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Research paper

Development of a model forecasting *Dermanyssus gallinae's* population dynamics for advancing Integrated Pest Management in laying hen facilities

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ABSTRACT

The poultry red mite, *Dermanyssus gallinae*, is the most significant pest of egg laying hens in many parts of the world. Control of *D. gallinae* could be greatly improved with advanced Integrated Pest Management (IPM) for *D. gallinae* in laying hen facilities. The development of a model forecasting the pests' population dynamics in laying hen facilities without and post-treatment will contribute to this advanced IPM and could consequently improve implementation of IPM by farmers. The current work describes the development and demonstration of a model which can follow and forecast the population dynamics of *D. gallinae* in laying hen facilities given the variation of the population growth of *D. gallinae* within and between flocks. This high variation could partly be explained by house temperature, flock age, treatment, and hen house. The total population growth variation within and between flocks, however, was in part explained by temporal variation. For a substantial part this variation was unexplained. A dynamic adaptive model (DAP) was consequently developed, as models of this type are able to handle such temporal variations. The developed DAP model can forecast the population dynamics of *D. gallinae*, requiring only current flock population monitoring data, temperature data and information of the dates of any *D. gallinae* treatment. Importantly, the DAP model forecasted treatment effects, while compensating for location and time specific interactions, handling the variability of these parameters. The characteristics of this DAP model, and its compatibility with different mite monitoring methods, represent progression from existing approaches for forecasting *D. gallinae* that could contribute to advancing improved Integrated Pest Management (IPM) for *D. gallinae* in laying hen facilities.

1. Introduction

The poultry red mite, *Dermanyssus gallinae*, is the most common ectoparasite of egg laying hens in many parts of the world, though this haematophagous mite may feed upon a range of other hosts, including humans (Sikes and Chamberlain, 1954; George et al., 2015). *Dermanyssus gallinae* has five developmental stages: egg, larva, protonymph, deutonymph and adult, with blood meals required for development from protonymph to deutonymph, to the adult stage, and for reproduction thereafter (Axtell and Arends, 1990). In a poultry house, the development of heavy infestations can occur within a short time period (30–70 days) (Maurer and Baumgartner, 1992), where favourable temperature and humidity drive rapid population growth. Highest *D. gallinae* population developmental rates and lowest *D. gallinae* mortality rates are generally seen between 20 and 37 °C (Maurer and Baumgärtner, 1992; Nordenfors et al., 1999). With temperatures in laying hen facilities typically kept between 18 and 21 °C, rising to 28–30 °C during the summer with higher outdoor temperatures

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(Klimaatplatform Pluimveehouderij, 2010), the *D. gallinae* lifecycle can be completed within 7 days (Maurer and Baumgartner, 1992).

High infestation rates of *D. gallinae* in egg-laying facilities may cause anaemia in hens (Kilpinen et al., 2005), and in extreme cases even hen mortality (Kilpinen et al., 2005; Arkle et al., 2006). Other negative effects of infestations include reduced animal welfare, reduced egg quality, and lower bird weight (Chauve, 1998). Lower egg production and increased feed and water intake have also been linked to *D. gallinae* infestation in laying hens (Mul et al., 2009). The costs for EU egg producers, have been estimated as € 0.29 per hen per one flock-year due to reduced production and € 0.14 per hen per one flock-year for control measures (Van Emous et al., 2005). *Dermanyssus gallinae* is known and suspected to vector numerous poultry pathogens (Valiente Moro et al., 2009), including Salmonella (Valiente Moro et al., 2007a,b) and the avian influenza A virus (H5N9) (Sommer et al., 2016). As well as presenting a threat to veterinary health, *D. gallinae* may also have an impact on human health as this species may also attack humans (Cafiero et al., 2011; George et al., 2015).

Control of *D. gallinae* is difficult. The mites' reclusive and nocturnal lifestyle makes this pest hard to target using available conventional acaricides, particularly as *D. gallinae* exist off-host and feed only intermittently (Maurer et al., 1988), potentially not encountering treated surfaces for several days after application. Increasingly stringent pesticide legislation in many parts of the world, as well as the tendency of *D. gallinae* to rapidly develop resistance, further exacerbate this issue (Sparagano et al., 2015). Consequently, there is an urgent need for alternative control strategies. Possibilities for future control of *D. gallinae* are described by Mul et al. (2009) and Sparagano et al. (2015). The current most promising approaches can be summarised as: a) a combination of control strategies, b) implementation of Integrated Pest Management (IPM), and c) the HACCP method (Hazard Analysis and Critical Control Points) (Mul et al., 2009; Harrington et al., 2011; Sparagano et al., 2015).

To deliver improved IPM for control of *D. gallinae*, advances have recently been made in the field of automated monitoring (Mul et al., 2015). For further improving IPM, development of better models to forecast mite population dynamics are now needed. For increased practical implementation of IPM, a model to quantify the total economic costs associated with given levels of *D. gallinae* infestation is required, as is a control algorithm to forecast and advise on timing of treatments when economic thresholds are exceeded (Benbrook et al., 1996; Legg, 2004; Mul et al., 2016). For effective advice, the control algorithm should incorporate input from both the population dynamics model and the economic model. Modelling ecosystem processes is nevertheless difficult, since the complexity of interactions and the effects of these interactions on pest population dynamics are broad and often unknown. Population dynamics models are nonetheless vital for forecasting and decision making in IPM programmes (Kogan, 1998).

Currently, two models are available describing the population dynamics of *D. gallinae* (Maurer and Baumgartner, 1994; Huber et al., 2011). Maurer and Baumgartner (1994) developed a population model to inform strategic and tactical decisions for control strategies, and to obtain knowledge to fill gaps in our understanding of *D. gallinae's* biology. Huber et al. (2011) developed a tactical model describing the population dynamics of *D. gallinae* and the effect of a treatment on that population. This model was based on that of Maurer and Baumgartner (1994) and showed the population development in time, depending on the egg production of adults, their fecundity, sex ratio and inter-laying time. In this model, the equilibrium or steady state of a *D. gallinae* population was defined when the number of eggs, nymphs and adults in the facility did not increase further. The treatment effect measurement was defined by two parameters: 1) The proportion of adults and nymphs killed, and 2) the time taken for the population to recover. In addition, the population measurements were simplified in the Huber model to three classes: eggs and larvae, nymph stages and adults. Practical implementation of both above models requires numerous and complex measurements of the mite population (with a differentiation between number of eggs, larvae, protonymphs, deutonymphs and adults at several points in time) and either the number of mites in the steady state, or the efficacy of the treatment. Obtaining this vital data, however, will be costly and time consuming, and is therefore currently not feasible.

In order to realise practical benefit and advancing improved IPM programmes, review of available literature (Kogan, 1998; Dent, 1995; Dent, 2000; Dively, 2017; Radcliffe et al., 2015) supports that models and their required inputs need to be: 1) labour-extensive with minimal staff input, preferably automatically implementing "real time" measurement data into models; 2) operational, providing easily interpretable data, forecasting pest population dynamics and the moment a defined action threshold will be exceeded (be this economic or hazard based); 3) able to compensate for different locations and time-specific-interactions and variables (e.g. management and temperature), enabling the handling of variability of the parameters of interest; 4) able to identify pest hotspots; 5) able to estimate and forecast treatment efficacy; and 6) applicable for different monitoring methods and therefore able to correct for monitoring measurement errors.

Where *D. gallinae* is concerned, and as shown in this paper, the variation of treatment effects on pests, and their population dynamics, are partly temporal, meaning that every flock has a different slope of the age effect, and a substantial unexplained part. This means that the population growth and the treatment effects on pests can vary between locations (facilities) and over time within a laying hen facility. This suggests that conventional population models are likely to be sub-optimal in forecasting *D. gallinae* population development and treatment efficacy. Under conditions of such high variation and different individual slopes, André et al. (2010) suggested that a time-series model with a dynamic approach (West and Harrison, 1997), also called dynamic adaptive model, can help to improve the forecasting accuracy.

For advancing the implementation of IPM programmes, an operational model helping the farmers in their management to control *D. gallinae*, is needed. Such an operational model, forecasting the mite population dynamics, applicable to all poultry facilities, and estimating the efficacy of a curative treatment, has yet to be described for *D. gallinae*. The aim of the current study was to develop and subsequently demonstrate a dynamic adaptive (DAP) model which can follow and forecast the population dynamics of *D. gallinae* in laying hen facilities. A further aim was to acquire an indication on the source of this variation.

2. Materials and methods

2.1. Source and compilation of datasets

To develop and demonstrate a model for forecasting the population dynamics of *D. gallinae*, and to gain insights into the source of the variation of the population growth, mite monitoring data was used from the Experimental Poultry Centre in Geel, Belgium and from a laying hen farm in Lyon, France.

At the Experimental Poultry Centre in Geel, mite monitoring data was collected in four laying hen houses (House) for a period of five flocks between 2005 and 2011. House A and C housed hens in large enriched cages (40 birds/cage), House B in an aviary system, and House D in small enriched cages (20 birds/cage). House A and C housed 2400 hens each, House B 2000 hens and House D 2160 hens. For monitoring the mite population in this farm, the Mite Monitoring Score method (MMS, Cox et al., 2009) was used (henceforth referred to as Dataset 1).

