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RESEARCH ARTICLE

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Relative abundance and damage by species in the Lepidoptera borer complex of macadamia nuts in the Barberton area, South Africa

M Enslin[1,2*], PS Schoeman[3], AE Timm[4], H du Plessis[2] and J van den Berg[2]

[1]*Insect Science South Africa, Tzaneen, South Africa.*
[2]*IPM program, Unit for Environmental Sciences and Management, North-West University, Potchefstroom, South Africa.*
[3]*South African Macadamia Association (SAMAC), East Rand, South Africa.*
[4]*Department of Agricultural Biology, Colorado State University, Colorado, United States.*

Larvae of the nut borer complex, which include *Thaumatotibia leucotreta, T. batrachopa, Cryptophlebia peltastica* and *Ectomyelois ceratoniae*, cause extensive economic damage to macadamias in South Africa. Monitoring the changing species composition in this complex over a growing season provides valuable information for managing populations. In this study, pheromone traps were placed in two orchards planted with two different cultivars and used to monitor moth numbers over a 28-week period, while larval numbers and nut damage were monitored weekly over a 21-week period from the onset of flowering. Larvae were identified using a combination of morphology and DNA sequences of ~658 bp of the cytochrome oxidase I (COI) gene. Both larval and moth numbers were dominated by *T. leucotreta*, followed by *T. batrachopa*, with respective trap catches of 69% and 27%. Spearman correlations indicated strong linear relationships between nut diameter and numbers of eggs per nut for both the Beaumont and 816 cultivars. Poor correlations were found between weekly moth numbers and the number of eggs per nut. A two- to three-week lag was observed between weekly *T. leucotreta* trap catches and egg numbers. In contrast, egg numbers correlated strongly with larval infestation levels and the incidence of damaged nuts. Although the numbers of eggs and larvae were higher in Beaumont than cv. 816 nuts, higher incidences of nuts with husk and kernel damage were recorded for cv. 816. This study highlights the importance of monitoring of moth and larval numbers in macadamia orchards and showed that such data could be used to predict pest incidence during the season. This study questions the norm in South Africa, which is that macadamia nut borer (MNB) is usually the most abundant species in the nut borer complex.

CORRESPONDENCE
M Enslin

EMAIL
enslinmarnus@gmail.com

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INTRODUCTION

Lepidopteran larvae of the nut borer complex in South Africa cause extensive economic damage to macadamia by reducing yields through direct feeding on nuts. Species comprising this borer complex are three Tortricidae species – *Thaumatotibia leucotreta* (Meyrick) (false codling moth, FCM), *Thaumatotibia batrachopa* (Meyrick) (macadamia nut borer, MNB), and *Cryptophlebia peltastica* (Meyrick) (litchi moth, LM) – and a Pyralidae, *Ectomyelois ceratoniae* (Zeller) (carob moth, CM). Mixed populations of these species are often reported in macadamia orchards (La Croix and Thindwa 1986; Timm et al. 2007; Schoeman 2016; Smith et al. 2022). Of these species, *T. leucotreta* is considered the most important internationally due to its quarantine status (Adom et al. 2021), although MNB and LM also have phytosanitary status for many markets.

Moths of all four species of the nut borer complex lay their eggs on developing and hard nuts. Resulting larvae cause substantial damage by burrowing into nuts, which typically results in fruit drop (La Croix and Thindwa 1986). When nuts are small, larvae may need to consume more than one kernel, and to do so, they usually move to adjacent nuts. Once macadamia nut shells are fully hardened, it cannot be penetrated by larvae and larval development is completed inside the husk (La Croix and Thindwa 1986). If vascular bundle tissue inside fully developed immature nuts are damaged by larval feeding, no further nut development takes place (Schoeman and De Villiers 2015).

Management of the nut borer complex is complicated by seasonal variation in pest population numbers, and varying activity peaks of the different species. Monitoring moth flight patterns and larval species composition provides information on which species are present, when seasonal flight activity commences, and how the moth and larval complexes vary over time (Witzgall et al. 2010). Moth numbers can be monitored using pheromone traps. However, since pheromone trap catches are influenced by environmental conditions (Jones 1995; Lösel et al. 2002), as well as bycatches and pheromone efficacy, the mere abundance of moths does not always indicate a high pest status. For example, poor correlations between moth catches and larval numbers inside fruit were reported for CM in citrus (Morland et al. 2019), and certain FCM species in litchi and macadamia (Jones 1995). Moth capture can therefore provide information on moth presence but may not always be an accurate predictor of the pest status of the different species in macadamia orchards (Smith et al. 2022). Although monitoring egg numbers on developing nuts can provide general information on the timing of pest infestation in macadamias, it was reported not to be a suitable predictor of damage (Jones 1994a). Determining larval numbers inside fruit is considered a more accurate indication of infestation levels of a particular species (Jones 1994b), although difficulty with larval species identification (Venette et al. 2003) often limits the feasibility of this monitoring method.

