   0.00   0.00   0.00   0.00   0.16   0.02   0.00   0.02   0.00   0.00   0.03   0.00   0.00   0.17   0.16   0.00   0.00   0.02   0.01
 2      0.00   0.00   0.00   0.00   0.00   0.00   0.03   0.05   0.01   0.00   0.00   0.00   0.01   0.00   0.01   0.00   0.00   0.00   0.02   0.00
 4      0.00   0.36   0.00   0.00   0.00   0.00   0.02   0.00   0.01   0.00   0.00   0.03   0.00   0.00   0.03   0.00   0.00   0.00   0.00   0.00
 6      0.00   0.00   0.00   0.00   0.05   0.00   0.02   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00
 8      0.00   0.00   0.14   0.00   0.10   0.23   0.07   0.00   0.08   0.00   0.32   0.00   0.05   0.00   0.16   0.00   0.00   0.00   0.03   0.00
 10     0.00   0.00   0.14   0.01   0.22   1.28   0.05   0.14   0.10   0.00   0.15   0.13   0.03   0.00   0.30   0.91   0.00   0.21   0.08   0.13
 12     0.08   0.28   0.28   0.14   0.26   1.11   0.14   0.13   0.24   0.05   0.41   0.46   0.50   0.35   0.40   0.76   0.31   0.37   0.35   0.17
 16     0.39   0.54   0.87   0.51   0.89   1.27   0.53   0.00   0.77   0.37   1.00   0.52   0.44   0.37   1.75   1.13   0.47   0.77   1.02   0.56
 20     1.61   1.61   0.98   1.17   1.24   1.50   1.36   1.37   1.09   0.88   2.61   1.50   1.42   0.91   0.72   0.97   2.49   1.20   1.34   1.38
 24     1.44   1.18   1.04   1.32   0.84   1.00   0.62   1.18   1.26   0.82   1.14   0.86   0.81   0.77   0.95   1.16   0.72   1.01   1.77   1.03
 28     1.32   1.09   1.36   1.10   1.25   0.81   1.24   0.93   1.03   0.70   0.95   0.84   0.56   0.73   1.57   0.72   1.56   0.85   0.94   0.89
 32     1.33   1.03   0.90   0.87   0.69   0.68   0.72   0.73   1.36   0.78   0.76   0.83   1.11   0.68   0.67   0.66   0.74   0.74   1.59   1.00
 36     1.04   0.64   1.47   0.60   0.94   0.34   0.94   0.44   0.86   0.55   0.61   0.29   0.76   0.52   1.46   0.46   1.51   0.37   0.83   0.53
 40     0.84   0.42   1.03   0.40   0.59   0.23   0.67   0.37   0.68   0.41   0.62   0.37   0.76   0.34   1.43   0.36   1.18   0.25   0.90   0.42
 44     0.78   0.55   0.89   0.43   0.51   0.25   0.54   0.27   0.54   0.40   0.58   0.62   0.48   0.50   1.01   0.37   0.84   0.64   0.71   0.48
 48     0.79   0.36   0.93   0.16   0.50   0.12   0.58   0.19   0.26   0.21   0.46   0.24   0.22   0.19   0.24   0.23   0.79   0.23   0.37   0.34
 56     0.21   0.21   0.45   0.14   0.25   0.10   0.27   0.18   0.16   0.25   0.79   0.25   0.64   0.08   0.15   0.14   0.15   0.15   0.36   0.20
 64     0.41   0.03   0.49   0.05   0.23   0.00   0.25   0.11   0.13   0.08   0.45   0.17   0.07   0.04   0.30   0.12   0.32   0.04   0.24   0.21
 72     0.26   0.03   0.33   0.04   0.13   0.00   0.14   0.09   0.15   0.00   0.05   0.09   0.25   0.01   0.39   0.08   0.23   0.02   0.36   0.12
 80     0.29   0.00   0.25   0.06   0.17   0.00   0.13   0.00   0.08   0.00   0.05   0.15   0.19   0.03   0.14   0.13   0.12   0.05   0.16   0.34
 88     0.07   0.02   0.13   0.00   0.07   0.00   0.06   0.08   0.07   0.00   0.00   0.00   0.11   0.11   0.20   0.00   0.06   0.05   0.12   0.00
 96     0.01   0.00   0.17   0.01   0.05   0.09   0.02   0.03   0.05   0.00   0.11   0.02   0.08   0.00   0.07   0.03   0.03   0.00   0.07   0.02
 108    0.00   0.00   0.00   0.00   0.03   0.00   0.02   0.01   0.02   0.00   0.00   0.00   0.00   0.00   0.15   0.02   0.00   0.00   0.07   0.02
 120    0.00   0.00   0.00   0.00   0.00   0.00   0.02   0.02   0.03   0.00   0.00   0.00   0.06   0.00   0.03   0.02   0.05   0.00   0.04   0.00
 132    0.00   0.00   0.01   0.00   0.00   0.00   0.01   0.01   0.04   0.00   0.00   0.00   0.00   0.00   0.05   0.00   0.01   0.00   0.00   0.00
 144    0.00   0.00   0.00   0.00   0.00   0.00   0.01   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.00   0.06   0.00   0.00   0.00   0.00
 192    0.02   0.00   0.06   0.00   0.00   0.00   0.10   0.00   0.07   0.00   0.00   0.00   0.04   0.00   0.09   0.13   0.04   0.00   0.05   0.01
 ;
```