In Lyon, France, mite monitoring data was collected at a single laying hen house of an egg production farm, housing 11,520 hens in enriched cages (60 hens/cage). In this farm, the mite population was monitored using two different monitoring methods; the Semi-Attractive water Trap method (SAT, Chiron et al., 2014) (henceforth referred to as Dataset 2) and the Simplified Passive tape Trap method (SPT, Roy et al., 2014; Chiron et al., 2014) (henceforth referred to as Dataset 3).

Table 1
Overview of the three datasets, housing systems, monitoring methods, the number of measuring points for calculating the Average Mite Infestation Level (AMIL), and the type of monitoring measurements used to obtain insight into the variation of the population growth, to develop or to demonstrate the dynamic adaptive model described herein for forecasting the population dynamics of *Dermanyssus gallinae*.

Dataset number	Type of housing system (laying hens/cage) (House ID)	Number of flocks	Monitoring method	Type of measurements	Used for	Number of measuring points for calculating AMIL[a]
1	Large enriched cages (40/cage) (House A)	5	MMS[b]	Classes (0–4)	Variation population growth, model development	36
	Aviary system (House B)	5	MMS[b]	Classes (0–4)	Variation population growth, model development	36
	Large enriched cages (40/cage) (House C)	5	MMSb[2]	Classes (0–4)	Variation population growth, model development	36
	Small enriched cages (20/cage) (House D)	5	MMS[b]	Classes (0–4)	Variation population growth, model development	36
2	Large enriched cages (60/cage)	1	SAT[c]	Counts	Demonstration	Max. 40
3	Large enriched cages (60/cage)	1	SPT[d]	Classes (0–3)	Demonstration	44

[a] Average Mite Infestation Level.
[b] Mite Monitoring Score method.
[c] Semi-Attractive water Trap method.
[d] Simplified Passive tape Trap method.

For all Houses and monitoring methods the Average Mite Infestation Level (AMIL) was determined as the average of all observation- or measuring points at a certain time of monitoring in a House. Table 1 gives an overview of the three datasets derived from different types of monitoring data.

2.1.1. Dataset 1, MMS method, Belgium

Dataset 1 from the Experimental Poultry Centre in Geel (Belgium) consisted of mite monitoring data from twenty flocks (or laying rounds) between 2005 and 2011 from four laying hen houses. The data were generated from mite monitoring based on the Mite Monitoring Score (MMS, Cox et al., 2009) covering five levels of *D. gallinae* infestation: 0 = no mites visible; 1 = mites visible in cracks and crevices; 2 = mites visual at unprotected places; 3 = clusters of mites (i.e. the size of all mites grouped together exceeds 1 cm^2) visible in cracks and crevices; 4 = clusters of mites visible at unprotected places in and on the housing equipment.

An employee of the Experimental Poultry Centre monitored all four laying hen houses. During the period 2005–2011, three different employees carried out the monitoring as follows. The houses were monitored every other week if no infection was present, or weekly after the first mite was detected, using the MMS method. In each house twelve designated locations were monitored, with scores returned for three heights per location (providing 36 observations overall). During the assessment, about 1 m^2 of the housing sub structure was inspected for mites, with the use of a torch, from top to bottom of the system around the measuring point. All 36 observation scores were averaged per house. For Dataset 1 the Average Mite Infestation Level (AMIL) was based on these 36 observation scores. All *D. gallinae* treatment dates and types of treatment were recorded, with silica being most typically used. A treatment was applied if AMIL was higher than 1, if a score higher than 3 was found anywhere in the house, or if workers reported *D. gallinae*-related dermatological complaints or bloodspots on eggs. The indoor temperature (ranging from 14.17 to 26.77 °C) was recorded every hour in each house, and the calculated weekly mean temperature was used in the models.

Dataset 1 was used to obtain insight into the sources of the variation of *D. gallinae* growth rate, and to develop the adaptive population model described herein.

2.1.2. Dataset 2, SAT method, France

Staff from the ITAVI (Institute Technique de l'AVIculture) collected Dataset 2 using the Semi-Attractive water Trap (SAT, Chiron et al., 2014) method, consisting of a 40-ml plastic vial, two-thirds of which were filled with water, with a screw cap. The vial was positioned on a metal wire (2.4 mm diameter) attached to the cap and to the grid near the egg belt, on the outside of the enriched cages present. The screw cap was perforated with seven holes of approximately 2 mm in diameter. The mites were attracted to the water and entered the vial via the metal wire through the holes in the screw cap. Liquid dish-washing detergent (from Paic and Carrefour) was added to the water at a rate of 0.01% (v/v) to make the mites drown and sink for subsequent assessment. The vials used for mite trapping were refreshed every two weeks. In the laboratory, the water/soap solution in each vial was filtered through a sieve (4 cm diameter, 150 µm mesh size) and the mites on the mesh were counted under a binocular microscope on a Petri dish divided into squares. The number of trapped mites was determined per trapping point and averaged for the number of trapping points available on the specific measuring date. For Dataset 2, the Average Mite Infestation Level (AMIL) was based on the total number of mites determined from the available number of trapping points which were maximum 40 trapping points, divided by the number of trapping points.

Seven traps were placed at cage level 1 along both sides of the cages at row 3 and 4. In row 1 and 2, four traps were placed at both sides of one half of the row on cage level 1. The *D. gallinae* population was monitored on a two-weekly basis with SAT for a period of 17 months

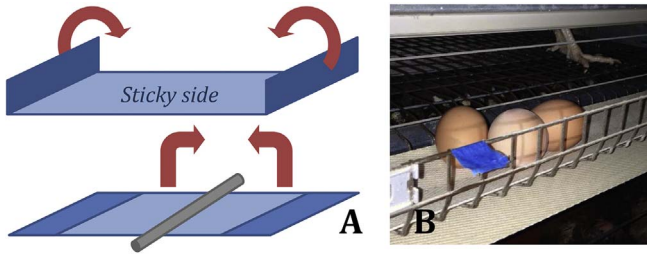

Fig. 1. Use of Painter's Masking Tape to produce a Simplified Passive tape Trap (SPT) for monitoring *Dermanyssus gallinae* (panel A) (adapted from Roy et al., 2014) and an example of fixation of the SPT in an egg laying facility (picture from A. Varescon) (panel B).

from July 2012 to December 2013. However, for the final thirteen weeks the mite population was monitored on a weekly basis. The temperature in this French laying hen house was recorded from the end of June 2012 until December 2013. The weekly mean temperature (ranging from 17.4 to 24.3 °C) was calculated and used in the model. Treatment dates and methods were recorded, again with silica being most typically used.

Dataset 2 was used to demonstrate the developed model's ability to perform given different monitoring methods and housing systems.

2.1.3. Dataset 3, SPT method, France

Staff from the ITAVI (Institute Technique de l'AVIculture) also collected mite monitoring data using the Simplified Passive tape Trap (SPT, Roy et al., 2014; Chiron et al., 2014) method, whereby a 5–8 cm long section of 3 cm wide painter's masking tape was wrapped around cylindrical bars in the poultry system, joining the two ends, but leaving a central space near the bar to serve as a mite refuge (see Fig. 1). The number of mites trapped on this sticky refuge was scored to four different levels: 0 = no mites visible in the trap; 1 = 1–9 mites visible in the trap; 2 = sparse groups of >10 mites visible in the trap; 3 = clusters of mites visible in the trap. SPT traps were assessed and renewed weekly at 44 trapping points. For Dataset 3, the Average Mite Infestation Level (AMIL) was based on the average scores from these 44 trapping points. Seven traps were placed along both sides of the cages in row 3 and 4 at cage level 1. In row 1 and 2, four traps were placed at both sides of one half of the row on cage level 1. The *D. gallinae* population was monitored for a period of 19 months from the end of April 2012 to December 2013. The temperature in the house was recorded from the end of June 2012 until December 2013. The weekly mean temperature (ranging from 17.4 to 24.3° C) was calculated and used in the model. Treatment dates and methods were recorded, again with silica being most typically used. Dataset 3 was used to demonstrate the developed model's ability to perform given different monitoring methods and housing systems.

2.2. Growth rate

On the assumption that mite populations observed at two closely related time points followed an exponential growth relation, and that population growth rate is in practice always density independent as a result of the treatments applied, all monitoring data was converted to a variable Rt describing the exponential "growth rate", derived from the exponential growth function as described in Edelstein-Keshet (1988).

$Y_t = Y_{t\text{-}1} * e^{Rt.\Delta t}$ into the equation (1)

$$Rt = \frac{Ln\left\{\frac{Yt}{Yt-1}\right\}}{\Delta t} \quad (2)$$

with
Ln = natural logarithm
Y_{t-1} = average mite infestation level at week t and
Δt = time step in weeks between t-1 and t.

To reduce measurement error, for our model's growth rate (R_t) per week was calculated as shown in Eq. (3).

$$Rt = \frac{Ln\left\{\frac{Yt}{\frac{Yt-1+Yt-2+Yt-3}{3}}\right\}}{\Delta t} \quad (3)$$

with
Ln = natural logarithm
Y_t = average mite infestation level at week t and
Δt = time step in weeks between t-3 and t.

Converting the infestation level to growth rate enabled the population dynamics model to work with both classes and counts as monitoring data (classes, counts).

Hereafter, weekly growth is referred to as growth rate. Growth rate was used as a response parameter to determine the source of variation of the *D. gallinae* population growth (Eq. (4)) (REMLmite model) and as a response parameter of the forecasting dynamic adaptive population model (Eq. (5)), DAP model.