The dynamic nature of pest populations necessitates continuous monitoring to tailor control strategies to specific pests that are present and dominant in macadamia orchards (Smith et al. 2022). Nevertheless, limited information exists on moth activity patterns and associated larval infestation levels in macadamia orchards in South Africa. If the information on seasonal abundance of moths can be successfully related to larval numbers (Witzgall et al. 2010), monitoring moth flight patterns can play an essential role in decision-making regarding pest control practices.

The aims of this study were to determine moth flight patterns, associated larval population structure and relative species abundance of the nut borer complex over one growing season in the Barberton area, Mpumalanga, South Africa. Possible relationships among weekly moth trap numbers, egg and larval numbers per nut and nut damage were also investigated.

MATERIAL AND METHODS

Study area

This study was conducted over an entire production season, from September 2020 to March 2021. The trial site was located on a commercial farm (25°44′43.3″ S, 31°00′51.8″ E) in the Barberton region, situated about 40 km from Nelspruit in the Mpumalanga province of South Africa. Crop management was carried out according to local agricultural practices. Insecticides used in the orchards and the times of application are listed in Table 1.

The study was conducted in two orchards, established 15 years ago, that are separated by a narrow dirt road. A single cultivar, Beaumont (Cultivar code 695), was grown in one orchard, while alternating rows of cv. 816 and Beaumont were grown in the other (mixed block). The tree spacing in these orchards was 8 m × 4 m (300 to 330 trees per ha), which is the standard industry spacing in macadamia orchards (SAMAC 2022).

Seasonal phenology and sampling timeline

To facilitate application of results of this study to regions where the seasonal crop phenology, for example, commencement of flowering, differs from that in the Barberton area, data are reported according to Julian calendar weeks. Moth numbers per week, for example, are reported according to the Julian calendar week of the year, with week one being the first week of January, rather than that of the specific date of a sampling event, which may vary between regions and over seasons.

Pheromone traps

Yellow delta traps (Insect Science (Pty) Ltd. Tzaneen, South Africa) with pheromone lures for FCM, MNB, LM and CM (Table 2) were placed inside the two orchards. Three sampling points, each consisting of a trap for each species, separated by 12 m (4 trees) within the same row of trees, were included per orchard. Seven to eight rows of trees separated each replicate. To limit possible trap interference, MNB and LM traps were placed at opposite ends of each replicate. Pheromone dispensers were replaced as indicated by the manufacturer's guidelines.

Trapping commenced six weeks prior to the onset of flowering, at Julian week 36 (September 7, 2020) and continued for 28 weeks until harvest (Julian week 11, March 8, 2021). Sticky liners were replaced at weekly intervals and the number of moths collected for each target species was recorded. Numbers of bycatch for each trap were also recorded, although these were not identified to species, except for large moths that occurred in FCM traps.

Sampling of nuts and larvae

Nuts were sampled over a 21-week period, from the commencement of flowering (October 19, 2020; Julian week 42) to harvest (March 8, 2021; Julian week 10). Sampling was interrupted for four weeks (Julian weeks 4, 6, 7 and 9) by the presence of cyclone Eloise during January 2021. Fixed rows were used for sampling – every second row in the Beaumont block, and every third row in cv. 816 in the mixed block. There were eight replicates per orchard, with each replicate consisting of a row of approximately 94 trees.

Twenty nuts that were identified as recently fallen were randomly collected from underneath the trees in each row (replicates) (160 nuts per block/week, total number of nuts = 5440). The nuts were stored in brown paper bags at temperatures of 4-6 °C to slow down larval development and limit husk rotting.

Table 1. Insecticides, active ingredients, and dates of application for pest control in the macadamia orchards at Barberton.

Date applied	Julian week number	Active ingredient and insecticide class	IRAC Group
07/10/2020	41	Chlorpyrifos (organophosphate)	1B
21/10/2020	43	Fipronil (phenyl pyrazole) Lambda-cyhalothrin (pyrethroid)	2B/3A
01/11/2020	44	Fipronil (phenyl pyrazole) Lambda-cyhalothrin (pyrethroid)	2B/3A
09/11/2020	45	Methomyl (carbamate)	1A
16/11/2020	46	Cypermethrin (pyrethroid)	3A
23/11/2020	47	Methomyl (carbamate)	1A
20/12/2020	51	Beta-cyfluthrin (pyrethroid)	3A
15/02/2021	7	Cypermethrin (pyrethroid)	3A

Table 2. Pheromone lures and trap type used for monitoring of *Thaumatotibia leucotreta*, *T. batrachopa*, *Cryptophlebia peltastica*, and *Ectomyelois ceratoniae* numbers in macadamia orchards in Barberton.

