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Sampling method evaluation and empirical model fitting for count data to estimate densities of *Oligonychus perseae* (Acari: Tetranychidae) on 'Hass' avocado leaves in southern California

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Abstract *Oligonychus perseae* (Acari: Tetranychidae) is an important foliar spider mite pest of 'Hass' avocados in several commercial production areas of the world. In California (USA), *O. perseae* densities in orchards can exceed more than 100 mites per leaf and this makes enumerative counting prohibitive for field sampling. In this study, partial enumerative mite counts along half a vein on an avocado leaf, an industry recommended practice known as the "half-vein method", was evaluated for accuracy using four data sets with a combined total of more than 485,913 motile *O. perseae* counted on 3849 leaves. Sampling simulations indicated that the half-vein method underestimated mite densities in a range of 15–60 %. This problem may adversely affect management of this pest in orchards and potentially compromise the results of field research requiring accurate mite density estimation. To address this limitation, four negative binomial regression models were fit to count data in an attempt to rescue the half-vein method for estimating mite densities. These models were incorporated into sampling plans and evaluated for their ability to estimate mite densities on whole leaves within 30-tree blocks of avocados. Model 3, a revised version of the original half-vein model, showed improvement in providing reliable estimates of *O. perseae* densities for making assessments of general leaf infestation densities across orchards in southern California. The implications of these results for customizing the revised half-vein method as a potential field sampling tool and for experimental research in avocado production in California are discussed.

Keywords *Oligonychus perseae* · Hass avocado · Sampling · Pest management · Count data · Negative binomial regression · GLMMs

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Introduction

Oligonychus perseae Tuttle, Baker and Abatiello (Acari: Tetranychidae) is an economically important foliar spider mite pest of avocado, *Persea americana* Miller (Lauraceae), in several countries (i.e., Spain, Costa Rica, Mexico, Israel, USA) (Lara and Hoddle 2015a). Recently, *O. perseae* was found infesting avocados in Italy and emerging research for this pest there is focused on developing management guidelines (Zappalà et al. 2015). In California (USA), attempts to develop a sustainable pest management program for *O. perseae* have investigated the role of resident and commercially available phytoseiids for suppressing pest populations (Hoddle et al. 2000; Hoddle and Morse 2012), expanding the selection of pesticide chemistries to mitigate resistance development (Humeres and Morse 2005), and examining the compatibility between pesticides and naturally occurring biological control agents, in particular, predatory phytoseiids (e.g., *Euseius* spp.) in avocado orchards (Zahn 2011). However, as with any pest management program designed for crop protection, success in implementing control measures depends on sampling methods that accurately estimate pest densities.

'Hass' avocado is a dominant commercial variety that is highly susceptible to feeding by *O. perseae* (Kerguelen and Hoddle 2000; CAC 2015). In California, *O. perseae* populations on 'Hass' can reach hundreds of mites per leaf and feeding injury to foliage contributes to defoliation which may result in sun-damaged fruit. Estimating densities of *O. perseae* can be challenging due to its small size and its propensity to shelter within webbed-nests on leaves, which further reduces visibility of all life stages (Aponte and McMurtry 1997). Leaf damage (i.e., necrotic spots) accumulates throughout the avocado growing season (April–September) and mites often do not inhabit these dead areas. Consequently, visual assessment of damage is not a reliable indicator of mite density at the time of sampling. Counting *O. perseae* for accurate density estimation of live stages requires the use of a microscope or hand-lens. However, complete enumerative sampling is a time-prohibitive strategy for pest managers and researchers. Lengthy processing time can result in leaf deterioration, mite death or leaf abandonment by mites. It is therefore imperative to maintain leaf sample quality as close to the original sample date to avoid biased estimates of treatment effects. This in turn requires rapid processing of leaf samples that produce accurate measures of mite infestations on individual leaves.

There have been technological advancements to facilitate mite counting such as brushing machines (Henderson and McBurnie 1943; Morgan et al. 1955) and photography-based counting (Sircom 2000), but for the purpose of *O. perseae* sampling these approaches are still time consuming or impractical due to this species' small size, webbed-nest life type, and potential to reach high densities. Alternative approaches for estimating *O. perseae* densities have focused on reducing counting efforts through regression techniques relating densities of mites, y, to some other reliable mite-density indicator, x, that can be readily measured for a fraction of the time and cost. In this regard, Machlitt (1998) developed a "half-vein" sampling method for monitoring field densities of *O. perseae* in California avocado orchards.

The half-vein method (Fig. 1) is based on a simple regression model that correlates mite counts along the upper portion of the second major leaf vein on left half of the leaf undersurface, hereafter referred to as UML2 (González-Fernández et al. 2009), with total mite counts on the leaf undersurface (Machlitt 1998). Specifically, UML2 is the second prominent half-vein encountered from the petiole end of the leaf and extends from the left side of the midrib to the left leaf margin. The regression equation with zero-intercept is

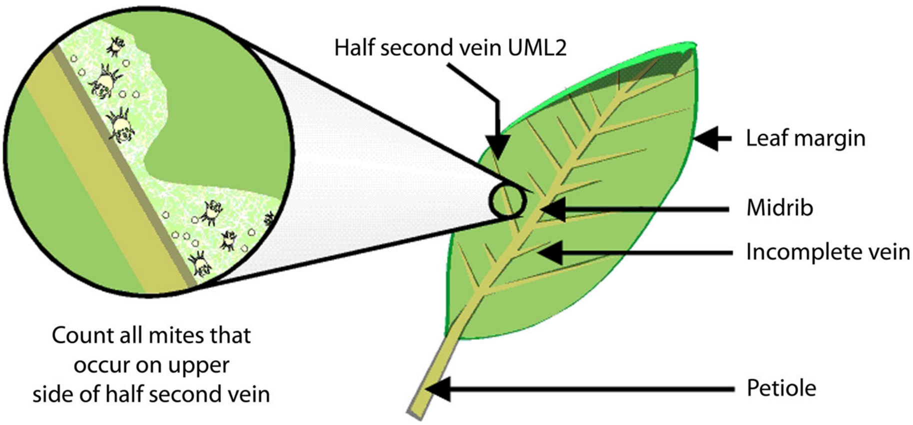

Fig. 1 Location of vein UML2 on leaf undersurface used to make partial mite counts and estimate densities of *Oligonychus perseae* according to the half-vein method (Machlitt 1998; González-Fernández et al. 2009)

$y = 12x$, where y is the estimated count of *O. perseae* on the undersurface of an avocado leaf, 12 is an estimated regression coefficient and x is the number of motile mites that occupy the upper margin of vein UML2 on 'Hass' avocado leaves (Machlitt 1998). Half-vein method estimates from a minimum sample size of 10 randomly selected leaves (i.e., one leaf per each of 10 trees) from neighboring trees are averaged to obtain the overall *O. perseae* density for the sampled orchard area. Correlation between *O. perseae* densities and partial mite counts on UML2 for four age categories of in-season avocado leaves (i.e., less than half-expanded, more than half-expanded, fully expanded, and combined leaves of all ages) was found to be greater than 0.85 in all cases and statistical modeling was based on mean values for sample batches ($n = 62$) consisting of 10 avocado leaves (Machlitt 1998).