2.3. Variation in population growth

To gain insight on the source of the variation of the population growth, the growth rate records from Dataset 1 were analysed with a linear random regression model (REML), using the statistical software package GenStat for Windows (17th edition, 2015) (Anonymous, 2006). This REML model enabled to determine the effects of a) housing, b) temperature and c) age in weeks of the flock of hens (flock age) on mite population growth rate.

Flock age is the age of the laying hen in weeks starting at 0 in the week they were hatched. In Belgium, most laying hens arrive on farm at age of 16–18 weeks (after hatching and being raised to this point at the rearing farm).

Parameters were estimated by REML (Searle et al., 1992).

The linear random regression model, further referred to as REMLmite model, used was:

$$\underline{R}_{ijkt} = \{\beta_0 + \pi_{0j} + \alpha_{0k} + \underline{\varepsilon}_{0ij}\} + \{\beta_1 + \pi_{1j} + \alpha_{1k} + \underline{\varepsilon}_{1ij}\}*A^{-1} + \beta_2*(T - 20) + \underline{\varepsilon}_{ijkt} \quad (4)$$

where: $\underline{R}_{ijkt}$ = weekly growth rate of flock (or laying round) i of House j after a treatment k (0,1) at week t (ln(AMIL)/week); A^{-1} = inverse of flock age of hens (in weeks); T = House temperature (in Celsius); β_0, β_1 = intercept and slope of effect of $\frac{1}{flockage}$ for House D when no treatment was applied; π_{0j}, π_{1j} = Difference in intercept and slope of effect of flock age^{-1} for other compartments (compared to D); α_{0k}, α_{1k} = difference in intercept and linear effect when treatment if applied compared to when treatment is not applied; β_2 = effect of temperature; $\underline{\varepsilon}_{0ij}$, $\underline{\varepsilon}_{1ij}$ = random effect (or difference in) of flock (or laying round) i of House j for intercept and slope of effect of $\frac{1}{flockage}$, $\underline{\varepsilon}_{it}$ = residual at week t, representing residual variation.

In the final model π_0 was omitted because it did not significantly contribute to the model.

The regression coefficient for the age effect of a flock of hens was modelled using the inverse of flock age of the hens $\left(\frac{1}{flock\ age}\right)$. The inverse of flock age was chosen since at low flock age the growth rate and treatment effects change more rapidly in time compared to high flock age.

2.4. Development of a dynamic adaptive population model

To enable forecasting of *D. gallinae* population dynamics in any specific farm situation, and to meet most of the requirements for a model contributing to the development and implementation of practical IPM programmes for *D. gallinae* in laying hen facilities, a dynamic adaptive population model was developed. Such a dynamic adaptive

model is suitable for forecasting near-future responses with temporal variation due to gradually changing factors. With *D. gallinae,* the factors contributing to the temporal variation are most likely elements of flock management and flock characteristics which are as yet unidentified or unmeasurable.

In dynamic adaptive models the parameter estimates are time-varying and regularly updated based on recent observations of the processes involved. Parameter estimation and forecasting future observations for these types of dynamic adaptive models are based on a Bayesian approach for recursive analysis of time series (West and Harrison, 1997).

The dynamic adaptive population model developed here, was a dynamic linear model (DLM) (West and Harrison, 1997). After each individual measurement of the *D. gallinae* population size, the parameters (priors) that enable forecasting the growth rate, being *C*0*t*, *C*1*t*, and *C*2*t* (see Eq. (5)), were evaluated and adjusted (posterior) by a dynamic linear model (DLM) (West and Harrison, 1997). Therefore, C_{0t}, C_{1t}, and C_{2t}, can change gradually in time. For further explanation about DLM, see Supplement S1.

In the developed model, further referred to as DAP model, it was assumed that the growth rate (R_t) at time t of Eq. (3) is a linear response to housing temperature (T_t) and treatment effect (D_t):

$$R_t = C_{0t} + C_{1t} * (T_t - 20) + C_{2t} * D_t \quad (5)$$

where: t = week t; C_{0t} = the intercept or base level (growth rate at indoor temperature of 20 °C, without treatment) in week t; C_{1t} = the linear effect of temperature in week t; C_{2t} = the linear effect of the treatment effect in week t.

Before the first data record was applied into the model, prior information (initially set priors) was incorporated. The structure, the matrix of known coefficients and the initial parameters of the DAP model were derived using the data from flock 1, Dataset 1. Final estimated parameters (posteriors) of the former measurement were used as prior values for the next measurement within the same House. A next measurement could also be the first measurement of the next flock in the same House. The influence of the initially set priors was less in flocks 2–5 when compared to the first flock. Therefore, the ranges of the time-dependent estimates of C_{0t}, C_{1t}, and C_{2t} were given only for flock 2–5 for all Houses of Dataset 1.

The correlations of the parameters for treatment effect and temperature were set at 0 at the start of the first flock. After five flocks, the correlations of parameter estimates were determined for all four Houses. These parameter estimates provided the correlations for the model as used with Datasets 2 and 3.

To convert the forecasted growth rate into a population forecast, Eq. (6) was used

$$\widehat{Y_t} = \left\{ \frac{Y_{t-1} + Y_{t-2} + Y_{t-3}}{3} \right\} * e^{\widehat{R}\, t * \Delta t} \quad (6)$$

where $\hat{Y}$ = the forecasted growth rate (in week t). This growth rate was generated by the model after input of monitoring data into the model. Y = the measured growth rate.

2.5. Model demonstration

The validation of the DAP model was demonstrated by assessing the model fit with the Mean Squared Prediction Error (MSPE). The MSPE assesses the quality of the prediction or forecast of the derived population model. The MSPE was calculated as the sum of squares of the difference between the forecasted growth rate and the measured growth rate:

$$MSPE = \frac{1}{n} \sum_{t=1}^{n} (\hat{Y}t - Yt)^2 \quad (7)$$

where $\hat{Y}$ = the forecasted growth rate (in week t). This growth rate was generated by the model after input of monitoring data into the model. Y = the measured growth rate.

The MSPE was determined, with and without outliers, for Datasets 1–3 with data obtained with the three different monitoring methods used. Differences in MSPE between Flocks 1–5 were also tested with a F-statistic using the statistical software package GenStat for Windows (17th edition, 2015) (Anonymous, 2006). To estimate the differences in accuracy of the model using the SPT and the SAT monitoring methods, the MSPE was determined for Dataset 2 and for Dataset 3, including the AMIL of the dates which were available in both datasets. Differences in MSPE between dataset 2 and 3 were tested with a F-statistic using the statistical software package GenStat for Windows (17th edition, 2015) (Anonymous, 2006). Due to significant differences between Belgian and French monitoring sites (hen breeds, housing system and flock management), no accuracy differences of the model were estimated between Dataset 1 and Datasets 2 and 3.

For graphic visualisation of the model, the fit of estimated forecasts of the mite infestation to real measurements (AMIL) were plotted.

3. Results

3.1. Dataset 1, MMS method, Belgium

The AMIL of the 36 measuring points was determined for all four Houses during five flocks (or laying rounds), as shown in Supplement S2. Fig. 2 shows, as an example, the mite population dynamics (AMIL) of the fifth flock in House D. Here, five silica based treatments were applied against *D. gallinae* at flock age 37, 43, 62, 67 and 75 weeks. Nest pads were cleaned at a flock age of 61 weeks. This cleaning, however, was not considered as a treatment by the staff.

Before the hens reached 60 weeks of age, the mite population increased to level 2. Shortly after hens had passed 60 weeks of age, the mite population decreased considerably to a little above level '1' due to cleaning of the nest pads, removing *D. gallinae*. The treatment applied just after the flock reached 70 weeks of age, and again just prior to 80 weeks, appeared to be less effective as there was no decline in the level of mite infestation at the first measurement after these treatments.

3.2. Dataset 2, SAT method, France

Dataset 2 is shown in Fig. 3. The AMIL is shown per monitoring date (flock age) and was ln transformed for improved clarity of the figure. The AMIL recorded using the SAT method reached 550 ($=e^{6.31}$) when the hens were around 80 weeks old. Silica treatments applied against *D. gallinae* were repeated 12 times on a weekly basis and resulted in a decrease of the number of mites trapped. On the ln scale the AMIL shows a linear increase with increasing flock age, meaning that on a normal scale there is an exponential growth of the mite population with increasing flock age. The solid line shows the model forecast which will be discussed in Section 3.6.

3.3. Dataset 3, SPT method, France

Dataset 3 (SPT method) is shown in Fig. 4. During the latter part of the laying round, 12 treatments were applied on a weekly basis. The highest Average Mite Infestation Level (AMIL) determined from 44 trapping points had a SPT score of almost 2.5 when hens were 83 weeks old. A remarkable observation can be seen in week 84 with a decline in AMIL without the application of a silica treatment. The solid line shows the model forecast which will be discussed in Section 3.6.