Species	Supplier (South Africa)	Lure replacement intervals	Active ingredient
Thaumatotibia leucotreta	Insect Science, Tzaneen	Not replaced. Lasts 28-30 weeks	E-7-dodecenyl acetate
Thaumatotibia batrachopa	Chempac, Paarl	Every 6 weeks	Z-8-dodecenyl acetate
Cryptophlebia peltastica	Insect Science, Tzaneen	Every 6 weeks	Z-8-dodecenyl acetate E-8-dodecenyl acetate
Ectomyelois ceratoniae	Chempac, Paarl	Every 6 weeks	(7Z,9E)-7,9,11- dodecatrienyl formate

The diameter of each nut was measured using a digital electronic calliper after which the number of Lepidoptera eggs on each nut were recorded. No distinction was made between eggs that had hatched and those that had not. Black eggs were recorded as parasitised. Nuts were then carefully dissected, and all larvae (dead and alive) removed. The numbers of dead larvae were included in the calculation of the total number of larvae per nut. The spatial distribution of larvae within the fruit was recorded as feeding either inside the husk or inside the kernel. All data were recorded within two days of nut collection.

Larval identification

Dead and live larvae that were recovered from nuts were individually preserved in 1.5 ml centrifuge tubes filled with 99% ethanol after which they were identified by means of morphological methods (Timm et al. 2008). Some of the larvae that could not be identified based on morphology were identified by means of molecular techniques. Larvae were identified morphologically by using a microscope to examine characters such as the location of primary setae, the arrangement of crochets on abdominal prolegs, the presence or absence of an anal comb and, if an anal comb was present, the number and arrangement of prongs on the anal comb. Since these structures can vary in young instars, only older instars (approximately 3rd-instar and older for Tortricidae) were examined. To confirm morphological identifications, 80 specimens were identified using DNA sequences. DNA was extracted using the Lucigen MasterPure Complete DNA and RNA Purification Kit (Lucigen Corporation, Middleton, WI, USA) by soaking whole larvae in the extraction buffer. After DNA extraction, larvae were removed, rinsed in ethanol, and stored at –80 °C to retain as voucher specimens. Approximately 658 bp of the cytochrome oxidase I (COI) gene was amplified with the primers LepF1/LepR1 (Hebert et al. 2004) using standard PCR protocols. PCR products were purified using ExoSAP-IT® (Applied Biosystems, Foster City, CA, USA). Purified PCR products were sequenced by the University of Chicago Comprehensive Cancer Center DNA Sequencing and Genotyping Facility with an Applied Biosystems 3730XL DNA sequencer (Applied Biosystems, Foster City, California, USA). Sequencing was performed in both directions using the same primers that were used for PCR amplification. The resulting sequences were trimmed, assembled, and aligned using Geneious Prime 2021.0.3 (www.geneious.com). Sequences were identified to species based on comparison to sequences in the BOLD Systems database. A sequence match of at least 98% was regarded as confirmation of a species, in addition to accurate placement on trees produced by the database using the Kimura Two-Parameter distance model.

Data analysis

The mean number of moths per trap per week was calculated for each of the four target species for each of the two orchards. Descriptive statistics were used to illustrate moth flight patterns for each orchard over time, as well as for data on nut diameter, mean number of eggs and parasitised eggs per nut. No distinction was made between newly laid unhatched eggs and eggs that already hatched and were still visible on the surface of the nuts. The number and position of larvae inside a nut (including husk), entry holes into the husk, as well as damage on the inside and outside of each nut were also analysed using descriptive statistics. Summary statistics were conducted by means of Microsoft Excel (Microsoft 365).

The weekly sampling provided sufficient data to determine relationships between pheromone trap catches, larval numbers and damage parameters over the 20-week sampling period. Simple correlation analyses were performed between variables. Spearman's rank correlations (rho) were used to assess the linear relationship between moth numbers, infestation levels and damage parameters. Cross-correlation analyses were done to determine relationships and the time lag between the following variables: mean weekly moth numbers of each species, mean weekly number of moths of the three species combined, mean numbers of eggs per nut, mean numbers of larvae per nut, nut diameter, and the various damage parameters. Data were analysed using IBM SPSS version 28.0.1.1 (15) (IBM 2021).

RESULTS

Moth flight patterns

A total of 1673 moths were captured in pheromone traps over the 28-week sampling period. The proportional contribution of the different species to the total number of moths during the season were as follows: FCM = 69%, MNB = 27% and LM = 4%. No CM moths were caught in any traps throughout the season.