Currently, the recommendation for using the half-vein method to assess *O. perseae* densities in commercial avocado orchards is to collect at least one in-season leaf, of mixed-age, for each of ten randomly selected trees (UC IPM 2011). However, the optimal sample size and the manner of leaf and tree selection to obtain reliable mite density estimates for a block of avocado trees were not determined and a robust performance evaluation of this sampling method for field use has not been conducted. Despite these limitations, the half-vein method has been used for *O. perseae* field research. In California, pesticide field trials for control of *O. perseae* relied on the half-vein method to compare treatment efficacy (Morse 2008, 2011). In Israel, the half-vein method was adopted to evaluate the biological control potential of phytoseiids for reducing *O. perseae* densities (Maoz et al. 2011). In Tenerife (Canary Islands), the half-vein method was used to evaluate the efficacy of pesticide treatments (Hernández-Suárez et al. 2010; Pérez-Fernández et al. 2015) and phytoseiid releases (Hernández-Suárez et al. 2010) for *O. perseae* control. Other mite density estimation properties associated with vein UML2 (i.e., the number of *O. perseae* occupied nests and necrotic spots caused by mite feeding damage) were used to assess the efficacy of conservation biological control practices (i.e., pollen provision for phytoseiids) for *O. perseae* suppression in Málaga, Spain (González-Fernández et al. 2009). These research-oriented studies demonstrate that there is a need for a regression method to accurately estimate whole leaf densities of *O. perseae* using a partial leaf count method.

The purpose of this study was to (1) evaluate the half-vein method performance in its original form, (2) validate assessments of the relationship between *O. perseae* densities and the number of mites found along vein UML2 using statistical analyses for count data and (3) provide guidelines for estimating *O. perseae* densities using the best method evaluated.

Materials and methods

Study sites and sample unit collection

In-season, mature 'Hass' avocado leaves were collected during the peak summer season of *O. perseae*, June–September (Yee et al. 2001), from 10 commercial avocado orchard sites in southern California. Enumerative mite counts for each sampled leaf were completed in the laboratory (Table 1). In California, avocado trees typically have a spring and summer growth flush period. Typically, the flushing period extends from April to July (UC IPM 2008) and recognition of each type of flush from current and previous seasons can be detected by examining bud scars on shoots (Cutting 2003).

A selection preference for mature leaves was based on availability during summer and that *O. perseae* populations on mature leaves reflected mite infestation densities within the sampled orchard. At each site, eight avocado leaves per tree (i.e., two leaves randomly selected per cardinal quadrant) were collected from trees arranged in 5 × 6 grids defined by rows and columns of trees. These 30 tree blocks were situated within larger blocks of avocado trees that were infested with *O. perseae*. For each site, data collected from leaf samples were partitioned for model development and validation analyses.

An 11th orchard located in Irvine, California was sampled monthly in 2012 and 2013 during the *O. perseae* season, approximately May–September, when monitoring for this pest is recommended (UC IPM 2011). The longitudinal data collected from orchard 11 was reserved for further validation of the improved half-vein method (see below) over two field seasons. At this site, ten 'Hass' avocado leaves from spring flush were collected per tree from two groups of untreated trees, 1 (n = 9 trees) and 2 (n = 8 trees), planted on an 18 × 14 grid. The only difference between these groups was that trees from group 2 were pesticide treated in 2003, 9 years before data collection for this evaluation commenced.

Table 1 Avocado leaf collection summary and observed *Oligonychus perseae* densities for each experimental orchard

Orchard	Sample date	No. of leaves	County	Mean no. of mites per leaf ± SEM	Range of mite counts per leaf
1	July 2009	247	San Diego	77 ± 5.8	0–607
2	Aug. 2009	240	Santa Barbara	42 ± 7.6	0–1088
3	Aug. 2009	240	Santa Barbara	342 ± 36.4	0–3016
4	Aug. 2009	240	Santa Barbara	37 ± 7.4	0–1411
5[a]	Aug. 2009	240	Santa Barbara	307 ± 21.8	1–2039
6	Sept. 2009	240	Santa Barbara	49 ± 6.7	0–567
7	June 2010	239	Santa Barbara	205 ± 18.6	0–1633
8	July 2010	240	Ventura	208 ± 12.7	0–1060
9	July 2010	256	Orange	519 ± 27.1	2–2850
10	Aug. 2010	240	Santa Barbara	18 ± 3.8	0–475

[a] Leaves were collected from an adjacent plot of 'Hass' avocado trees 8 days after having been collected at Orchard 3

Leaf sample sets from group 1 (March, May and July 2012) and group 2 (March and April 2012) were omitted from validation analyses because not all trees were sampled on a particular sampling date and/or no mites were found on foliage. Furthermore, in this study, a selection preference for spring leaves over summer leaves was made to widen the observation window of *O. perseae* densities on aging leaves (i.e., less than half-expanded to fully expanded leaves).

For each sampled leaf across all eleven sites, information was recorded for three variables: (1) y_{obs}, the total number of motile *O. perseae* mites (all stages except eggs) on the entire leaf undersurface, (2) x_1, the number of motile *O. perseae* mites situated along the upper margin of vein UML2, and (3) x_2, leaf length (cm) which was measured as the direct distance along the midrib between the leaf tip and base proximal of the petiole. Leaf length was recorded to test the null hypothesis that higher mite counts were not correlated with larger leaves.

Evaluation of the original half-vein method

The mite count database comprised of sites 1–9 was divided into two subset databases, A (n = 1212 leaves) and B (n = 1210 leaves). Since orchards 1–9 had two replicates per cardinal direction per tree (i.e., 8 leaves per tree), the data from the first and second replicates were assigned to databases A and B, respectively. Database B had partial data missing for two leaf sample units and these were not included in the analyses, whereas database A was complete with all four leaves available per tree. For orchard 10, mite count data from two adjacent 5 × 6 blocks were assigned to each database because there was only 1 replicate set of leaves (i.e., 4 leaves) for each sampled tree. Database A was first used to evaluate the performance of the original half-vein method for each orchard and then was used as a training set to generate a new model that redefined the relationship between mite counts on the entire leaf undersurface and partial mite counts on vein UML2. Database B and the data collected from site 11, were used to cross-validate the newly described relationship.