3.4. Variation in population growth

In order to achieve insight into the cause of the high variation of *D. gallinae* population growth rate, Dataset 1 growth rate records were analysed using the linear regression (REMLmite) model as described in

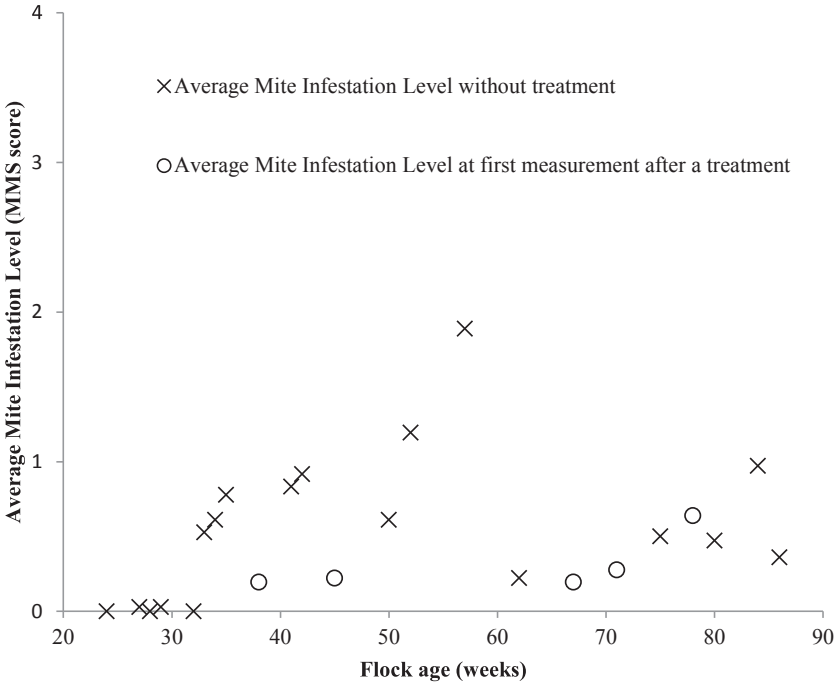

Fig. 2. Population dynamics of *Dermanyssus gallinae* over 90 weeks with the Average Mite Infestation Level versus flock age (weeks). The Average Mite Infestation Level (AMIL) is the average score of the 36 monitoring points in House D, of the fifth flock of the Experimental Poultry Centre in Geel (Belgium). The measured AMIL without treatment is shown by "X"; The measured AMIL after a treatment is shown by "○". The AMIL was determined using the Mite Monitoring Score method (Cox et al., 2009).

Eq. (4). The analyses revealed that:

a) The effect of flock age on the growth rate of a *D. gallinae* population in an average flock was estimated with β_0 (intercept of effect of $\frac{1}{flock\ age}$ without treatment) = −0.22 (95% Confidence Interval: −0.07, 0.37), and β_1 (regression coefficient for the effect of $\frac{1}{flock\ age}$ without treatment) = 16.4 (95% Confidence Interval: 7.8, 25). At high flock age (from 75 weeks of age) the growth rate of a *D. gallinae* population will reach a negative growth rate without applying any treatment as the extrapolated estimate for infinite flock age is −0.22 (P = 0.003).

For example, at a flock age of 40 weeks, the population growth rate was −0.22 + 16.4 (1/40) = 0.19, meaning that the mite population increased by ($e^{0.19}$ = 1.209) 21% in one week compared to the last measured population size. It is worth noting that this was the case without a treatment in House D and at a temperature of 20° C.

b) The effect of treatment was age dependent and was estimated with α_0 (difference in intercept of effect of $\frac{1}{flock\ age}$ post treatment, P = 0.033) = 0.24 (0.02, 0.46) and α_1(difference in linear effect of $\frac{1}{flock\ age}$ post treatment, P < 0.001) = −19.9 (-31.7, −8.1).

For example, when a treatment was applied at a flock age of 40 weeks, the mite population growth rate was (−0.22 + 0.24) + (16.4–19.9) * (1/40) = −0.0825, meaning that the mite population would be ($e^{-0.0825}$ = 0.9208) 92% of the last measured population size, i.e. a population reduction of 8%. The estimated effect of flock age on growth rate post treatment and without treatment in Dataset 1 are displayed graphically in Fig. 5.

c) The effect of temperature is independent from treatment, flock age or compartment, as the interactions with temperature were found to be non-significant (P > 0.05), and thus described as an additional effect. The effect of temperature on growth rate was estimated with β_2 = 0.019 (95% Confidence interval: 0.002, 0.036). This means, for example, that at a temperature of 25 °C, the growth rate will increase by 0.019 * (25–20) = 0.095 when compared to a temperature of 20 degrees Celsius. The *D. gallinae* population in a 40 week old flock without a treatment at a temperature of 25 °C was estimated to increase by ($e^{0.19+0.095}$ = 1.33) 33% in one week.

d) The effect of House was age dependent and was estimated with

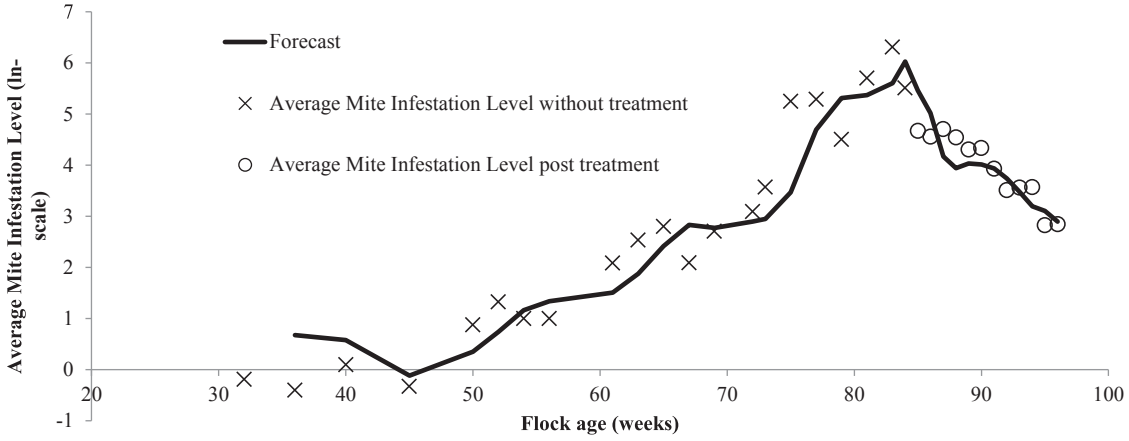

Fig. 3. Population dynamics of *Dermanyssus gallinae* over a period of 64 weeks from Dataset 2 with the Average Mite Infestation Level (AMIL) (ln- scale) versus Flock age (weeks). The Average Mite Infestation Level (AMIL) was determined using a maximum of 40 monitoring points collected in a French laying hen farm using the Semi-Attractive water Trap (SAT) method. The line shows the dynamic adaptive (DAP) model forecast of the AMIL one week in advance. The measured growth rate without treatment is shown by "X"; The measured growth rate after a treatment is shown by "○".

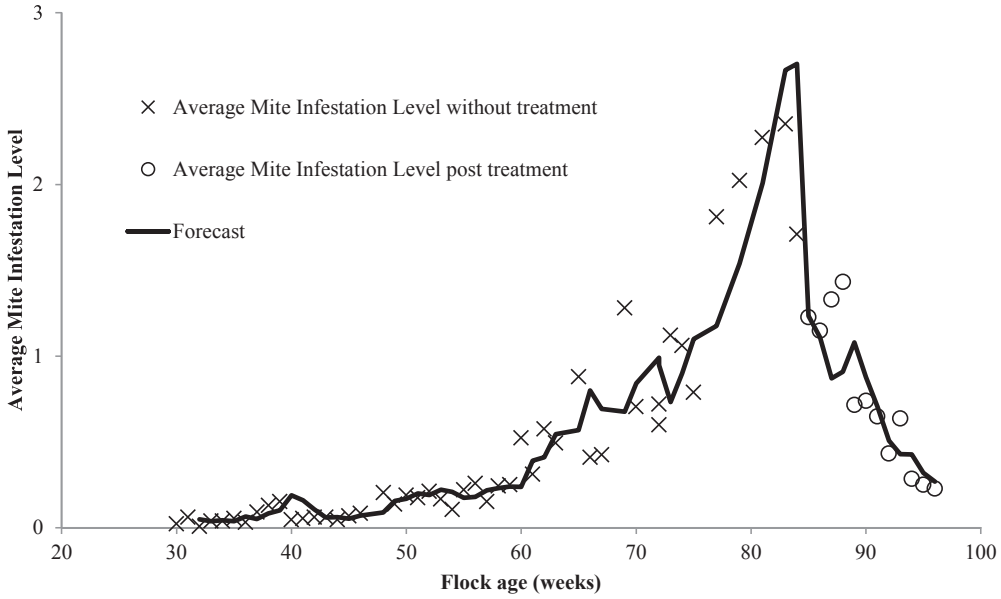

Fig. 4. Population dynamics of *Dermanyssus gallinae* over a period of 66 weeks from Dataset 3 with the Average Mite Infestation Level (AMIL) versus Flock age (weeks). AMIL was determined using the 44 data points collected in a French laying hen farm with the Simplified Passive tape Trap (SPT) method. The line shows the dynamic adaptive (DAP) model forecast of the AMIL one week ahead. The measured growth rate without treatment is shown by "X"; The measured growth rate after treatment is shown by "○".

π_{1j} (difference in linear effect of flock age compared with House D) = +6.88 (95% Confidence Interval: 0.41, 13.35) for House A, −6.55 (−13.02, −0.082) for House B and −0.93 for House C (−7.4, 5.54). The effect of flock age in House A and B was significantly different (P = 0.01). For example, the growth rate post treatment in House B at a flock age of 40 weeks and at a temperature of 20° C was estimated to be (−0.22 + 0.24) + (16.4 − 19.9 − 6.55) * (1/40) = − 0.231, which is lower compared with the same situation in House D (with the estimation of −0.0825).