Mean numbers of moths per trap per week showed similar patterns in the two orchards (Figure 1A, C). The first FCM and MNB moths were captured in the first week of the season (Julian week 36), six weeks prior to the commencement of flowering (Figure 1A, C). Numbers of MNB and FCM moths were very low (< 7 moths/trap) during the first 11 weeks (Julian weeks 36–46) of trapping. FCM moth numbers started to increase five weeks after flowering had commenced (Julian week 42) with a peak in activity during weeks 47–51. MNB numbers remained low (< 5 per trap/week) throughout the season, with a peak during Julian weeks 3–5. Numbers of LM moths were very low (< 2 per trap/week) throughout the season (Figure 1A, C) and virtually no captures were made after Julian week 2.

Bycatches per week were low (< 5/trap) throughout the season, except for the FCM trap during week 40 and the LM trap during week 11 (Figure 1B, D). The bycatch in FCM traps included large moths, most notably *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae) and *Chrysodeixes acuta* (Walker) (Lepidoptera: Noctuidae).

Nut size and egg numbers per nut

Nut size increased steadily until approximately 16 weeks after commencement of flowering (Julian week 5), after which they were fully developed (Figure 2). It was only in the period from nine to 12 weeks after onset of flowering (Julian weeks 50-1) that differences in nut size between varieties could be observed. Nuts of cv. 816 developed faster during this period. At full maturity, the mean diameter of nuts of both Beaumont and cv. 816 was 32 mm.

Correlations between the mean nut diameter and number of eggs per nut were very strong in both the Beaumont ($r = 0.930$, $p < 0.001$) and 816 ($r = 0.884$, $p < 0.001$) orchards (Table 3). Eggs were only encountered once nuts reached a mean diameter of 17.6 mm and 18.7 mm for the Beaumont and 816 cultivars respectively, during Julian week 49 (Figure 2). Very low numbers of eggs (< 3/nut) were detected on nuts during the first nine weeks after onset of flowering (Julian weeks 42-51) when nut diameter was < 25 mm. Mean egg numbers per nut differed between the two cultivars, with higher numbers occurring in Beaumont throughout the sampling period (Figure 2). For both cultivars, egg numbers increased 12 weeks after the onset of flowering and peaked at 15 weeks (Julian week 5), with a mean of 23.5 and 12.4 eggs per nut for Beaumont and cv. 816, respectively. The incidence of egg parasitism was low throughout the season (Figure 2), with parasitism levels of at least 6% only recorded during weeks 43, 3 and 10.

Larval species complex

A total of 1449 larvae of all four species of the macadamia nut borer complex were collected during the sampling period. Of these, 528 could be identified to species level, including those identified by means of molecular methods. Early-instar larvae