```
data marcelo;
 title 'cinética de passagem de partículas: A. M. Fernandes (unpublished
 results)';
 input time     a1 a2 a3 a4 a5 a6;
 y = a1 - a6;
 n = 23;

 datalines;
 0   0.0     0.0     0.0   0.0    0.0   0.0
 4   0.0     16.8    0.0   1.1    0.0   0.0
 8   0.0     12.1    0.0   4.7    0.0   0.0
 12  936.1   215.7   0.0   40.2   179.1 0.0
 16  441.8   496.7   0.0   352.2  0.0   243.8
 20  1555.2 495.7  38.7   370.2 478.1  296.0
 24  1598.2 673.3  62.6   490.8 690.8  286.3
 28  1300.2 947.6  54.3   626.3 678.4  352.5
 32  1740.2 944.6  65.5   522.8 924.5  367.9
 36  1785.2 1205.6 70.8   614.4 754.3  477.1
 40  1797.2 1046.6 0.0    699.5 822.8  790.1
 44  1055.2 905.6  126.5  610.5 852.4  673.1
 48  900.3   872.9   107.7 490.8  763.3 748.4
 56  753.4   855.3   59.1  607.8  553.3 753.7
 64  573.4   789.9   36.5  505.6  454.8 657.4
 72  427.3   478.2   27.0  341.8  344.2 825.0
 80  329.2   460.3   22.9  301.3  257.6 465.8
 88  208.4   429.2   7.8   184.7  166.4 600.0
 96  105.0   136.5   7.3   244.5  114.7 513.8
 108 63.0    107.7   0.0   102.1  41.6  452.0
 120 17.1    49.0    0.0   64.3   14.4  352.2
 132 9.9     28.8    0.0   36.4   69.5  139.2
 144 5.2     0.0     0.0   20.5   9.5   84.8
 ;
```

Cobalto

```
data marcelo;
 title 'cinética de passagem de partículas:Favoreto (2008)';
 input time     a1 a2 a3 a4 a5 a6 a7 a8;
 y = a1 - a8;
 n = 24;