Including the random regression term in the REMLmite model resulted in a significant model improvement (P < 0.05) explaining 17.1% of the variation instead of 13.2% without the random regression term. This means that the systematic factors (flock age, house temperature, and treatment) do not fully describe and explain the variation in the population growth rate. A substantial part of the variation is unexplained. Moreover, a part of the variation among flocks was temporal meaning that flocks had different slopes for the age effect as displayed graphically in Fig. 6. The population growth rate of the first flock in House A and C cannot be seen as the Average Mite Infestation Level (AMIL), and consequently the growth rate of the mite population, was almost always equal to zero.

The results of the analysis, which are described above, are summarised in Table 2.

3.5. Development of a dynamic adaptive population model

For estimating responses with unexplained temporal variations, as evidenced in the preceding section, a dynamic adaptive model (DAP model) was developed to forecast the growth rate of a *D. gallinae* population in any flock (see Eq. (5)). The following parameters were included in the model: C_{0t} = the intercept or base level (growth rate at indoor temperature of 20° C, without treatment) in week t; C_{1t} = the linear effect of temperature in week t; C_{2t} = the linear effect of the treatment effect in week t.

During the five flocks and in four Houses of Dataset 1, the mean, (minimum and maximum) values of C_{0t}, C_{1t}, and C_{2t} in the developed DAP model were:

a) 0.05 (−0.1, 0.4) for the intercept (C_{0t}),
b) 0.05 (0.02, 0.13) for temperature (C_{1t}),
c) − 0.07 (−0.29, 0.23) for treatment (C_{2t}).

The ranges of the values for treatment and the intercept were higher when compared with the values for temperature.

3.6. Model demonstration

In this section, we demonstrate the forecasting quality of the DAP model by comparing the forecasted population growth rate from this model with the actual measured and observed population growth rate.

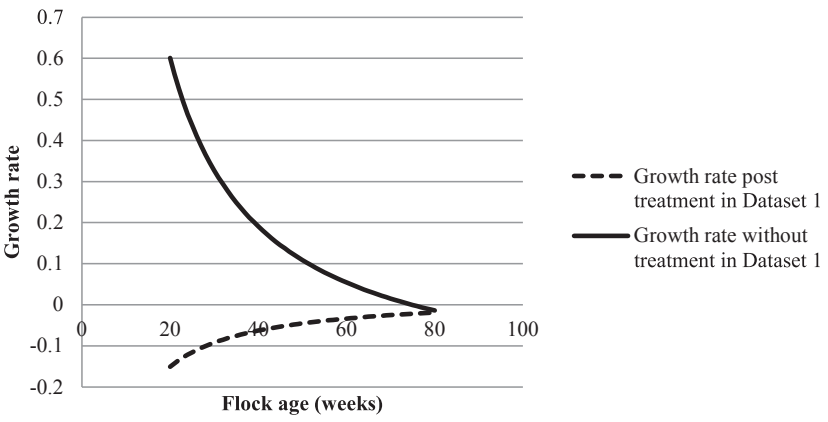

Fig. 5. Effect of flock age on the population growth rate (Rt) of *Dermanyssus gallinae* post treatment and without treatment in Dataset 1. Fixed effects of flock age and treatment are estimated with $\underline{R}_{kt} = \{\beta_0 + \alpha_{0k}\} + \{\beta_1 + \overline{\pi_1} + \alpha_{1k}\}^* A^{-1}$ where β_0, β_1 = intercept and slope of effect of $\frac{1}{flockage}$ for House D when no treatment was applied; α_0, α_1 = difference in intercept and linear effect when treatment is applied compared to when treatment is not applied; $\overline{\pi_1}$ = weighted average of house-specific flock age effects.

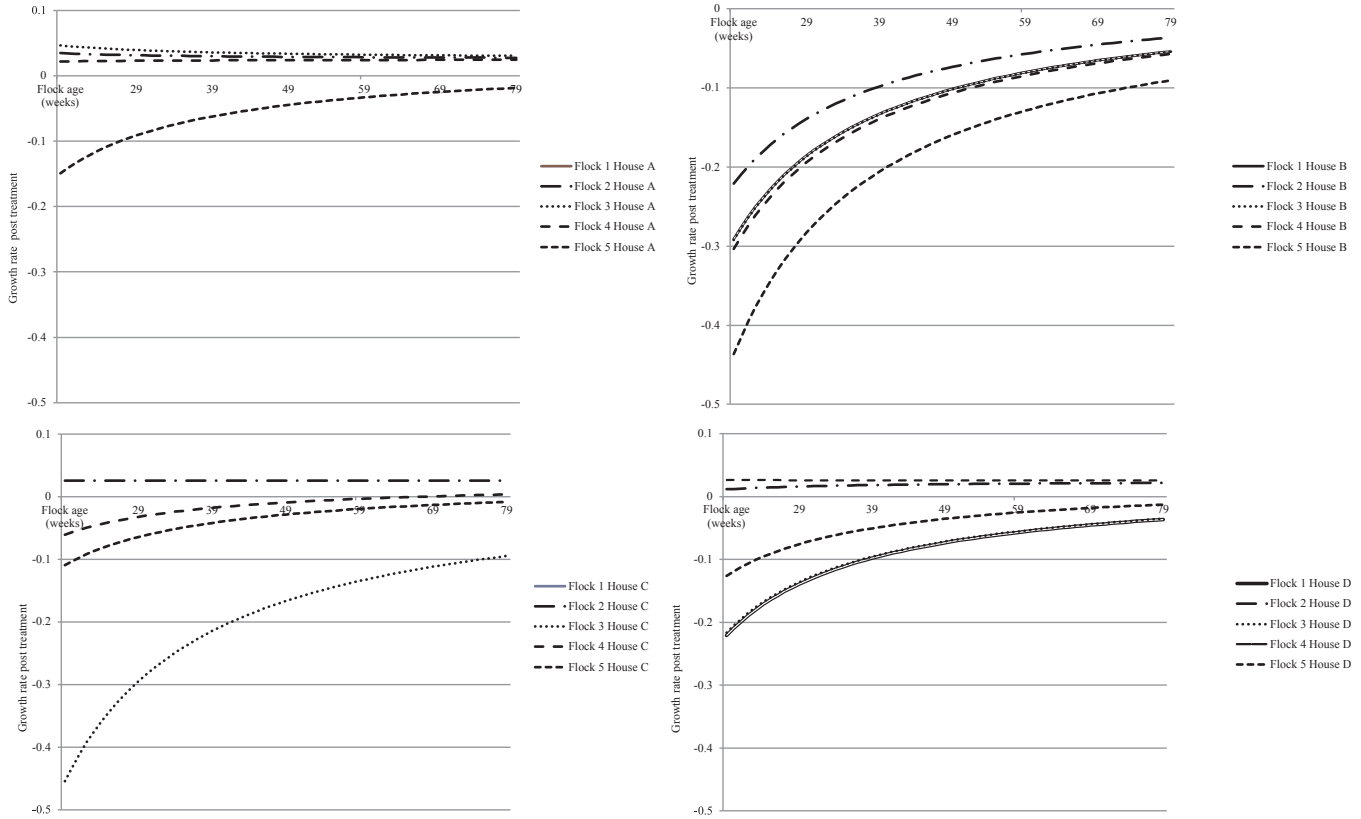

Fig. 6. Population growth rate (Rt) of *Dermanyssus gallinae* post treatment versus Flock age (weeks) per flock (flocks of House A − D) of Dataset 1 with monitoring data obtained with the Mite Monitoring Score method. $\underline{R}_{ijkt} = \{\beta_0 + \alpha_{0k} + \underline{\varepsilon}_{0ij}\} + \{\beta_1 + \overline{\pi_1} + \alpha_{1k} + \underline{\varepsilon}_{1ij}\} * A^{-1}$.
where β_0, β_1 = intercept and slope of effect of $\frac{1}{flockage}$ for House D when no treatment was applied; α_{0k}, α_{1k} = difference in intercept and linear effect when treatment is applied (k = 1) compared to when treatment is not applied (k = 0); $\overline{\pi_1}$ = weighted average of house-specific flock age effects; $\underline{\varepsilon}_{0ij}$, $\underline{\varepsilon}_{1ij}$ = random difference in intercept and slope of effect of $\frac{1}{flockage}$ for House j in flock i.

Table 2
Model parameter values for the effect of flock age, treatment, temperature and hen house on the *Dermanyssus gallinae* population growth rate, their confidence interval and P-values for the linear random regression model (REMLmite model) enabling to gain insight in the source of the variation of the *Dermanyssus gallinae* population growth.