For each orchard within database A, the mean of mite counts for vein UML2 was multiplied by 12 to predict the average number *O. perseae* per leaf. This multiplication factor, as it appears in published pest management guidelines (UC IPM 2011), accommodates leaves of all age classes (Machlitt 1998). The predicted mite densities were compared to the observed densities for each orchard site using the percent error formula as a measure of accuracy: $100 \times [(y_{predicted} - y_{observed})/y_{observed}]$. Negative percent error values indicated that the expected mite density has been underestimated and positive values indicated that the expected mite density has been overestimated. Ideally, the percent errors for a model should be close to zero.

Statistical analyses for improving the half-vein method

Correlation between response and predictor variables

A preliminary assessment of pooled data from database A for sites 1–10 indicated the possible existence of a curvilinear relationship between total *O. perseae* counts and UML2 (Fig. 2), suggesting that the total number of *O. perseae* mites cannot increase linearly on individual avocado leaves without reaching some level of carrying capacity. Naturally, as mite densities increase, negative feedback mechanisms such as leaf tissue death, intraspecific competition for nesting sites and a reduction in available feeding surface area

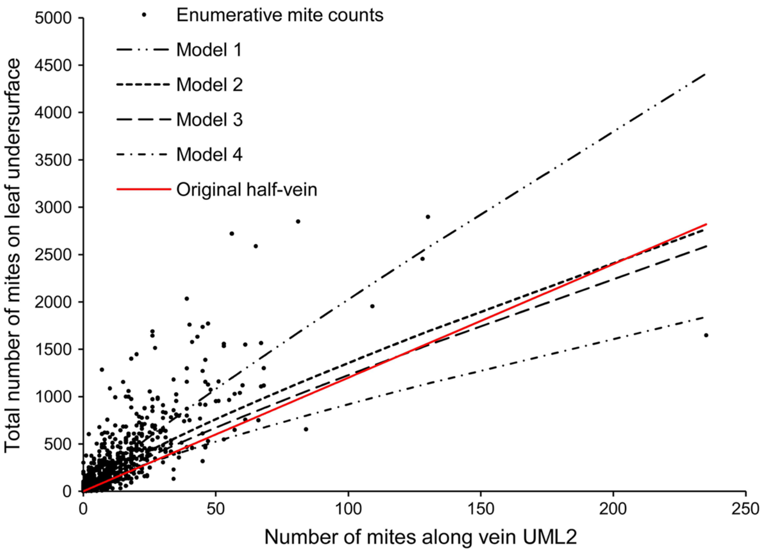

Fig. 2 Comparison of fitted models, original half-vein method and observed *Oligonychus perseae* counts on avocado leaves across ten sites from validation database B based on the response scale

function to counter population growth on heavily infested leaves. As *O. perseae* infestations increase on trees motile stages will disperse in the wind in an attempt to reach new, favorable colonization and feeding sites (Hoddle and Morse 2012). Consequently, for each site, the degree of association between observed total mite counts, x_1 and x_2 was evaluated by determining Spearman's correlation coefficient for each variable pairing using PROC CORR in SAS 9.3 (SAS Institute 2011). Spearman's rank correlation was selected because interpretation of this measure is not contingent on the assumption of normality and that pairs of variables are linearly correlated, only that the relationship be monotonic (McDonald 2009).

Redefining the relationship between total mite counts and vein UML2

Oligonychus perseae count data for training data sets (database A) were not collected longitudinally and therefore, fitting biological growth curve models (e.g., logistic, Gompertz, Chapman-Richards, Bertalanffy) (Kaufman 1981) to collected mite infestation data was not appropriate. Instead, an empirical modeling process based on the observed relationship between total mite counts and UML2 was adopted and is described below. The added caveat of working directly with *O. perseae* count data is that it generally cannot be characterized by the normal distribution and use of linear regression modeling is inappropriate. Furthermore, power transformations (Box and Cox 1964) of the data did not satisfy normality assumptions. Consequently, these factors guided the a posteriori framework of statistical analyses needed to improve and validate the half-vein method for field use.

The relationship between observed mite counts and x_1 was defined using negative binomial regression under the framework of generalized linear mixed models (GLMMs) to account for the non-normal distribution of the count data (confirmed by examining Q–Q plots and Shapiro-Wilk tests for individual sample dates, results not shown), its overdispersion behavior, and the potential contribution of random effects from orchards and avocado trees in explaining the observed response variation.

Under the GLMM framework, the canonical log link function was used to restrict the expected mean response to positive values, a scale parameter (k) was used to model variance as a function of the mean and, when specified, random effects were accounted for through the linear predictor (i.e., as G-side random effects). Although the response variable did not need to be transformed, transformation of the predictor variable x_1 (Faraway 2006) was needed to linearize the relationship on the link scale. Initially, linear (i.e., 1st and 2nd order polynomials) and nonlinear model equations with a single fixed effect were selected by screening an extensive compilation of functions reviewed by Ratkowsky (1990) and subsequently re-parameterized to obtain linear predictors for final model fitting. More than 20 models were evaluated but some of them provided similar curves (not shown here). Final candidate models were selected from this initial group on the basis of parameter parsimony and ability to represent a potential range of observed mite densities. On the response scale based on the inverse exponential link, the models selected for further evaluation were:

$$y = \exp[\alpha + \beta \ln(x_1 + 0.31)] \tag{1}$$

$$y = \exp[\alpha + \beta \ln(x_1 + 0.31) + u] \tag{2}$$

$$y = \exp[\alpha + \beta \ln(x_1 + 0.31) + v] \tag{3}$$

$$y = \exp[\alpha + \beta \ln(x_1 + 0.31) + u + uv], \tag{4}$$

where y refers to the expected mean of total *O. perseae* counts on a leaf given the presence of random effects; x_1 is the partial count of *O. perseae* along vein UML2; α and β are estimated parameters for the fixed effect and u and v represent random effects attributed to avocado orchards and trees, respectively. The term uv represents the interaction between orchard (block) and individual avocado trees at each site. When specified in the models, these random effects can account for the clustered data collection process given that a subset of orchards and nested levels of individual trees were sampled from a larger population in southern California.

Because x_1 can assume a value of zero, an estimated constant, $\gamma = 0.31$, was added to the equations to avoid calculation errors (i.e., natural logarithm of zero) and obtain a linear predictor for GLMMs. An estimate of γ was obtained by first fitting the template of model 2 using PROC NLMIXED and the TruReg estimation method for non-linear models in SAS 9.3 (SAS Institute 2011) and then applying this adjustment constant to all other models. Once γ was fixed at 0.31, all models were refitted with PROC GLIMMIX and the Laplace estimation method in SAS 9.3 (SAS Institute 2011). The Laplace estimation method represents an actual likelihood to fit probability distributions for counts (i.e., Poisson, negative binomial) and allows Pearson Chi square/df values to be calculated for model-fit diagnosis (Gbur et al. 2012).