 datalines;
 0   0.0    0.0     0.0    0.0    0.0    0.0    0.0   0.0
 4   0.0    0.0     0.0    0.0    0.1    0.1    0.2   0.0
 8   22.9   11.8    47.3   1.4    15.8   92.8   16.5  16.9
 12  116.6  124.6  107.6  127.0  88.6   148.9  78.3  124.0
 16  127.5  118.7   96.6   93.8   110.3  90.2   78.1  113.9
 20  103.6  71.0    57.7   63.5   85.2   63.2   62.2  97.7
 24  56.0   77.7    37.9   62.5   57.3   40.9   41.0  76.6
 28  53.6   48.5    26.1   61.5   54.9   27.5   38.1  68.3
 32  33.1   43.6    16.2   52.1   48.1   25.1   30.0  52.8
 36  22.6   35.5    14.3   34.3   22.3   13.8   20.5  15.6
 40  20.7   22.8    18.5   22.1   17.0   19.6   15.9  13.1
 44  16.2   12.9    15.4   16.1   13.7   17.0   18.8  16.7
 48  18.2   22.1    11.3   24.8   16.2   24.7   19.0  16.9
 56  18.8   14.1    5.3    15.8   11.2   8.8    11.9  8.6
 64  6.4    6.4     3.3    5.8    7.5    7.6    11.2  7.3
 72  4.4    4.2     1.6    5.0    3.1    5.5    7.7   4.0
 80  2.1    2.5     0.6    4.0    1.2    2.6    5.9   0.7
 88  3.1    0.8     0.0    1.7    0.3    1.6    4.3   2.8
 96  1.3    0.2     0.0    36.2   0.0    0.7    2.8   0.0
 108 0.0    0.0     0.0    0.0    0.0    0.0    1.1   0.0
 120 0.0    0.0     0.0    0.0    0.0    0.0    0.0   0.0
 132 0.0    0.0     0.0    0.0    0.0    0.0    0.0   0.0
 144 0.0    0.0     0.0    0.0    0.0    0.0    0.0   0.0
 192 0.0    0.0     0.0    0.0    0.0    0.0    0.0   0.01
 ;
```

```
data marcelo;
 title 'cinética de passagem de partículas:Santos (2011)';
 input time    a1 a2 a3 a4 a5 a6 a7 a8 a9 a10;
 y = a1 - a10;
 n = 28;

 datalines;
 0     0.00  0.00  0.00  0.00  0.00  0.00  0.00  0.00  0.00  0.00
 1     0.00  0.00  0.06  0.00  0.07  0.00  0.05  0.00  0.00  0.01
 2     0.00  0.00  0.00  0.01  0.01  0.03  0.00  0.00  0.00  0.02
 4     0.06  0.04  0.06  0.01  0.07  0.01  0.05  0.00  0.07  0.03
 6     0.05  0.00  0.28  0.06  0.17  0.06  0.04  0.02  0.08  0.30
 8     0.12  0.65  1.66  0.76  0.86  1.70  0.33  0.58  0.92  0.27
 10    0.24  1.42  1.77  2.06  1.06  1.45  0.40  1.32  1.20  1.33
 12    1.08  1.95  2.16  2.60  1.42  1.59  0.96  1.64  1.59  1.54
 16    1.20  1.87  1.79  2.29  1.45  0.90  1.36  1.77  1.07  1.64
 20    1.02  1.02  0.83  1.54  0.76  0.69  1.12  1.14  1.26  1.25
 24    0.81  0.80  0.50  0.66  0.47  0.52  0.43  0.68  0.57  0.80
 28    0.52  0.55  0.39  0.51  0.47  0.41  0.36  0.47  0.30  0.56
 32    0.48  0.47  0.35  0.37  0.34  0.33  0.38  0.39  0.33  0.55
 36    0.35  0.27  0.32  0.35  0.30  0.14  0.28  0.36  0.28  0.45
 40    0.32  0.23  0.36  0.19  0.24  0.12  0.23  0.21  0.25  0.28
 44    0.33  0.17  0.27  0.13  0.23  0.10  0.21  0.12  0.11  0.22
 48    0.12  0.15  0.12  0.11  0.11  0.09  0.10  0.13  0.17  0.17
 56    0.11  0.11  0.13  0.09  0.11  0.12  0.09  0.10  0.03  0.13
 64    0.06  0.07  0.03  0.07  0.03  0.05  0.02  0.07  0.10  0.10
 72    0.02  0.04  0.00  0.07  0.02  0.03  0.00  0.06  0.02  0.06
 80    0.01  0.02  0.00  0.03  0.01  0.02  0.00  0.01  0.00  0.07
 88    0.00  0.04  0.00  0.03  0.00  0.07  0.00  0.04  0.00  0.05
 96    0.00  0.01  0.00  0.01  0.00  0.07  0.00  0.03  0.00  0.04
 108   0.02  0.00  0.02  0.00  0.03  0.01  0.00  0.00  0.03  0.01
 120   0.00  0.01  0.00  0.00  0.00  0.00  0.00  0.01  0.02  0.04
 132   0.00  0.00  0.00  0.04  0.01  0.00  0.00  0.01  0.02  0.04
 144   0.00  0.00  0.00  0.04  0.00  0.00  0.00  0.00  0.01  0.00
 192   0.07  0.00  0.06  0.00  0.00  0.00  0.06  0.00  0.09  0.01
 ;
```