Expected growth rate	E(Rt) =	Model parameter	Explanation	Value	Confidence- interval	P- value
Effect of flock age on growth rate	$\{\beta_0+\beta_1\} * A^{-1}$	β_0	Intercept of effect of flock age without treatment	−0.22	−0.07, 0.37	0.003
		β_1	Regression coefficient for the effect of flock age without treatment	16.4	7.8, 25	<0.001
Effect of treatment	$\{\beta_0 + \alpha_{0k}\} + \{\beta_1 + \alpha_{1k}\} * A^{-1}$	α_0	Difference in intercept of effect of flock age post treatment	0.24	0.02, 0.46	0.003
		α_0	Difference in linear effect of flock age post treatment	−19.9	−31.7, −8.1	<0.001
Effect of temperature	$\beta_2 * (T - 20)$	β_2	Effect of temperature on growth rate	0.019	0.002, 0.036	0.031
Effect of House	$\beta_0 + \{\beta_1 + \Pi_{1j}\} * A^{-1}$	Π_{1j}	Effect of House A compared to D	6.88	0.41,13.35	0.082
			Effect of House B compared to D	−6.55	−13.02, −0.082	0.01
			Effect of House Compared to D	−0.93	−7.4, 5.54	0.78

The model forecast (one week ahead) of the growth rate with Dataset 1, and the measured growth rate (if available) is shown in Supplement S3. The DAP model enabled forecasting of *D. gallinae* population growth for all three housing systems. As an example, the forecast line (one week ahead) for growth rate and the determined growth rate as measured with the MMS method is shown in Fig. 7 for the fifth flock of House D. At a flock age of 38 weeks, the effect of a treatment on mite population growth rate, as forecasted by the DAP model, was higher than the measured effect. This is probably best explained by the effect of the posterior transferred from the end the fourth flock of House D, with old laying hens, to the start of the fifth flock of House D. With more measured data available, the model automatically adapted and improved itself. The measurement at a flock age of 33 weeks was considered as an outlier by the DAP model. This outlier could be explained by the fact that the measured AMIL at the start of the fifth flock was very close to zero, where small changes in individual monitoring (MMS) scores will result in relatively high fluctuations in the growth rate as a result of Eq. (3).

Fig. 8 shows the DAP model forecast line of the AMIL for the fifth flock of House D and the measured AMIL.

The DAP model was also able to forecast the mite population growth rate with monitoring data obtained with other monitoring methods aside from the Mite Monitoring Score method from Dataset 1. In Figs. 9 and 10 the DAP model forecast validity is presented with Datasets 2 and 3, with data obtained with the SAT method and the SPT method, respectively. In Fig. 3, the DAP model forecast with Dataset 2 is shown

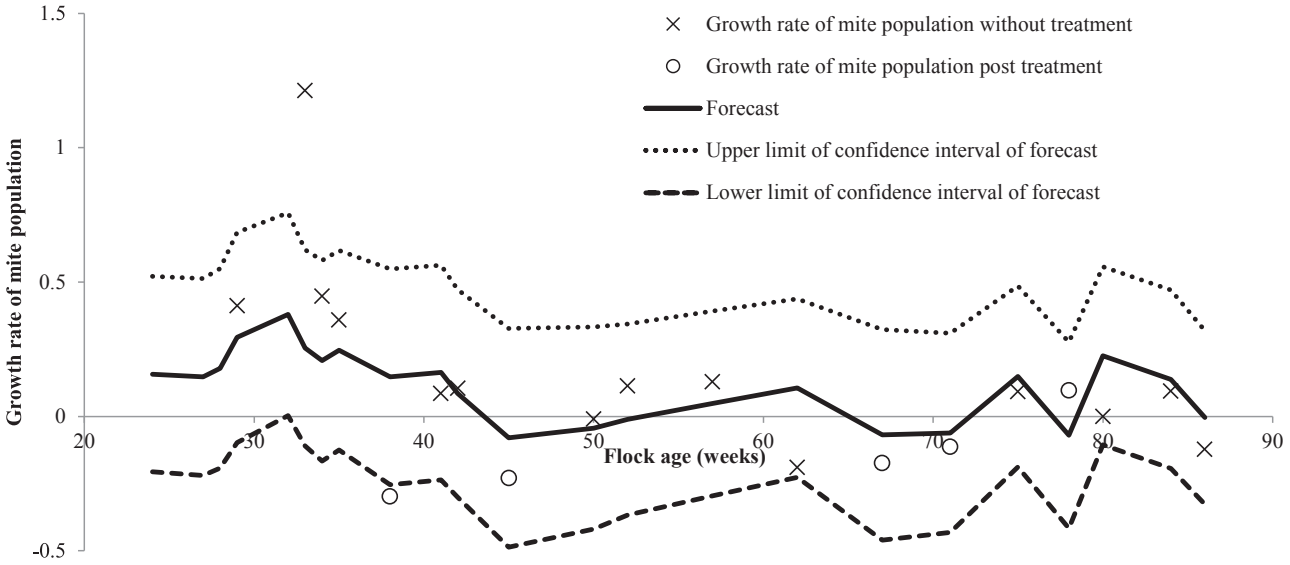

Fig. 7. Dynamic adaptive (DAP) model forecast (black solid line) of the population growth rate (one week ahead) and the observed growth rate (X: observed growth rate without treatment; ○: observed growth rate post treatment) of *Dermanyssus gallinae* versus Flock age (weeks), determined with monitoring data from House D during the fifth flock of Dataset 1, obtained with the Mite Monitoring Score method.

with the forecasted AMIL and the measured values. Fig. 9 shows the DAP model forecast of the population growth rate and the true values determined with Dataset 2. In Fig. 4, the DAP model forecast with Dataset 3 is shown with the forecasted AMIL and the measured values. Fig. 10 shows the DAP model forecast of the growth rate and the true values determined with Dataset 3.

In Fig. 9 the measured population growth rate and the forecast growth rate are both positive until silica treatments were applied, which resulted in negative growth rates as would be expected. A sudden increase of the population growth was observed, but not forecasted at a flock age of 75 weeks.

In Fig. 10, the three outliers between a flock age of 30 weeks and 42 weeks, occurred in the period when the AMIL oscillated around zero. Small fluctuations around growth rate "0" may result in bigger growth rate fluctuations compared to small fluctuations around growth rate "2" because of the equation used for the growth rate calculation (see Eq. (3)).

The DAP model forecasts of Datasets 2 and 3 showed highly comparable negative growth rates at a flock age of 96 weeks, being −0.265 and −0.270 respectively. This could be expected as the data was obtained in the same farm with the same mite population, though with different monitoring methods. These relatively comparable forecasted growth rates shows that the DAP model is able to forecast with different monitoring methods.

The prediction or forecast quality of the DAP model is shown in Table 3 with all assessed MSPE of Dataset 1. The forecast quality of the DAP model, expressed as MSPE excluding outliers, increased considerably from flock 1 (House A–D) to flock 2 (House A-D), as shown by a significant lower MSPE ($P < 0.05$). The models forecast quality showed relatively small changes between flock 2–5 with an MSPE around 0.024. The MSPE of flock 2–5, excluding outliers, showed no significant differences ($P > 0.05$).

Table 4 shows the MSPE assessed with Dataset 2 and a reduced Dataset 3. The reduced Dataset 3 includes monitoring data from dates

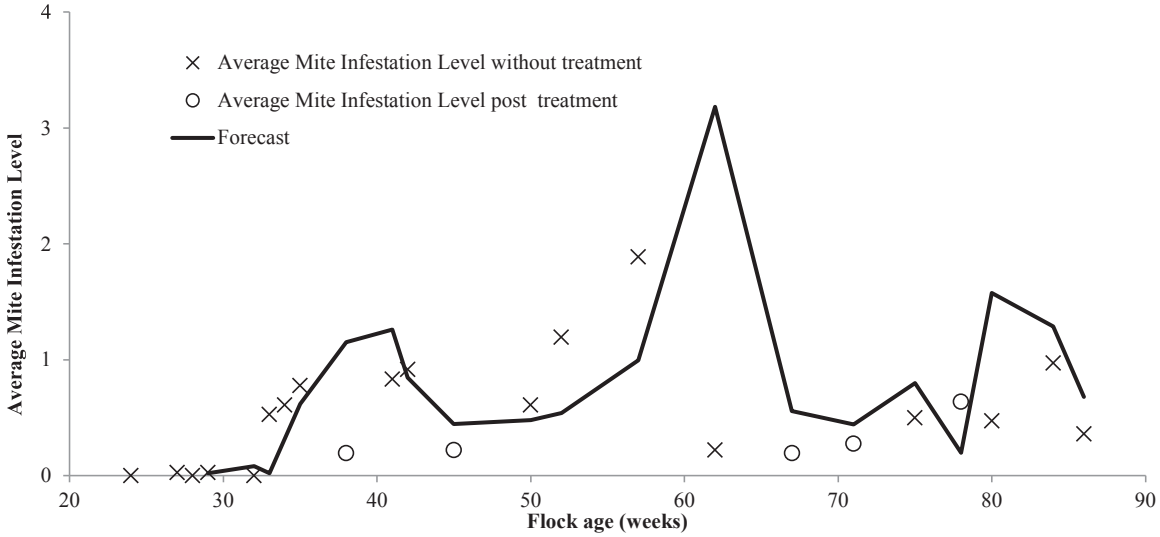

Fig. 8. Dynamic adaptive (DAP) model forecast (one week ahead) of the Average Mite Infestation Level (AMIL) (black solid line) versus Flock age (weeks), determined with *Dermanyssus gallinae* monitoring data from House D during the fifth flock of Dataset 1, using the Mite Monitoring Score method and the observed AMIL (X: observed AMIL without treatment; ○: observed AMIL after treatment).