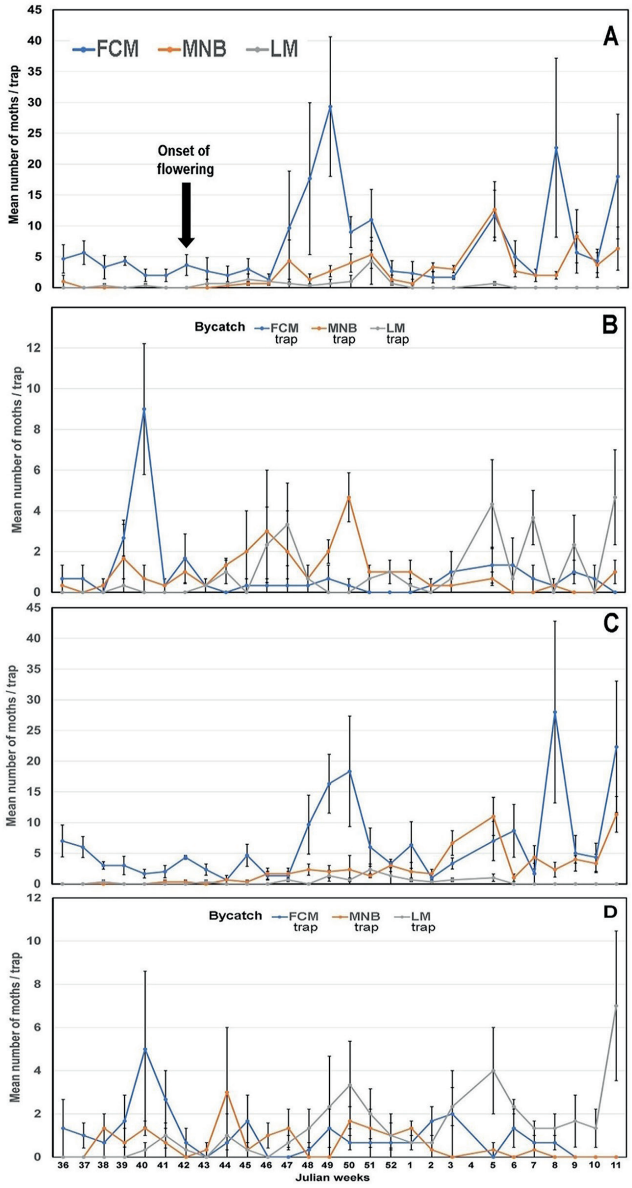

Figure 1. A) Mean numbers of false codling moth (FCM), macadamia nut borer (MNB), and litchi moth (LM) moths per trap the Beaumont cultivar orchard, B) bycatch in the FCM, MNB and LM trap in the Beaumont cultivar orchard, C) Mean numbers of FCM, MNB, and LM moths per trap in the cv. 816 orchard, and D) bycatch in FCM, MNB and LM traps in the cv. 816 orchard. Sampling of nuts started at week 42, when flowering commenced.

(921) could not be identified. The proportional contribution of each species to the overall weekly larval numbers are presented in Figure 3. The overall larval complex was dominated by FCM (67%), followed by MNB (19%), CM (10%) and LM (4%). Larvae that could not be identified are not represented in Figure 3.

During the first five weeks after flowering commenced (Julian weeks 43–47), only FCM and MNB larvae were recovered from fallen nuts (Figure 3). MNB made up 67%, 54%, 64% and 100% of the population for the first four weeks, after which FCM dominated for the remainder of the growing season. From week five after onset of flowering (Julian week 46) onwards, FCM comprised between 50% and 82% of the population on a weekly basis. CM only occurred from Julian week six onwards and remained present for the rest of the growing season. The proportional contribution of CM larvae varied over time with the highest abundance (27%) during Julian week 47. CM was only present in very low numbers towards the end of the season. LM larvae made up the smallest percentage of the pest complex and did not occur until Julian week 48.

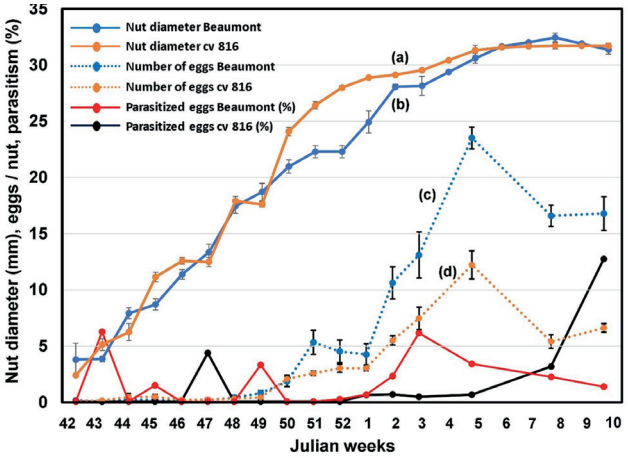

Figure 2. Mean nut diameter (mm), mean number of lepidoptera eggs per nut and incidence of parasitized eggs on fallen nuts sampled from Beaumont and cv. 816 orchards. Flowering commenced at week 42. Lines (a) and (b) indicate nut diameter. Lines (c) and (d) indicate numbers of eggs per nut. Dashed lines indicate percentage parasitism. Bars indicate standard error.

Very low numbers of the following species were also recorded: *Lobesia vanillana* (De Joannis) (Tortricidae) (3), *Nola imitata* (Van Son) (Nolidae) (1), *Janseodes melanospila* (Guenée) (Erebidae) (2), and *Ariathisa* sp. (Noctuidae) (1).

Larval infestation patterns

Larval infestation patterns were similar for the two cultivars, with an increase in numbers at Julian week 51, and a decrease in numbers late in the season (Figure 4A). Mean numbers of larvae per nut were similar for the two cultivars until a sharp increase in larval numbers was recorded during Julian week 49. The mean number of larvae per nut after week 49 was higher for Beaumont than cv. 816 (Figure 4B), with the mean number of larvae per nut during weeks 50-5 ranging between 1.1–2.4 for Beaumont and 0.9–1.2 for cv. 816.

Spatial distribution of larvae and damage inside nuts

Differences in the spatial distribution of larvae inside nuts were observed between the two cultivars. The total number of larvae encountered was higher in Beaumont than cv. 816 nuts (Figure 4A). Different patterns were observed in spatial distribution inside nuts of the two cultivars. While the numbers of larvae feeding inside the husk tissue were higher for Beaumont than cv. 816 nuts (Figure 4B), the numbers of larvae inside the shell were lower for Beaumont nuts from Julian week 1 onwards (Figure 4C).