```
data marcelo;
 title 'cinética de passagem de partículas:Pádua (2009)';
 input time     a1 a2 a3 a4 a5 a6 a7 a8 a9 a10 a11;
 y = a1 - a11;
 n = 29;

 datalines;
 0     0.0    0.0    0.0    0.0    0.0    0.0      0.0    0.0    0.0    0.0    0.0
 4     0.0    0.0    0.0    0.0    0.0    0.0      0.0    0.0    0.0    0.0    0.0
 8     1.5    5.7    2.1    1.9    0.0    0.0      1.8    0.0    10.9   0.0    1.6
 12    53.1   151.7  162.8  57.0   5.9    5.1      175.6  76.2   140.1  0.0    51.8
 16    186.4  0.0     378.4  368.6  610.8  132.5  577.7    417.4  285.9  0.0    250.8
 20    233.9  289.0  306.3  492.3  321.1  261.8    471.6  322.1  362.3  0.0    237.6
 24    288.9  343.9  0.0    273.0  248.0  420.7    384.4  0.0    309.7  294.6  179.6
 28    253.0  292.9  196.7  223.3  189.2  0.0      205.9  217.5  256.6  379.2  149.6
 32    211.5  271.0  158.8  178.9  0.0    0.0      0.0    188.1  0.0    402.4  90.3
 36    0.0    0.0    135.9  165.1  140.5  210.1    169.6  161.5  189.5  373.5  0.0
 40    0.0    208.5  125.0  125.4  116.0  183.2    0.0    140.7  142.8  323.1  65.1
 44    112.0  182.8  97.7   79.7   77.9   0.0      0.0    87.2   94.0   284.2  36.9
 48    68.0   86.9   71.3   54.6   51.3   136.8    58.7   63.5   62.2   249.8  26.7
 56    57.7   56.1   36.5   43.4   34.6   69.0     53.0   42.8   31.7   0.0    17.2
 64    42.7   41.0   29.2   28.6   24.8   59.1     31.6   29.8   29.8   93.3   20.6
 72    0.0    0.0    0.0    0.0    0.0    0.0      0.0    0.0    0.0    0.0    12.6
 80    0.0    23.8   25.7   21.9   20.1   40.6     22.8   24.6   20.5   19.5   14.3
 88    22.3   0.0    19.3   19.3   0.0    33.5     21.1   22.5   19.2   0.0    16.5
 96    0.0    22.3   14.1   12.6   11.5   12.2     11.1   0.0    8.5    11.4   9.0
 108   9.6    0.0    0.0    15.2   10.2   11.9     10.0   0.0    8.6    8.5    0.0
 120   0.0    16.7   12.8   14.3   12.8   12.6     17.3   14.6   9.5    0.0    8.7
 132   14.7   11.8   10.8   11.0   12.9   19.1     15.8   17.4   0.0    0.0    0.0
 144   18.2   19.5   18.6   0.0    0.0    18.9     0.0    19.5   0.0    0.0    0.0
 156   0.0    21.9   0.0    0.0    0.0    22.2     0.0    0.0    0.0    4.9    4.2
 168   6.7    4.4    3.8    3.8    4.8    4.8      3.4    5.1    5.0    7.8    4.1
 180   6.0    3.7    5.4    5..  4    6.3    6.4    1.6    2.4    1.7    0.0    3.9
 192   1.4    3.7    2.4    1.6    2.8    2.9      2.4    1.8    1.1    2.3    2.9
 204   4.5    3.3    3.3    1.5    4.3    3.6      2.5    2.6    3.5    4.5    3.3
 216   4.2    5.0    2.9    3.9    5.1    5.4      3.8    5.4    5.2    4.5    4.1
 ;
```