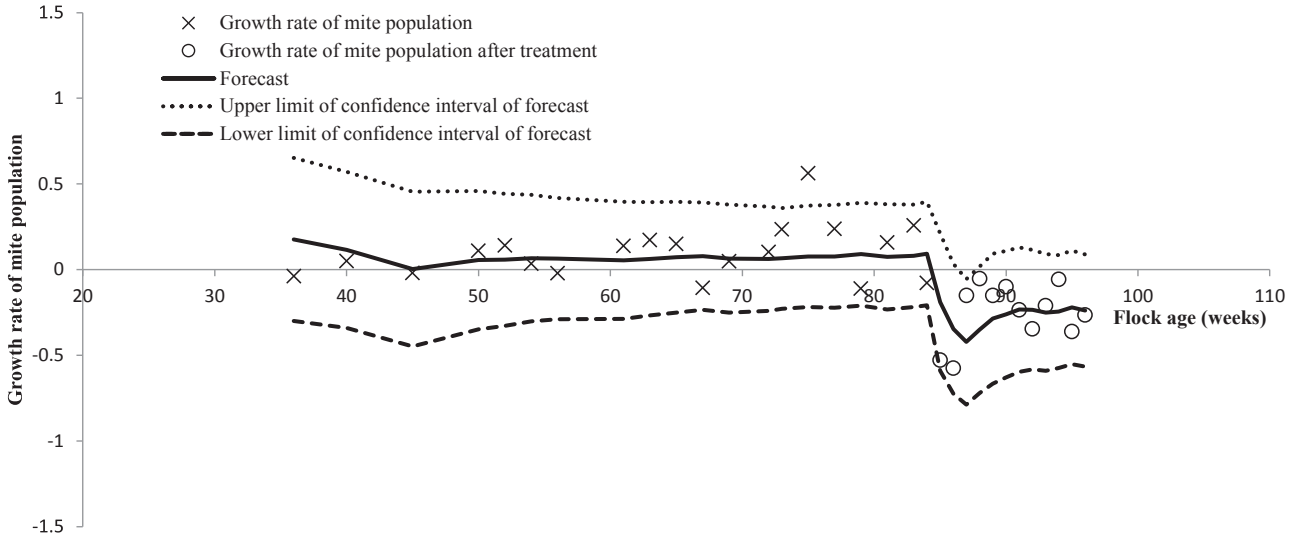

Fig. 9. Dynamic adaptive (DAP) model forecast (black solid line) of the population growth rate and the measured growth rate (X: measured growth rate without treatment; ○: measured growth rate after treatment) of *Dermanyssus gallinae* versus Flock age (weeks), determined with monitoring data from Dataset 2 obtained with the Semi-Attractive water Trap (SAT) method.

which were available in both Dataset 2 and 3, and therefore excludes dates which were only available in Dataset 3. The difference between the assessed MSPE (excluding outliers) of Dataset 2 (SAT method) and Dataset 3 (SPT method) was not significant ($p > 0.05$).

4. Discussion

The current study shows a high variation in the growth rate of *D. gallinae* populations in laying hen houses. This high variation was partly explained by house temperature, treatment, hen house and flock age. A substantial part of the total variation, however, was temporal and unexplained. This in mind, the model developed herein to forecast the population dynamics of *D. gallinae* in laying hen facilities utilised a dynamic adaptive approach, adjusting itself after each measurement to forecast the population dynamics of *D. gallinae*. In this section, we discuss the practicalities of further model development. This

Table 3
Forecast quality of the *Dermanyssus gallinae* dynamic adaptive population (DAP) model per flock, expressed as Mean Squared Prediction Error (MSPE) including and excluding outliers. The MSPE was assessed with Dataset 1, which includes monitoring data obtained with Mite Monitoring Score method in House A-D from the Experimental Poultry Centre, Geel, Belgium.

Flock (House A-D)	Number of records (monitoring data)	Number of records with information on growth rate	Number of records identified as outlier	MSPE*	MSPE, excluding outliers
1	228	61	2	0.154[a]	0.130[a]
2	123	88	2	0.049[c]	0.032[b]
3	106	54	9	0.094[b]	0.024[b]
4	50	31	2	0.039[c]	0.026[b]
5	81	54	4	0.063[bc]	0.024[b]

*Mean Squared Prediction Error.
[a-c]MSPE within a column without a common superscript differ significantly ($P < 0.05$).

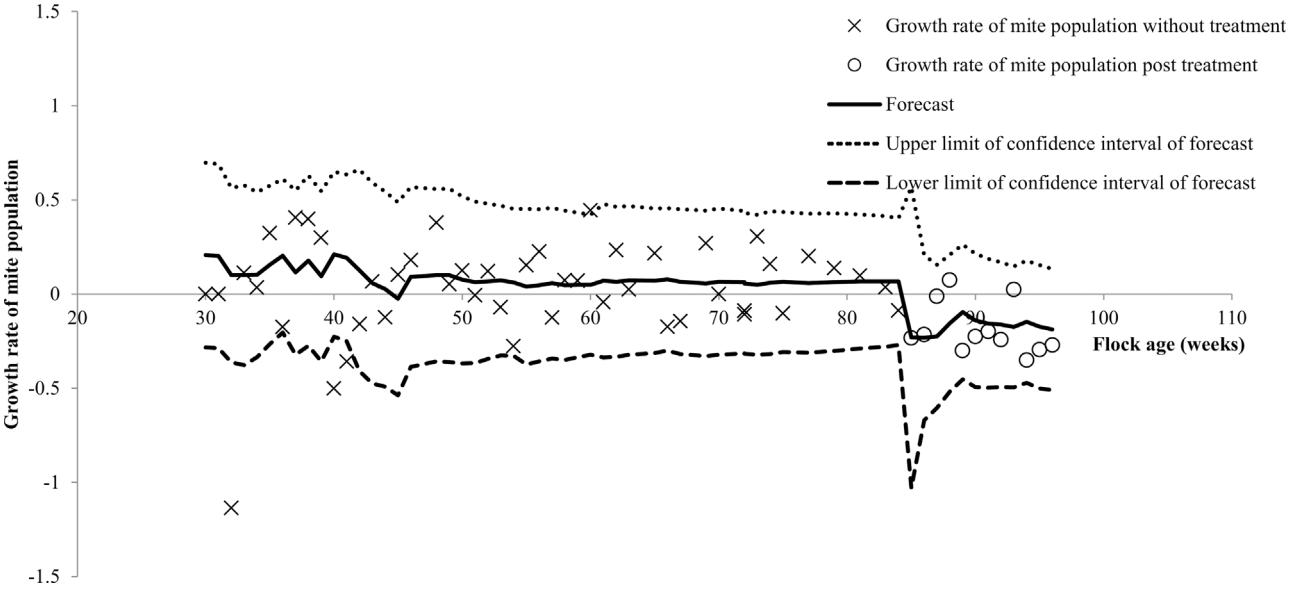

Fig. 10. Dynamic adaptive (DAP) model forecast (black solid line) of the population growth rate and the measured growth rate (X: measured growth rate without treatment; ○: measured growth rate after treatment) of *Dermanyssus gallinae* versus Flock age (weeks), determined with monitoring data from Dataset 3 obtained with the Simplified Passive tape Trap (SPT) method.

Table 4
Forecast quality of the dynamic adaptive population (DAP) model, expressed as Mean Squared Prediction Error (MSPE), assessed with Dataset 2, obtained with Semi-Attractive water Trap (SAT) method and Dataset 3, obtained with Simplified Passive tape Trap (SPT) method with data from the same measuring dates.

Monitoring method	Number of records (monitoring data)	Number of records with information on growth rate	Number of records identified as outlier	MSPE	MSPE, excluding outliers[b]
Dataset 2 (SAT)	33	32	1	0.030	0.024
Dataset 3 reduced[a] (SPT)	33[a]	33	0	0.016	0.016

[a] Dataset 3 without data from dates which were only available in Dataset 3.
[b] Differences between dataset 2 and 3 were not significant ($p > 0.05$).

development would optimise uptake of automated *D. gallinae* monitoring and its contribution to advancing the implementation of improved IPM for *D. gallinae* in laying hen facilities.

To develop the dynamic adaptive population (DAP) model described, and to acquire an indication on the source of the high variation observed, all monitoring data were converted to 'growth rate'. The growth rate expresses relative increase or decrease of the mite population per week, assuming exponential growth in periods without treatment. Density independent growth rate was also assumed in practice; no correlation between 'growth rate' and 'AMIL' was found in Dataset 1 (correlation coefficient = 0.01), confirming that growth rate, in the level of the mite infestation, is independent where exponential growth can be assumed. This independency, however, may not always be present. If treatments are not applied to limit population growth, for example, it might be expected that growth rate would be density dependant, as supported by work elsewhere (Maurer and Baumgartner, 1994; Huber et al., 2011). Nevertheless, in a commercial setting it would be highly unlikely that mite populations would be allowed to reach such levels without treatment intervention.

The overall growth rate post-treatment of the mite population from Dataset 1 was estimated using the linear random regression model (REMLmite model). The results of this REMLmite model show that with increasing age of the hens, the growth rate of the mite population gradually declines, even without treatment. This effect can also be seen in data published elsewhere. Arkle et al. (2004), for example, observed declining *D. gallinae* populations from the start of a trial with laying hens of 52 weeks of age. Other work reports fluctuations in mite numbers (Nordenfors et al., 2001; Chirico and Tauson, 2002), or declines after treatment (Meyer-Kühling et al., 2007; George et al., 2010). More mite monitoring data from flocks older than 40 weeks may confirm the observed effect of flock age on mite population size, and is a worthy area for future research. It is perhaps plausible that the laying hens' immunological reaction to *D. gallinae* may contribute this effect (Arkle et al., 2006; Harrington et al., 2010), regardless of any treatment, though this hypothesis remains to be explored. The accumulation of dust and debris in laying hen houses over time, hampering the efficacy of acaricides due to absorption and/or reduced adherence to surfaces, could similarly explain reduced efficacy of treatment with flock age (Maurer and Perler, 2006; Kilpinen and Steenberg, 2009).