Competing models were evaluated using the Akaike information criterion (AIC) (Akaike 1974), Bayesian information criterion (BIC) (Schwarz 1978), Pearson Chi square/df values, graphical fit of the models to observed count data, hypothesis testing for the statistical significance of the covariance parameters and results from sampling simulations described in the next subsection (Stroup 2013). Smaller values of AIC and BIC generally indicated improved fit of the models. Pearson Chi square/df values (ideally close to one) were used to assess correct specification of the conditional distribution of the response (Stroup 2013).

Cross sectional model validation

The utility of the four models to estimate densities of *O. perseae* within blocks of avocado trees was evaluated with sampling simulations using PROC SURVEYSELECT in SAS 9.3 (SAS Institute 2011). For each model, 500 simple random sample iterations, without replacement, were conducted for each of twelve stratified sampling combinations using database B. With some exceptions, these combinations consisted of a total sample size of 10, 20, and 30 avocado leaves with a stratified specification of 1, 2, 3, and 4 leaves sampled per tree. For the scenario of 3 leaves per tree, a total of 9 and 21 leaves were sampled when the target total sample size was 10 and 20 leaves, respectively, to maintain a balanced sample size between trees. For the same reason, a total of 12 and 32 leaves were sampled when the target sample size of 10 and 30 leaves was specified with a 4 leaf per tree combination. For each leaf sample batch, the mean number of *O. perseae* per leaf was estimated using only the fixed effects of the four negative binomial regression models listed above (i.e., the marginal estimates of the model), the original half vein model and the recorded enumerative mite counts. These estimates were compared against the observed densities, calculated from enumerative *O. perseae* counts on all leaves, using the percentage error formula values averaged over all iterations. These results were used to determine how to sample within a block of avocado trees.

Longitudinal model validation

Validation over time was possible using data collected from the two groups of trees at orchard 11 across two field seasons. For each sample date and group combination ($n = 18$ datasets), a simple random sample of 1 leaf per tree was conducted for 500 iterations. This sampling structure was determined from the validation results of database B and was considered appropriate due to the small number of trees (<10) within both groups. For each leaf sample batch, the number of *O. perseae* per leaf was estimated using models 1–4, the original half-vein model, and recorded enumerative counts of mites on entire leaves. Similar to the cross-sectional validation analyses, the estimated *O. perseae* densities from all selected models were compared against the expected *O. perseae* densities on all leaves using the percent error formula (see above).

Results

Evaluation of the original half vein method

Table 2 lists the estimated *O. perseae* densities based on original half-vein method using vein UML2. When compared to the enumerative mite counts, the percent errors revealed that the half vein method underestimated *O. perseae* densities at sampled orchards over a range of 41–60 %. A notable exception was site four with 15 % error (Table 2).

Table 2 Percent errors for *Oligonychus perseae* densities estimated using enumerative counts and the original half vein method (Machlitt 1998) for database A

Orchard	No. of leaves	Observed mite density	Half-vein estimate	Percent error
1	124	93	37	−60
2	120	47	19	−60
3	120	358	216	−40
4	120	36	30	−15
5	120	339	182	−46
6	120	48	28	−41
7	120	213	103	−51
8	120	227	124	−45
9	128	564	236	−58
10	120	17	7	−60

Statistical analyses for improving the half-vein method

Correlation between response and predictor variables

Spearman correlation coefficients between total *O. perseae* mite counts on the undersurface of 'Hass' avocado leaves and partial counts of this mite along vein UML2 ranged from 0.50 to 0.89 and were statistically significant across all orchard sites 1–10 (Table 3). These results provided the justification for conducting follow-up model analyses in an attempt to improve estimates of *O. perseae* densities using the half-vein method with partial mite counts along UML2 as a predictor variable (x_1). At orchards 5, 8, and 9 there was a statistically significant association between total *O. perseae* counts and leaf length, but overall correlation coefficient values ranged from −0.12 to 0.23 (Table 3) and were not

Table 3 Spearman correlation coefficients between total counts of *Oligonychus perseae*, partial counts along vein UML2 and avocado leaf length

Orchard	Total mites versus UML2	Total mites versus leaf length	UML2 versus leaf length
1	0.77***	0.04	0.04
2	0.74***	0.08	0.10
3	0.86***	−0.03	0.03
4	0.70***	0.10	0.11
5	0.85***	0.20*	0.23*
6	0.83***	−0.01	0.02
7	0.89***	0.10	0.01
8	0.84***	0.23*	0.26**
9	0.72***	0.19*	−0.005
10	0.50***	−0.12	−0.12

Significant at: * $p < 0.05$; ** $p < 0.005$; *** $p < 0.0001$

Table 4 Spearman correlation coefficients between total counts of *Oligonychus perseae*, partial counts along vein UML2 and avocado leaf length at orchard 11 for spring flush leaves starting in April (2012 and 2013) in Irvine, Orange County, California

Set	Sample date	No. of leaves	Total mites versus UML2	Total mites versus leaf length	UML2 versus leaf length
1	June 2012	90	0.43***	0.22*	0.17
	July 2012	49	0.48**	0.18	0.12
	Aug. 2012	89	0.67***	0.53***	0.22*
	April 2013	90	0.56***	−0.03	0.002
	May 2013	90	0.46***	−0.22*	−0.15
	June 2013	90	0.56***	0.11	0.02
	July 2013	89	0.77***	0	−0.07
	Aug. 2013	89	0.65***	0.31**	0.21*
2	July 2012	80	0.34**	0.15	0.05
	Aug. 2012	80	0.57***	0.31*	0.01
	April 2013	80	0.62***	0.11	−0.01
	May 2013	80	0.48***	0.17	0.09
	June 2013	80	0.60***	−0.04	0.72
	July 2013	80	0.75***	0.16	0.04
	Aug. 2013	80	0.69***	0.20	0.17

Significant at: * $p < 0.05$; ** $p < 0.005$; *** $p < 0.0001$

consistently significant at all sites to warrant the addition of a second predictor variable (i.e., leaf length) to the selected regression models.

Similarly, correlation analyses for orchard 11 (Table 4) indicated that there was a consistent and statistically significant association between total *O. perseae* mite counts and partial counts along vein UML2 over time at this orchard. However, there was a pattern of encountering lower correlation coefficients, in the range of 0.34–0.77 (Table 4), in comparison to orchards 1–9 (Table 3). In general, correlations for orchard 11 were higher in later summer months (i.e., July, August) when mite activity was increasing. Leaf length was found to be correlated with total mite counts and partial counts in only 5 and 2 sample dates for the first and second group of trees, respectively. Consequently, leaf length was not a consistent indicator of mite densities during the growing season and was not included as a predictor variable.