```
data marcelo;
 title 'cinética de passagem de partículas:A. M. Fernandes (unpublished results)';
 input time     a1 a2 a3 a4 a5 a6 a7 a8 a9 a10 a11 a12 a13 a14;
 y = a1 - a14;
 n = 23;

 datalines;
 0    0.0      0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0
 4    0.0      0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.5     0.0     0.0     1.5     0.0     0.0
 8    0.0      0.0     0.0     0.0     0.0     0.0      335.5  0.0     0.0     0.0     0.0     2.3     0.0      467.0
 12   2422.8  16.0    1194.0  171.9   8.8     310.5   1423.8  0.0     1237.3  2283.6  0.0     175.3   0.0     1290.2
 16   1135.8  1562.7  2567.0  966.0   514.8   1146.4  798.6   1983.6  2896.3  888.6   318.1   1753.0  142.5   634.2
 20   2118.8  2061.7  1856.0  1620.3  905.1   1311.4  752.4   2234.6  2616.3  1636.6  1192.9  1987.0  1251.0  1249.2
 24   1652.8  1502.7  1420.0  1694.3  1863.8  1169.4  420.1   2110.6  64.0    878.3   1112.9  1608.0  1552.0  1027.2
 28   1226.8  1619.7  1444.0  1292.3  1673.8  1120.4  360.7   1213.6  1464.3  342.5   968.9   1382.0  1247.0  833.8
 32   1146.8  1618.7  1446.0  1351.3  1514.8  887.1   390.9   1097.6  1494.3  250.6   1016.9  930.5   1839.0  511.8
 36   1302.8  964.2   1160.0  1187.3  1055.8  979.3   17.1    1007.6  1250.3  185.1   1040.9  755.1   1635.0  378.2
 40   1118.8  723.9   1205.0  967.6   1189.8  621.6   226.7   839.7   695.2   122.9   0.0     450.2   1639.0  251.2
 44   468.6   800.0   970.0   944.8   1426.8  541.4   164.5   820.4   656.7   119.9   867.9   348.3   1540.0  157.8
 48   297.3   500.4   800.7   826.7   1109.8  424.5   142.8   672.4   0.0     88.2    716.7   289.0   1198.0  106.2
 56   228.2   371.8   474.5   421.3   1013.8  368.9   91.1    135.9   452.0   39.6    190.2   192.4   995.0   55.2
 64   136.5   249.4   298.1   289.3   874.5   240.1   55.4    89.9    233.1   19.8    85.3    58.0    901.0   35.7
 72   95.4     140.8   176.1   213.0   661.1   133.0   25.7    64.8    150.9   8.7     28.0    42.2    696.4   28.4
 80   72.2     99.4    105.1   158.9   596.2   90.0    30.4    61.1    103.4   6.9     108.0   31.4    533.4   24.7
 88   51.7     45.3    67.3    145.0   372.8   53.9    21.2    47.5    69.3    3.9     82.2    5.3     510.4   14.8
 96   32.2     35.1    44.6    104.6   201.3   43.2    11.9    31.8    33.4    2.1     83.4    7.1     112.1   7.7
 108  23.3     22.8    19.1    35.6    165.4   21.7    12.0    23.5    26.8    1.6     30.2    5.4     164.6   4.0
 120  12.3     6.8     5.2     22.6    124.2   6.7     8.5     14.9    0.3     0.7     24.3    4.2     89.1    3.6
 132  9.1      0.6     3.1     9.4     80.3    2.7     5.4     10.3    3.4     0.6     12.6    1.7     41.4    5.1
 144  6.8      0.0     5.6     9.4     56.9    0.9     1.4     6.4     0.0     0.8     10.9    2.0     21.5    1.5
```