The effect of house temperature on the growth rate of a *D. gallinae* population was found to be 0.019, meaning that with every 1 °C temperature increase or decrease starting from 20° C, the growth rate of the mite population respectively increases or decreases with 0.019 (equal to 2%). This higher growth rate with increasing temperature is in agreement with the findings of Maurer and Baumgartner (1992), Nordenfors et al. (1999) and Tucci et al. (2008). However, Maurer and Baumgartner (1992) and Tucci et al. (2008) both suggest maximum growth or lifecycle development at temperatures higher than 30° C. Monitoring data at such high temperatures was not available in Dataset 1; indeed, the operational accuracy of the REMLmite model used remains to be confirmed outside the temperature range of 14.2–26.8 °C.

The effect of (hen)House was found to be age dependent. Furthermore, a significant difference of this effect was determined between House A and B with House B having a larger reduction in population growth rate when compared to House A. In this case, housing type is not the explaining factor as there was no significant difference between House C and B with House C having the same large enriched cages as House A. The staff from the Experimental Poultry Centre in Geel (Belgium) with the four hen Houses, also could not explain the difference as the management measures in all Houses were the same.

With the REMLmite model used, the residual effects of treatment on *D. gallinae* population responses could be explained for 17.1 percent by flock age, house temperature, treatment and hen house; a substantial part of the population growth rate variation could not be explained. The effect of management measures and the measurement error of the monitoring methods, were potentially responsible for at least part of this unexplained variation. The MMS method (Dataset 1) is not validated in a sense that the actual number of mites in a laying hen house is unknown for all MMS scoring levels. Consequently, there is no insight in the measurement error of the used MMS method and thus this may lead to incorrect conclusions related to the source of the high variation of the growth rate. A dataset, obtained with a validated monitoring method and with a known measurement error, will give more insight in the presence and the source of the high variation of the growth rate.

The Average Mite Infestation Level, AMIL, was the average score or number of mites of all measuring points in a laying hen house. The growth rate was determined using this AMIL. This average includes all monitoring data thus also including the measuring points with relative high scores. By including these "exceptional" scores a better impression will be obtained about the future of the mite population as these so called "hotspots" can be the precursor of the development of the future of the mite population. Using the median, "ignoring" the highest and the lowest scores, instead of the average, however, could have reduced the variation of the population growth.

Unexplained temporal variation of the residual effects will limit accurate forecasting of the population growth rate via a fixed effects model, including a REML model. These types of models will exclude flock specific effects. With an adaptive model, however, such flock specific effects are, with increasing numbers of available flock data, increasingly incorporated in the forecasting. Examples of such adaptive models are models with a Kalman filter (Harvey, 1989), or dynamic adaptive models (West and Harrison, 1997). To illustrate that the forecasting quality is limited with a model with fixed effects (e.g. linear random regression model), compared to a dynamic adaptive model, the quality of the forecast of the DAP model (one measurement ahead) was compared with a new linear regression (REMLmite) model with a fixed temperature and treatment effect. The fixed effects were estimated with data from the third flock in all Houses of Dataset 1 and subsequently used to forecast the growth rate in flock 4. The MSPE of the new REMLmite model was 0.051 and thus an increase in MSPE of 32% compared with the MSPE of the DAP model (0.039). As both MSPE were determined with the same dataset, an increase in the measurement bias was avoided and the increase of the MSPE of the new REML mite model could only be explained by an increased model bias of that new REMLmite model. We therefore conclude that in this case the DAP model has a better forecasting quality when compared to the new REMLmite model.

In the developed DAP model, the population growth rate followed a linear response to housing temperature and treatment effect. The effect of temperature in the DAP model was found to be higher when compared to the temperature effect in the REMLmite model. A possible explanation for this may be the posterior input in the DAP model. However, this could not be confirmed with temperature effects fluctuating between hen House and flocks from 0.02 to 0.076. The difference in handling correlations of information between the two types of models, e.g. correlation of higher temperatures and occurrence of treatment, may be another explanation for the difference in temperature effect observed.

For the DAP model, the determined MSPE showed a significant reduction for the second laying round compared with the first, which may have resulted from the priors for the parameter values being theory-based at the start of the first laying round. During this first laying round, these parameter values were gradually adapted by the model to more suitable parameters, resulting in lower MSPE for the second flock. After the first laying round, the MSPE is more likely to reflect flock (or laying round) dependent measurement errors (accuracy) of the monitoring method and could be partially explained by a lack of fit of the model. It can be expected that monitoring techniques employing a scale method are less sensitive and less temporally robust than count methods. With AMIL of the MMS method (scale) close to zero, the DAP model may provide more outliers when compared to AMIL of the SAT method (counts) as a result of a) the characteristics of Eq. (3), and b) the monitoring method with MMS having a relatively large step between scale 0 (no mites visible) and scale 1 (mites visible in cracks and crevices). In short, it is difficult to detect mites in cracks and crevices unless these harbourages are well populated and effectively 'full' with mites. The relative insensitivity of scale methods when compared to counts methods, however, was not supported when comparing the determined MSPE using Dataset 2 (counts) to the determined MSPE using Dataset 3 (scale). It should be noted, however, that the scale in Dataset 3 was clearly defined and dependent on counts (0, <10, >10, clusters (=uncountable)), possibly resulting in higher interrater reliability and agreement (Kottner et al., 2011) than the MMS method.

Improvements of the DAP model forecast may be achieved by including extra model parameters (e.g. flock age or management measures). As mentioned previously, in Fig. 8 an unexpected decline was shown at the first measurement after reaching a flock age of 60 weeks. This decline followed mechanical cleaning of nest pads to remove *D. gallinae*, which was not considered as a treatment, but rather as a general husbandry measure to reduce the mite population. Incorporating such husbandry measures into the model may improve its forecasting quality. Additionally, a correction for hen age may also result in model improvement, particularly considering the reduction of treatment effect with increasing hen age described herein. Modifying the estimated treatment effect at the end of the laying round for age effect, to have better priors for the next laying round at the Experimental Poultry Centre in Geel, resulted in an improvement of the DAP model forecast quality for the first treatments in a laying round (data not shown). This age effect, however, was not included in the DAP model, as this model should be generic. Furthermore, additional variables could improve DAP model forecast accuracy for a specific farm, they would need to be carefully selected and included with caution, if at all. Including additional variables is not recommended here, as with increasing numbers of variables the stability of dynamic adaptive models generally decreases (as the model determines all variances and covariance's for all parameters).

The current work confirms that monitoring methods based on either scales or counts are compatible with the DAP model developed to forecast the population dynamics of *D. gallinae* in a layer house, though it is likely that the sensitivity of monitoring method may influence the number of outliers as discussed above. Further improvement of the DAP model forecasting quality may occur with more frequent monitoring, but achieving this via manual assessment would necessitate a significant increase in labour. The use of an automated monitoring device (Mul et al., 2015), however, could assist in regular (e.g. daily) assessment of population levels to improve model forecasting without requiring additional labour input.

The DAP model described has the potential to contribute to improved IPM of *D. gallinae*, as well as for many other pests. As shown in the results presented, the DAP model could satisfactorily forecast the population dynamics and response to treatment of *D. gallinae* given only three easily obtainable input parameters: monitoring data, layer house temperature and treatment date. Furthermore, the DAP model functioned equally well given data from different monitoring methods utilising both infestation classes and count data, also correcting for location specific interactions. Moreover, the DAP model was able to handle time dependent and highly variable factors, e.g. different types of laying hens, feed, climates, management and treatment regimes. Therefore, most requirements for practical models for advancing improved IPM programmes or the required input are fulfilled with this DAP model.

To further improve the DAP model described for use on-farm, future developments are already being researched by the authors. These include the development of a population dynamics DAP model able to forecast in 4D (time and three dimensions of the laying hen facility) as well as a treatment advice module. This 4D model should be able to forecast the population dynamics of pest 'hot spots' and thus advise on localised treatments. The treatment advice module will incorporate the forecast of the DAP model and production outputs of the laying hens (e.g. number of eggs, egg weight, egg quality, feed conversion) in order to determine the exact moment when the economic threshold will be exceeded. The treatment advice delivered to farmers will be based on this economic threshold, fulfilling another key requirement of IPM programmes.

5. Conclusion

The population growth rate of *D. gallinae* could, with the available data, partly be explained by house temperature, flock age, treatment and House. A substantial part of the total variation in mite population growth is temporal and unexplained, thus supporting a dynamic approach to forecast population development. A dynamic adaptive (DAP) model was therefore developed to forecast a *D. gallinae* population in any laying hen house using only frequently measured population monitoring data, indoor temperature data and date of treatment application. The DAP model was able to forecast the population dynamics of *D. gallinae* and growth rate post-treatment and without treatment compensating for location (laying hen house) and time specific interactions (e.g. temperature, management), and coped with the variability of the parameters of interest (e.g. variation in growth rate after a treatment). This in mind, and with its ability to work with data obtained using different monitoring methods, the developed DAP model could contribute to adopting improved Integrated Pest Management for *D. gallinae* in laying hen facilities.

Conflict of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.vetpar.2017.07.027.

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