Redefining the relationship between total mite counts and vein UML2

Table 5 lists the fixed effect parameter estimates, fitting criteria, and covariance parameter estimates of random effects, when specified, for each candidate model. A graphical comparison of the estimated means from fixed effects of each fitted model, the original half-vein method and observed mite counts for database A is shown on the response scale in Fig. 2 and the log link scale in Fig. 3. Pearson Chi Square/DF values for model 1 (1.83) and model 2 (1.96), were greater than one and this result was interpreted as overdispersion. Pearson Chi Square/DF values for models 3 (0.78) and 4 (0.87) were closer to the ideal value of 1 and these results implied an improved model fit. Model 4 had the lowest AIC (12,126) and BIC (12,127) values which suggested a better fit than competing models

Table 5 Parameter estimates for the four nonlinear negative binomial models tested

Model	α	β	k	Covariance parameters		AIC	BIC	Pearson Chi square/DF
				Orchard	Trees			
1	3.41	0.91	1.38			12,475	12,490	1.83
2	3.36	0.84	1.20	0.23*		12,343	12,344	1.96
3	3.08	0.87	0.71		1.03*	12,232	12,247	0.78
4	3.07	0.81	0.69	0.53*	0.64*	12,126	12,127	0.87

* Significant at $p < 0.0001$

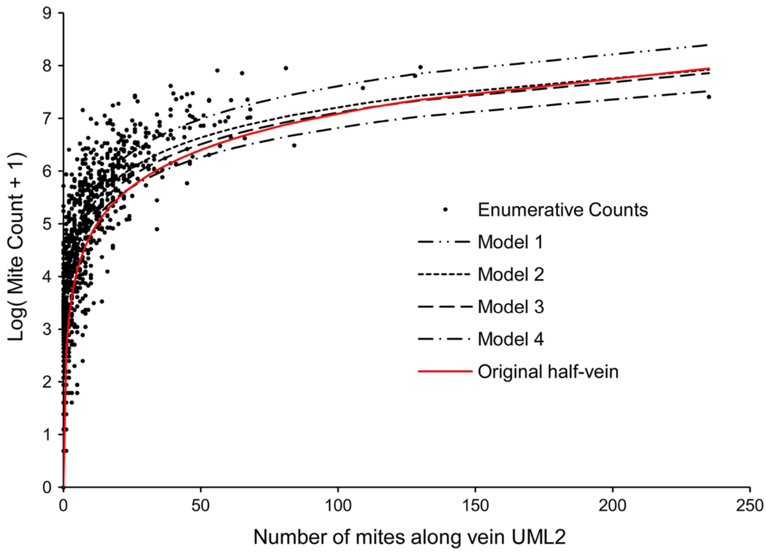

Fig. 3 Comparison of fitted models, original half-vein method and observed *Oligonychus perseae* counts on avocado leaves across ten sites from validation database B based on the log link scale

(Table 5). Graphically, however, model 4 was conservative in estimating the counts of *O. perseae* on avocado leaves (Fig. 2) and would be prone to underestimating mite densities. The opposite problem was detected for model 1 which overestimated counts of *O. perseae* (Fig. 2).

Model 3 generated an intermediate fit for the observed count data (Fig. 2) and lower paired values of AIC (12,232) and BIC (12,247) than models 1 and 2 and the combination of these results implied an overall better fit for model 3 (Table 5). A potential explanation for these results was explained by the covariance parameters. Covariance parameters ranged from 0.23 to 1.03 and formal hypothesis testing indicated that they were significantly different from zero (Table 5). This implied that incorporation of random effects were needed for improved interpretation of the observed data. Model 4 distinguished between the random effect associated with orchards as a block effect and interaction with individual trees, but because trees were not subjected to any type treatment, the specification of an interaction term may introduce some level of redundancy. The structure of

Table 6 Comparison of estimated *Oligonychus perseae* densities and percent errors for sampling methods based on 500 simple random sampling (SRS) iterations and a sample size of 30 avocado leaves with 1 leaf sampled per 30 trees

Site	E(y)[a]	Estimated density for models[b]						Mean percent errors for models[c]					
		EM	HV	1	2	3	4	EM	HV	1	2	3	4
1	61	61	23	61	52	42	38	−1	−62	−1	−15	−32	−38
2	37	37	23	57	48	39	35	−1	−38	55	29	5	−6
3	327	326	208	387	280	243	195	0	−36	18	−14	−26	−40
4	38	36	37	83	66	55	47	−4	−2	118	73	44	24
5	275	273	158	312	236	201	166	0	−42	14	−14	−27	−39
6	50	51	31	71	58	48	42	0	−39	42	15	−6	−17
7	196	198	97	199	153	129	108	1	−50	1	−22	−34	−45
8	189	190	96	202	158	132	112	0	−49	7	−17	−30	−41
9	474	476	192	374	281	240	197	1	−60	−21	−41	−49	−58
10	19	19	5	22	20	16	15	−1	−72	16	8	−17	−19

[a] Expected density, E(y), on the response scale was determined from enumerative counts of all sampled leaves for each orchard within database B

[b] Estimated densities based on enumerative counts (EM), the original half-vein method (HV) and negative binomial regression models (1–4)

[c] Mean percent errors were calculated between the expected and estimated mite densities across all sampling iterations for enumerative counts (EM), the original half-vein method (HV) and negative binomial regression models (1–4)

model 3 represented a possible solution to this problem. Even though model 3 specified only a tree effect, this model implicitly accounted for effects at the orchard level and this was reflected in the increased value for the covariance parameter estimate (Table 5).

Cross sectional validation

Cross sectional performance evaluation of fitted models was based on sampling simulations for twelve stratified avocado leaf sampling combinations using database B. An assessment of all combinations for the enumerative counts indicated that an overall sample of 30 leaves, with one leaf sampled per tree, generated lower percent errors in comparison to a 20 and 10 leaf sample (results not shown). The results of the percent errors for all models based on a 30 leaf sample with 1, 2, 3, or 4 leaves per tree are listed in Tables 6, 7, 8 and 9. In these analyses, lower percent errors were achieved with a stratified sample of 1 leaf per tree and this would be the recommended sampling structure within a 5 × 6 sampling block. The lowest percent errors across all sites, ranging from −4 to +4 %, were associated with enumerative mite counts. Percent errors for the original half-vein method ranged from −1 to −72 % across all sites and sample sizes. The original half-vein model consistently underestimated mite densities (Fig. 2).