```
data marcelo;
 title 'cinética de passagem de partículas: A. M. Fernandes (unpublished results)';
 input time     a15 a16 a17 a18 a19 a20 a21 a22 a23 a24 a25 a26 a27 a28 ;
 y = a15 - a28;
 n = 23;

 datalines;
 0    0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0
 4    0.78    1.9     0.0     0.0     0.0     0.0     0.0     4.1     0.45    0.98    0.0     0.0     0.0     0.0
 8    176.9   1.1     15.4    0.0     0.0     2.1     126.5   413.7   7.9     0.5     0.0     0.0     0.0     1.6
 12   1259.9  1237.9  689.6   1572.6  0.0     421.3   2103.2  9.9     41.0    3403.1  24.3    0.0     436.4   43.3
 16   1354.6  1490.9  1112.5  2867.6  1345.9  2369.3  0.0     3672.9  2919.0  2439.1  1831.1  568.7   2072.1  1191.1
 20   1467.6  1561.9  884.7   3232.6  1933.9  2526.3  1731.2  2912.9  3147.0  2060.1  1921.1  1836.6  2983.1  2071.1
 24   1257.6  1162.9  645.7   1564.6  2373.9  2132.3  1551.2  2475.9  3432.0  1805.1  1852.1  2321.6  2937.1  2047.1
 28   872.1   1065.9  767.9   1812.6  2294.9  1985.3  1282.2  4376.9  2957.0  1203.1  1897.1  1347.6  2737.1  2318.1
 32   823.1   0.0     568.5   1031.6  2225.9  1896.3  1278.2  3236.9  2985.0  892.5   1510.1  1322.6  2502.1  2650.1
 36   783.9   727.6   327.0   674.0   2053.9  1272.3  635.1   1691.9  2520.0  587.5   1559.1  1128.6  1727.1  2304.1
 40   246.5   0.0     328.7   929.1   1910.9  0.0     530.9   2687.9  1642.0  2124.1  1559.1  782.8   1348.1  521.6
 44   229.5   433.8   213.4   515.1   1759.9  910.2   436.8   1433.9  1167.0  515.6   1250.1  537.2   1256.1  2166.1
 48   128.1   460.6   145.3   338.8   1548.9  796.6   532.4   980.5   919.8   219.2   1146.1  471.3   845.5   2084.1
 56   81.2    173.1   230.0   111.8   1317.9  353.2   152.6   274.5   713.5   144.0   1465.1  270.9   466.1   1853.1
 64   31.4    125.1   86.3    24.5    56.9    129.7   105.3   216.2   334.2   60.8    664.2   107.4   175.9   1480.1
 72   23.2   77.5    42.4    48.9    595.3   55.3    57.3    250.0   194.8   24.5    426.1   71.4    48.6    1044.1
 80   9.5    43.3    34.1    21.7    509.4   44.1    44.6    82.5    154.4   20.9    235.1   14.7    8.8     1194.1
 88   3.4    37.5    12.4    6.0     340.1   11.2    33.3    48.7    81.9    10.7    186.5   16.8    31.1    718.3
 96   3.7    25.0    27.1    6.2     270.7   10.9    36.1    64.2    53.5    11.0    149.2   4.5     20.4    514.6
 108  1.3    11.7    8.8     1.4     250.3   11.6    13.3    35.0    37.2    8.1     133.6   0.0     11.9    294.9
 120  0.0    6.9     4.3     0.3     112.5   1.9     3.4     23.4    15.9    2.3     65.9    0.0     4.2     159.4
 132  0.0    3.8     2.0     0.0     64.9    0.0     61.9    16.4    2.5     4.4     47.9    0.0     3.4     96.8
 144  0.0    2.2     1.0     0.3     0.0     0.0     17.3    7.3     0.0     4.0     21.9    0.0     4.9     58.1
```

Lantânio