The incidence (%) of nuts with damage to the husk tissue (Figure 4D) and damaged kernels (Figure 4E) were higher for cv. 816 for most of the season. A near perfect correlation (r = 0.997) was recorded between the incidence of nuts with husk damage and those with kernel damage in cv. 816. The correlation between these two variables was slightly lower in Beaumont nuts (r = 0.856).

Moth trap data and numbers of larvae, eggs and damage to nuts

Spearman correlation analyses (Table 3) showed that the mean combined weekly numbers of moths did not correlate significantly with any of the other parameters. Weekly FCM moth numbers also were not significantly correlated with the numbers of eggs or larvae per nut, or damage parameters in the same week, in any of the two orchards. However, weekly MNB moth numbers correlated significantly with the numbers of eggs per nut (r = 0.567, p < 0.035) and larval numbers per nut (r = 0.576, p < 0.031) (Table 3).

Table 3. Spearman correlation values indicating linear relationships between weekly trap catch numbers, egg numbers per nut, larval infestation levels and damage parameters.

cv. 816	Mean nr. of FCM moths / week	Mean nr. of MNB moths / week	Mean of total weekly nr. of moths	Mean nr. of eggs / nut	Mean nr. of larvae / nut	Mean % nuts with damaged husks	Mean % nuts with damaged shells
Mean number of eggs per nut	0.072	0.567*	0.330	--			
	$p = 0.807$	$p < 0.035$	$p = 0.249$				
Mean nr. of larvae per nut	0.279	0.576*	0.519	0.895**	--		
	$p = 0.333$	$p < 0.031$	$p = 0.057$	$p < 0.001$			
Mean % nuts with damaged husks	0.117	0.518	0.335	0.958**	0.871**	--	
	$p = 0.691$	$p < 0.058$	$p = 0.242$	$p < 0.001$	$p < 0.001$		
Mean % nuts with damaged shells	0.123	0.527	0.338	0.964**	0.874**	0.997**	--
	$p = 0.676$	$p < 0.052$	$p = 0.237$	$p < 0.001$	$p < 0.001$	$p < 0.001$	
Mean nut diameter				0.884**	0.815**	0.858**	0.874**
				$p < 0.001$	$p < 0.001$	$p < 0.001$	p < 0.001
Beaumont	Mean nr. of FCM moths / week	Mean nr. of MNB moths / week	Mean of total weekly nr. of moths	Mean nr. of eggs / nut	Mean nr. of larvae / nut	Mean % nuts with damaged husks	Mean % nuts with damaged shells
Mean number of eggs per nut	-0.066	0.653*	0.316	--			
	$p = 0.822$	$p < 0.011$	$p = 0.27$				
Mean nr. of larvae per nut	-0.068	0.551*	0.228	0.938**	--		
	$p = 0.816$	$p < 0.041$	$p = 0.433$	$p < 0.001$			
Mean % nuts with damaged husks	-0.234	0.536*	0.135	0.953**	0.942**	--	
	$p = 0.421$	$p < 0.048$	$p = 0.645$	$p < 0.001$	$p < 0.001$		
Mean % nuts with damaged shells	0.040	0.567*	0.277	0.830**	0.934**	0.856**	--
	$p = 0.893$	$p < 0.035$	$p = 0.337$	$p < 0.001$	$p < 0.001$	$p < 0.001$	
Mean nut diameter				0.930**	0.829**	0.873**	0.718**
				$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.004$

*Correlation is significant at the 0.05 level (2-tailed)