Models 1–3 displayed improved performances in reducing percent errors and mitigating underestimation compared to model 4 and the original half-vein method, but significant patterns were detected across sampling combinations (Tables 6, 7, 8, 9). Estimates of percent errors for model 1 revealed a strong pattern for overestimating mite densities, and in some cases, such as in orchards 2, 4, and 6, the absolute percent error values exceeded

Table 7 Comparison of estimated *Oligonychus perseae* densities and percent errors for sampling methods based on 500 simple random sampling (SRS) iterations and a sample size of 30 avocado leaves, 2 leaves per 15 trees

Site	E(y)[a]	Estimated density for models[b]						Mean percent errors for models[c]					
		EM	HV	1	2	3	4	EM	HV	1	2	3	4
1	61	62	24	62	54	43	39	0	−61	2	−13	−30	−36
2	37	37	23	58	48	39	35	1	−37	57	30	6	−5
3	327	330	211	392	283	246	197	1	−35	20	−13	−25	−40
4	38	40	38	84	67	56	48	4	0	122	77	46	26
5	275	277	159	314	238	202	167	1	−42	14	−13	−26	−39
6	50	51	31	73	59	48	42	1	−38	44	17	−4	−16
7	196	194	96	196	151	127	107	−1	−51	0	−23	−35	−46
8	189	191	97	203	159	133	113	1	−49	7	−16	−30	−40
9	474	474	191	374	280	239	196	0	−60	−21	−41	−50	−59
10	19	19	5	22	20	16	15	−1	−72	17	8	−17	−19

[a] Expected density, E(y), on the response scale was determined from enumerative counts of all sampled leaves for each orchard within database B

[b] Estimated densities based on enumerative counts (EM), the original half-vein method (HV) and negative binomial regression models (1–4)

[c] Mean percent errors were calculated between the expected and estimated mite densities across all sampling iterations for enumerative counts (EM), the original half-vein method (HV) and negative binomial regression models (1–4)

Table 8 Comparison of estimated *Oligonychus perseae* densities and percent errors for sampling methods based on 500 simple random sampling (SRS) iterations and a sample size of 30 avocado leaves, 3 leaves per 10 trees

Site	E(y)[a]	Estimated density for models[b]						Mean percent errors for models[c]					
		EM	HV	1	2	3	4	EM	HV	1	2	3	4
1	61	62	24	61	53	42	39	1	−61	0	−14	−31	−37
2	37	36	23	57	47	38	34	−2	−38	54	28	4	−7
3	327	328	210	390	282	245	196	0	−36	19	−14	−25	−40
4	38	35	36	81	65	54	46	−7	−4	114	71	41	22
5	275	275	159	313	237	201	167	0	−42	14	−14	−27	−39
6	50	52	32	73	59	49	43	3	−37	46	18	−3	−15
7	196	196	96	197	151	128	107	0	−51	0	−23	−35	−45
8	189	191	97	204	160	134	114	1	−49	8	−16	−29	−40
9	474	473	192	375	281	240	197	0	−59	−21	−41	−49	−58
10	19	20	6	23	21	16	16	5	−71	20	10	−15	−17

[a] Expected density, E(y), on the response scale was determined from enumerative counts of all sampled leaves for each orchard within database B

[b] Estimated densities based on enumerative counts (EM), the original half-vein method (HV) and negative binomial regression models (1–4)

[c] Mean percent errors were calculated between the expected and estimated mite densities across all sampling iterations for enumerative counts (EM), the original half-vein method (HV) and negative binomial regression models (1–4)

Table 9 Comparison of estimated *Oligonychus perseae* densities and percent errors for sampling methods based on 500 simple random sampling (SRS) iterations and a sample size of 32 avocado leaves, 4 leaves per 8 trees

Site	E(y)[a]	Estimated density for models[b]						Mean percent errors for models[c]					
		EM	HV	1	2	3	4	EM	HV	1	2	3	4
1	61	62	23	61	52	42	38	1	−62	−1	−15	−32	−38
2	37	37	23	57	48	39	35	−1	−38	55	29	5	−6
3	327	321	205	382	277	241	193	−2	−37	17	−15	−26	−41
4	38	40	40	87	69	57	49	5	4	130	81	51	30
5	275	272	157	310	235	200	165	−1	−43	13	−15	−27	−40
6	50	52	31	73	59	48	42	3	−38	45	17	−4	−16
7	196	203	99	202	155	131	110	3	−49	3	−21	−33	−44
8	189	191	98	204	160	134	114	1	−49	8	−16	−29	−40
9	474	471	191	373	280	239	196	−1	−60	−21	−41	−50	−59
10	19	19	5	22	21	16	15	−1	−72	17	9	−17	−19

[a] Expected density, E(y), on the response scale was determined from enumerative counts of all sampled leaves for each orchard within database B

[b] Estimated densities based on enumerative counts (EM), the original half-vein method (HV) and negative binomial regression models (1–4)

[c] Mean percent errors were calculated between the expected and estimated mite densities across all sampling iterations for enumerative counts (EM), the original half-vein method (HV) and negative binomial regression models (1–4)

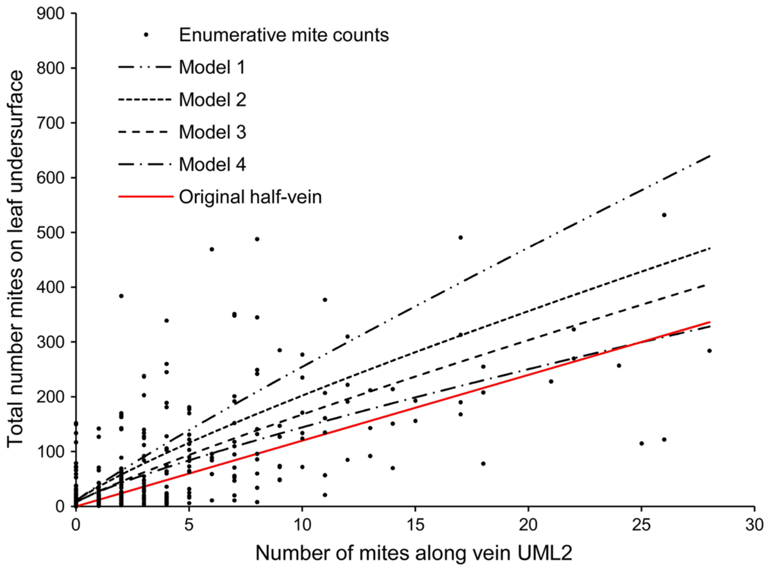

Fig. 4 Comparison of fitted models, original half-vein method and observed *Oligonychus perseae* counts on avocado spring flush leaves from dataset 1 of orchard 11 based on the response scale