```
data marcelo;
 title 'cinética de passagem de partículas: A. M. Fernandes (unpublished results);
 input time  a1 a2 a3 a4 a5 a6 a7 a8 a9 a10 a11 a12 a13 a14 a15;
 y = a1 - a15;
 n = 23;

 datalines;
 0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0
 4    0.0    0.0    0.0    0.0    0.0    0.0    5.7    0.0    0.0    0.0    0.9    0.0    0.0    0.0    0.0
 8    0.0    0.0    0.0    0.0    0.0    0.0    4.6    0.0    0.0    0.0    3.1    0.0    0.0    0.0    0.0
 12   388.5  0.0    10.1   3.6    0.5    2.2    3.4    123.1  123.1  33.1   23.1   0.0    0.0    6.2    0.0
 16   167.1  415.0  350.8  204.5  115.4  20.7   142.5  484.2  484.2  35.9   145.5  8.2    57.2   470.3  0.0
 20   695.7  867.6  505.3  315.4  382.4  67.7   151.4  538.2  538.2  107.5  329.8  30.5   374.8  503.3  216.3
 24   491.1  824.7  504.4  456.3  499.6  434.1  270.0  587.4  587.4  269.3  475.4  0.0    495.7  581.2  365.8
 28   410.9  700.8  537.0  305.2  458.2  485.7  213.7  676.3  676.3  602.7  443.5  174.5  502.0  546.2  433.5
 32   485.3  789.2  583.7  377.4  537.1  473.6  208.5  654.0  654.0  642.7  402.1  235.3  533.1  436.3  517.0
 36   466.5  452.4  563.2  334.3  582.4  313.3  168.2  10.5   10.5   642.6  372.4  392.3  554.9  410.0  598.1
 40   460.0  519.0  657.8  290.0  500.5  470.5  197.3  449.1  449.1  507.5  291.9  431.3  0.0    275.1  579.6
 44   209.9  637.9  529.1  295.8  418.1  571.7  129.5  340.5  340.5  515.6  246.0  426.3  504.3  211.4  596.0
 48   141.3  458.9  450.9  193.3  412.9  493.6  123.6  276.2  276.2  0.0    188.3  399.1  461.8  193.7  510.4
 56   135.3  321.7  288.7  100.6  196.5  540.0  188.9  196.4  196.4  446.6  89.3   0.0    235.4  154.2  443.8
 64   86.2   287.7  198.3  97.2   154.7  430.8  147.8  127.5  127.5  259.0  50.6   245.5  171.9  54.1   425.6
 72   61.3   181.7  137.7  56.2   119.5  360.2  95.0   62.4   62.4   182.3  22.0   220.0  131.5  45.3   351.4
 80   44.5   136.9  84.7   23.0   62.0   322.0  62.5   56.6   56.6   137.8  16.0   92.9   77.4   33.6   280.7
 88   28.0   73.3   68.0   22.6   74.1   221.3  39.9   46.9   46.9   104.0  7.5    79.8   58.0   8.9    271.6
 96   15.1   67.7   47.6   11.8   50.5   122.4  34.9   13.5   13.5   101.8  3.9    48.1   60.6   9.3    61.7
 108  9.7    45.2   22.2   7.0    16.0   103.7  16.8   7.5    7.5    50.5   1.7    16.8   21.0   0.0    99.7
 120  4.1    18.6   9.7    3.0    11.6   75.8   7.8    1.8    1.8    16.3   0.5    14.7   16.4   0.0    57.4
 132  1.8    12.1   4.7    3.2    3.1    51.3   4.6    0.0    0.0    22.1   1.1    8.8    6.8    0.0    28.0
 144  1.8    6.5    5.1    2.5    2.9    31.8   3.4    0.0    0.0    0.0    0.3    7.4    4.9    0.0    14.1
 ;
```