**Correlation is significant at the 0.01 level (2-tailed).

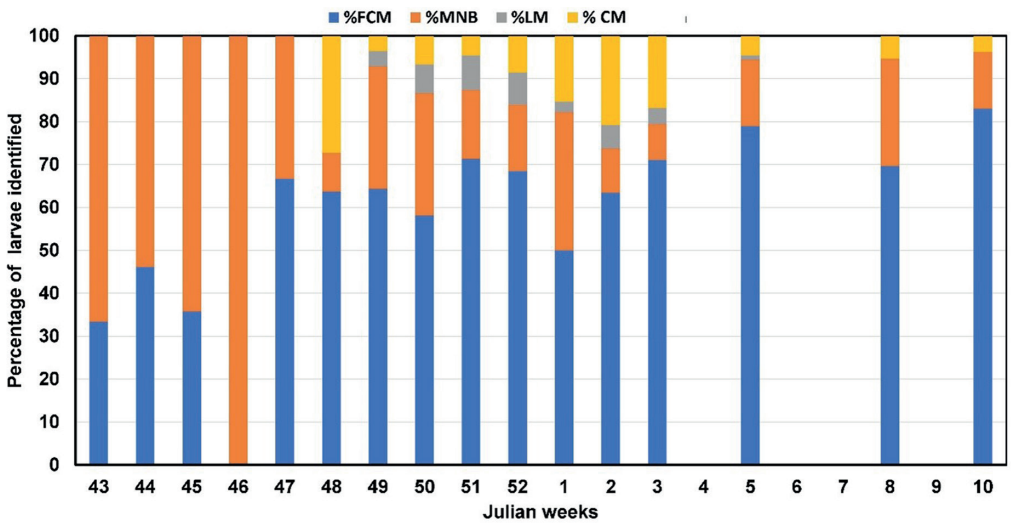

Figure 3. Percentage of larvae of *Thaumatotibia leucotreta* (FCM), *Thaumatotibia batrachopa* (MNB), *Cryptophlebia peltastica* (LM) and *Ectomyelois ceratoniae (*CM) recorded from fallen nuts at weekly intervals after onset of flowering at week 42. No sampling was possible in Julian weeks 4, 5, 6 and 9. Harvest commenced during week 10.

There was a strong positive correlation between egg numbers and larvae per nut in the 816 ($r = 0.0.895$, $p < 0.001$) and Beaumont ($r = 0.938$, $p < 0.001$) orchards. Similarly, strong positive and highly significant correlations were recorded between egg numbers per nut and the incidence of nuts with damaged husks and kernels.

Cross correlation analyses yielded both negative and positive correlations, indicating lag times between certain variables (Table 4). Only *r*-values > 0.5 are presented in Table 4. In some cases, strong correlations were observed when the two time series were compared without a time offset (week 0). These time series comparisons indicates that certain variables, for example weekly moth numbers, can be used as a predictor of egg numbers per nut and larval infestation levels at later time periods.

Weekly FCM moth numbers (Column A) correlated poorly with egg numbers per nut in the weeks following the trap catches in both orchards, except for weeks 5 and 6 (Table 4, column A). There was a lag of 2–3 weeks between weekly FCM trap catches

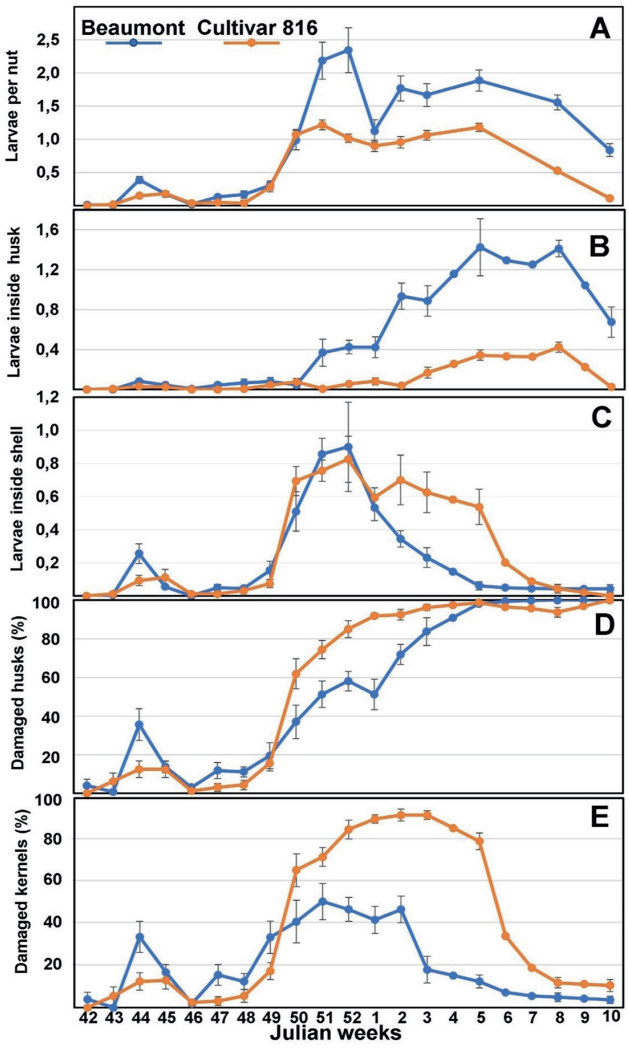

Figure 4. A) Mean number of larvae per nut, B) mean number larvae inside the husk, C) mean number of larvae inside shell, D) mean number of nuts with damaged shells and E) mean number of nuts with damaged kernels. Bars indicate standard error.

and eggs numbers per nut, and damage to husks and shells in both orchards. The time lags between weekly MNB moth numbers (Column B) and the various parameters were notably shorter that between FCM moth numbers and these variables. MNB weekly trap numbers correlated strongly (r = 0.769) with the numbers of eggs per nut, 4 weeks later, as well as with the numbers of larvae, 1 (r = 0.583) and 4 (0.607) weeks later. In the 816 orchard, the numbers of eggs per nut lagged MNB moth numbers by 0 (r = 0.506) and 1 week (r = 0.759). The time lag between overall moth numbers (Column C) and other variables were mostly longer than 3 weeks and only correlated with egg numbers per nut, 5–6 week later (r = 0.549-0.652).