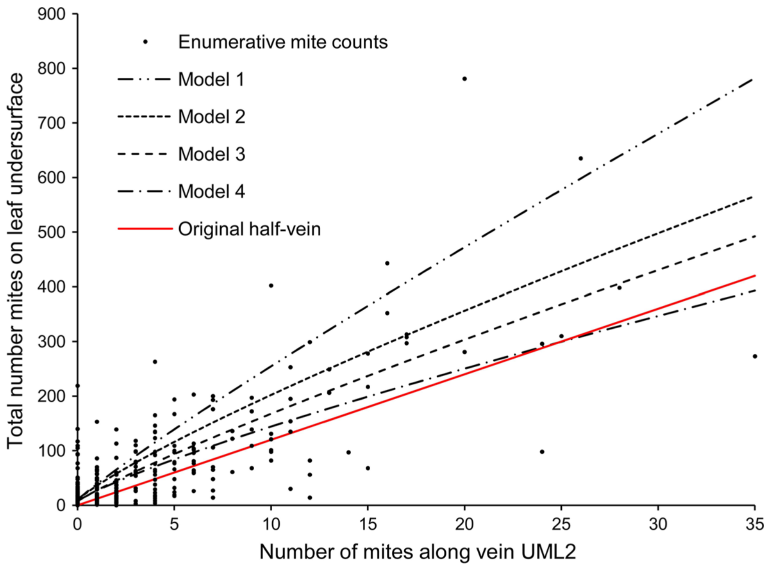

Fig. 5 Comparison of fitted models, original half-vein method and observed *Oligonychus perseae* counts on avocado spring flush leaves from dataset 2 of orchard 11 based on the response scale

those of the original half-vein model (Tables 6, 7, 8, 9). With the exception of orchard 4, the absolute percent error values for models 2 and 3 indicated that these models performed better than model 1 in estimating mite densities (Tables 6, 7, 8, 9). While model 3 demonstrated a tendency for slight underestimation, model fit criteria reported in Table 5 supported the statistical validity of model 3 over model 2 for estimating whole leaf mite densities using partial counts along UML2.

Longitudinal validation

A graphical comparison of mite density estimates from models 1–4, the original half-vein method, and observed mite counts for the two groups of trees sampled over time are shown in Fig. 4 for dataset 1 and Fig. 5 for dataset 2. Enumerative mite counts on the leaf undersurface and vein UML2 at this site were not as high as in database A and B, but the estimated percent errors and mite density values from sampling simulations (Table 10) offered an objective approach for model evaluation. *O. perseae* densities predicted from total enumerative counts generated the lowest percent errors and consequently, this continued to be the most accurate sampling approach. The half-vein method underestimated *O. perseae* densities in an absolute range of 29–60 % at densities greater than 16 mites per leaf. By comparison, lower percent errors in an absolute range of 1–29 % were generated with model 3 at mite densities greater than 16 mites per leaf during summer months. Therefore, model 3 would be a better alternative than the original half-vein model and models 1, 2, and 4 for the purposes of estimating per leaf densities of *O. perseae* in an orchard. At densities lower than 16 mites per leaf, the original half-vein method performed better than the new fitted models but the predicted mite densities from model 3 were still within an acceptable practical range that would have indicated that *O. perseae* population densities were relatively low.

Table 10 Comparison of estimated *Oligonychus perseae* mean densities and percent errors for sampling methods based on 500 simple random sampling (SRS) iterations and a sample size of 1 avocado leaf per tree at orchard 11

Set	Sample date	E(Y)[a]	Estimated density for models[b]						Mean percent errors for models[c]					
			EM	HV	1	2	3	4	EM	HV	1	2	3	4
1	June 2012	0.60	0.58	0.37	11	12	8	9	−4	−39	1790	1827	1310	1382
	Aug. 2012	51	52	20	54	46	37	34	3	−60	6	−9	−27	−34
	April 2013	7	7	9	29	26	20	19	−2	23	308	264	185	170
	May 2013	0.16	0.17	0.50	12	12	9	9	7	222	7343	7439	5432	5686
	June 2013	6	6	11	34	31	24	23	2	82	481	423	307	288
	July 2013	87	86	48	111	92	75	66	−2	−45	27	5	−14	−24
	Aug. 2013	126	127	89	190	151	125	108	1	−29	51	20	−1	−15
2	May 2012	0.18	0.12	0.69	12	12	9	9	−34	296	6721	6748	4946	5144
	June 2012	0.74	0.80	0	10	11	8	8	8	−100	1322	1368	967	1032
	July 2012	1	0.95	0.82	12	12	9	10	−2	−15	1185	1193	852	891
	Aug. 2012	17	17	9	30	28	21	20	0	−45	83	66	29	23
	Sept. 2012	0.33	0.29	0	10	11	8	8	−11	−100	3127	3230	2322	2469
	April 2013	6	6	7	25	22	17	16	−2	11	291	249	172	158
	May 2013	1	0.95	1	13	13	10	10	−6	30	1222	1207	871	897
	June 2013	6	6	8	29	26	20	19	0	50	413	365	261	246
	July 2013	112	111	72	155	124	102	89	−1	−36	39	11	−8	−21
	Aug. 2013	102	103	58	131	106	87	76	1	−43	28	4	−15	−25

[a] Expected density, E(y), on the response scale was determined from enumerative counts of all sampled leaves for each orchard within database B

[b] Estimated densities based on enumerative counts (EM), the original half-vein method (HV) and negative binomial regression models (1–4)

[c] Mean percent errors were calculated between the expected and estimated mite densities across all sampling iterations for enumerative counts (EM), the original half-vein method (HV) and negative binomial regression models (1–4)

Discussion

Populations of *O. perseae* were first detected in California in 1990 (Bender 1993). Since that time, this non-native species has become the key foliar pest of 'Hass' avocados throughout the commercial growing region in southern California and this has created the need for developing effective control and sampling tools (UC IPM 2011). The motivation for this study was to evaluate the performance of the original half-vein model (Machlitt 1998) for the purpose of estimating *O. perseae* densities using partial counts of this pest along the upper margin of leaf vein UML2 (a single predictor, x_1) and, if necessary, to update the structure of the original model and provide validated sampling guidelines that would facilitate its potential application in avocado orchards.

The initial evaluation based on all leaf samples provided strong evidence that the original half-vein approach underestimated mite densities in a range of 15–60 %. These results indicated that the half-vein method in its original form was not reliable for estimating *O. perseae* densities on infested leaves collected from commercial Hass avocado orchards (Table 2). The consistent underestimation pattern implied that the current relationship of *O. perseae* counts and vein UML2 may be influenced by abiotic (e.g., weather variables) and biotic (e.g., tolerance of Hass foliage for higher mite densities) factors since the time the original analyses were conducted (Machlitt 1998). The nature of this potential change is unclear as access to the original datasets Machlitt (1998) used for generating the original half leaf vein sample method were not available for re-analysis. Nevertheless, the consistent significant correlation across sites (Table 3, 4) detected between the response and predictor variable for UML2 implied that an updated model for estimating *O. perseae* densities using partial counts was necessary if this partial count method was to provide accurate estimates of mite densities on whole leaves.