```
data marcelo;
 title 'cinética de passagem de particulas: A. M. Fernandes (unpublished results);
 input time  a16 a17 a18 a19 a20 a21 a22 a23 a24 a25 a26 a27 a28 a29 a30;
 y = a16 - a30;
 n = 23;

 datalines;
 0   0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0
 4   0.0    0.5    0.2    0.0    0.0    0.0    2.9    0.0    0.0    0.0    0.0    0.0    0.0    0.0    0.0
 8   0.0    26.5   1.4    0.0    0.0    0.0    0.0    0.0    0.0    4.4    0.0    0.2    0.0    1.6    1.1
 12  254.5  198.1  68.5   14.9   0.0    0.0    11.5   189.4  0.0    2.7    66.2   0.0    0.0    6.4    1.2
 16  360.0  377.1  296.9  196.9  7.3    118.1  484.6  0.0    67.6   324.4  503.1  254.0  3.0    147.9  89.9
 20  461.9  450.8  386.3  201.6  63.9   312.2  539.6  570.1  142.1  703.1  574.9  305.1  161.1  451.7  365.8
 24  424.3  472.8  392.1  192.6  180.5  490.6  509.7  565.5  433.0  1023.9 533.4  326.8  269.2  661.8  469.0
 28  390.2  419.9  419.3  247.6  220.2  505.6  635.9  530.8  1140.1 1024.9 497.0  407.6  280.8  716.6  558.1
 32  290.7  433.1  0.0    194.0  311.9  512.7  632.0  591.3  976.2  1040.9 368.5  420.6  289.3  810.2  716.1
 36  246.7  441.7  473.1  159.6  336.7  566.1  465.9  359.9  1337.1 883.0  248.9  418.9  310.0  664.3  829.4
 40  172.2  187.8  0.0    175.3  327.2  548.6  0.0    288.7  1247.1 739.6  680.4  621.1  273.9  568.2  290.9
 44  129.5  194.3  329.7  113.3  293.8  518.9  368.0  364.4  1484.1 599.4  223.8  438.4  181.5  585.3  796.8
 48  80.2   121.8  371.2  78.1   300.7  494.5  362.1  302.1  1026.1 547.1  110.7  474.7  186.1  459.3  726.5
 56  45.5   48.1   155.9  104.8  180.3  460.5  212.2  139.1  614.6  419.9  74.8   468.0  118.2  278.8  703.6
 64  23.8   43.0   121.3  55.6   93.0   6.8    94.7   91.8   517.6  229.7  38.3   353.9  58.4   151.5  550.1
 72  16.0   35.6   85.2   33.2   104.4  245.6  49.0   62.4   541.7  152.6  15.3   260.4  41.5   66.9   456.4
 80  11.7   16.7   48.3   26.7   92.4   212.2  35.2   34.5   249.6  131.3  11.0   152.1  50.1   46.5   517.0
 88  7.4    8.5    44.5   10.9   28.5   139.0  11.8   28.5   145.2  78.6   3.9    150.7  8.4    24.5   282.5
 96  1.1    7.3    28.6   19.6   30.6   106.8  9.7    11.0   180.0  51.9   0.0    117.4  3.9    11.0   261.0
 108 0.0    4.5    18.0   5.9    6.6    140.8  3.5    4.5    82.1   39.6   0.0    100.5  2.8    6.3    120.3
 120 0.0    0.0    9.6    2.6    4.0    61.3   0.0    0.5    41.5   17.0   0.0    51.2   1.6    0.0    78.7
 132 0.0    0.0    5.7    1.4    0.0    36.8   0.0    15.5   24.3   5.4    0.0    24.0   0.0    0.0    49.7
 144 0.0    0.0    3.4    0.3    0.0    47.1   0.0    3.2    12.5   2.1    0.0    10.3   0.0    0.0    24.4
 ;
```