Consequently, improvement and validation of the half-vein method, as part of an empirical modeling process, was adopted to determine whether it still held practical application for sampling of *O. perseae*. This approach included one generalized linear model (i.e., model 1) and three generalized linear mixed models (GLMMs) (i.e., models 2–4) which were better suited for handling non-normal data and accounting for potential random effects (Bolker et al. 2009). The performance of these models was compared with the original half-vein model and enumerative counting through simulated sampling of additional cross-sectional and longitudinal field data not used in the modeling process. As expected, the enumerative counting strategy consistently provided the highest level of accuracy (Tables 6, 7, 8, 9, 10) but this approach is time consuming and not suitable for field work. The overall results from the model-fit statistics (Table 5) and sampling simulations (Tables 6, 7, 8, 9, 10) suggested that model 3 with a random effect from avocado trees performed better than competing models and could potentially be customized as an alternative time-saving sampling tool to better estimate per leaf densities of *O. perseae* in California by making partial counts on vein UML2 on sampled leaves.

As a GLMM, the fixed effect components of model 3 inherently provided an estimate of *O. perseae* counts on a leaf for the average tree within an orchard for values of x_1. In this study, more than 300 trees were sampled across different sites and years, and these were representative of the types of trees that might be sampled by pest control managers or growers to assess levels of *O. perseae* in orchards. Due to the design of the data collection process, the use of model 3 for estimating mite densities is compatible with making a general assessment of *O. perseae* densities over 30-tree blocks with 1 in-season mature leaf randomly sampled per tree (Tables 6, 7, 8, 9, 10) during the summer (e.g. July–August) when elevated densities, as indicated by the presence of these mites on the leaf undersurface and the prominence of necrotic spots (i.e., feeding damage), are suspected in relatively small sections of the orchard. The use of model 3 early in the season during spring months when *O. perseae* populations may be low (e.g., April–May) is not recommended because this model is likely to overestimate densities as was shown from the validation results of orchard 11 (Table 10). However, because mite densities are low at this time of year, whole leaf counts could be used to estimate average mite numbers per leaf. Once densities exceed an average of 16 mites per leaf, use of the fixed effect component of model 3 as validated in this study, $y = \exp[\alpha + \beta \ln(x_1 + 0.31)]$, is recommended for estimating densities of *O. perseae* on whole avocado leaves. For each leaf collected within the block of interest, vein UML2 can be examined with a 20× hand lens to count the number of *O. perseae* occupying the upper margin of this vein. Individual values of x_1, along with parameters values α and β for model 3 (Table 5), are entered into the respective model Eq. (3) to produce estimates of *O. persea* at the leaf level. These estimates are averaged over the number of leaves sampled (e.g., 30 leaves comprised of 1 randomly selected in-season leaf from each of 30 trees) and a final mite density assessment for the 30-tree block is made. In this study, 95 % of the x_1 values across all datasets (n = 3849 leaves) were less than or equal to 26 *O. perseae* mites. With training, it takes approximately 30 s to 1 min per leaf to obtain values for x_1 and therefore the density assessment for blocks of 30 trees should take approximately 15–30 min.

When the objective is to characterize the severity of mite infestation over larger spatial areas (e.g., 200 × 200 tree blocks or smaller) relatively quickly, our recommendation is to use a binomial sampling structure with a minimum sample size of 30 leaves (Lara and Hoddle 2015b). Binomial sampling can be used to effectively classify densities of *O. perseae* as being above or below a working action threshold of 50 mites per leaf throughout the period of the growing season (i.e., April–September in California) when mite populations need to be monitored for potential control. The binomial sampling plan developed by Lara and Hoddle (2015b) accounts for potential spatial correlation of *O. perseae* (DePalma et al. 2012; Li et al. 2012) and reduces the sampling effort because no mite counting is required, only the proportion of leaves that are infested with at least one mite is recorded and used to estimate per leaf densities of *O. perseae*. In small 30-tree blocks, however, either binomial sampling or the validated half-vein method (model 3) presented here can be used to sample for *O. perseae* which together expand the range of sampling tools available to pest managers and researchers.

Growers can combine the information from the sampling tools described above with information from visual inspection of feeding damage, current and anticipated weather conditions [observations have been made that *O. perseae* populations decline under periods of high summer temperatures (UC IPM 2011)], time of year (mite populations usually peak during the summer and decline in fall), known information on the history of mite infestations in monitored orchards, and availability and potential application timing of pest control materials (i.e., releases of commercially available phytoseiids or pesticide applications) to make an informed decision on the appropriate control strategy at the orchard level. Although improvements have been made to the *O. perseae* sampling program, work is still needed to expedite sampling data collection and processing through the use of a customized agricultural software application designed for use on smartphones or tablets. The potential benefits for implementing this electronic technology for systematic information management has been demonstrated for other field-based systems (Aanensen et al. 2009; Kennedy et al. 2013; Olson et al. 2014). If developed for the avocado system, this type of technology would enable pest managers to readily enter and store sampling data (e.g., presence-absence or x_1 values) directly into handheld devices and software would perform numerical model calculations and provide an estimate of mite densities. This information could be relayed directly to growers electronically with information on the recommended treatment, if necessary. Furthermore, the readily accessible electronic records of these assessments and any other type of complementary data collected at the time of sampling (e.g., pictures of feeding damage, GPS coordinates of trees sampled) could be used to build a spatial and temporal pest profile for the orchard that could be used to identify and target areas with a known history of pest pressure for monitoring.

Finally, for research experiments where highly accurate mite density estimates are required to compare the pest-control effectiveness of treatment applications such as different pesticide materials or natural enemy species, enumerative counting should always be considered as the first option and this procedure can be facilitated with the aid of a microscope in the laboratory and leaves can be cool-stored to preserve quality and reduce mite activity until counting. The original half-vein model (Machlitt 1998) was specifically designed with the intention of assisting growers and pest managers with quickly assessing densities of *O. perseae* populations in commercial avocado orchards and model 3 was customized to better meet this objective. In this study, we did not evaluate the performance of the original half-vein method under an experiment research design with a series of replicated treatments. However, the underestimating behavior pattern of original half vein model suggests that additional error may be introduced into the estimates of mite densities and could potentially affect the interpretation of treatment comparisons. Future research should determine if different types of treatment applications (e.g., pesticides vs. natural enemies) will affect the empirical relationship between total mite counts and partial counts along UML2 as seen on untreated trees used in this study. The results of such studies may provide an indication of the appropriate sample size needed for reliable sampling results.

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