There was a lag of 1–3 weeks between the numbers of eggs and larval numbers per nut, with notably strong correlations in both orchards (Beaumont: r = 0.793; 816: r = 0.889) between these two variables when the two time series were compared without a time offset (week 0) (Table 4) (Column D). A very strong correlation (r = 0.914) (Column D) was observed between the number of eggs per nut and incidence (%) of nuts with damage to husk tissue, when the two time series were compared without a time offset.

DISCUSSION

This study is the first of its kind in macadamia orchards in South Africa. Together with that of Smith et al. (2022) are the only studies to use molecular tools for species identification of pest ecology in macadamia orchards. Due to the small size of larvae, their cryptic feeding habits, and similarity between some of the species, accurate identification to species level is difficult (Morland 2015). Larval identification by means of molecular methods is the most reliable way to establish the relative dominance of different species of this pest complex within orchards. Although moths of only three of the species were recorded in pheromone traps, molecular markers also identified larvae of CM. Other species identified as larvae inside nuts using molecular means during this study were *Lobesia vanillana* (Tortricidae), *Nola imitata* (Nolidae), *Janseodes melanospila* (Erebidae) and *Ariathisa* sp. (Noctuidae), although very low numbers of each were present. Of these species, only *L. vanillana* is a known pest of economic importance, whose polyphagous nature results in feeding damage to a variety of crops, including vanilla (Brown et al. 2014), citrus (Morland et al. 2019) and grapes (du Preez et al. 2021).

A recent study of the nut borer complex in South Africa reported that MNB represented 95% of the larvae in damaged nuts across all growing regions in the country (Smith et al. 2022), making it the most important species in this pest complex. When MNB was first identified as a macadamia pest in South Africa in 1999 (de Villiers 2001), it was the dominant species and made up 90% of the species complex, followed by FCM (8%), and LM and CM, which contributed 2% (Bruwer 2001). In this study, however, the dominant species in the Barberton region was FCM, which constituted 67% of the larvae that were identified. The results of this study question the norm in South Africa, which is that MNB is usually the most abundant species in the nut borer complex. The occurrence of LM and CM larvae in nuts also contrasts with a recent study (Smith et al. 2022), which did not record any of these two species during a survey of the macadamia nut borer complex in South Africa, indicating that species complexes vary between production areas, as well as within and between seasons. It is not expected that the presence of LM and CM was due to any specific environmental factor. The general landscape in the study area is largely similar to those of other macadamia producing areas and the study site was adjacent to other macadamia farms and open savanna veld.

Information on species dominance in the nut borer complex has largely been based on the occurrence of larvae inside nuts (Mlanjeni et al. 2004; Smith et al. 2022). For example, in the early 2000's the nut borer infestations composition in the Levubu region (Limpopo province) dominance varied interchangeably between MNB and FCM within a season (Mlanjeni et al. 2004). Mlanjeni et al. (2002) reported that MNB contributed to between 63–76% of the species complex during certain months, while FCM made up 55–71% during other months. LM and CM were of minor importance in the latter studies and although CM made up 13% of the species complex during certain periods, the overall contribution to the species complex was low (5%) (Mlanjeni et al. 2002). Similar changes in the nut borer complex were reported in Malawi (La Croix and Thindwa 1986) where long-term monitoring (1980–1987) found that MNB increased in abundance over the years to become the dominant species, while FCM numbers decreased (La Croix 1990).

Establishing the dominance of different species through moth trap catches only, may provide inaccurate results. Based on pheromone trap catches alone, this study showed that the borer complex in the Barberton region was dominated by FCM moths (68%), followed by MNB (27%). FCM moth numbers peaked between six and nine weeks after the onset of flowering in both orchards. FCM moth numbers again started to increase towards a possible 2nd peak during the latter part of the season (week 5 onwards). Unfortunately, due to a cyclone, no data could be obtained to confirm a 2nd peak in FCM moth numbers. Based on the single small peak in MNB moth numbers late in the season (weeks 3–5) it could have been incorrectly concluded that

Table 4. Cross correlation function (CCF) values (*r*) indicating linear relationships and time offset (lag) between weekly moth numbers, egg numbers per nut, larval infestation levels and damage parameters. Variables listed in column headings were the lead variable in each correlation analyses. The lag of 0 represents no time offset, meaning both time series are compared in their original alignment.

Beaumont	Time lag (week)	Mean nr. of FCM moths per week	Time lag (week)	Mean nr. of MNB moths per week	Time lag (week)	Mean of total number of moths	Time lag (week)	Mean number of eggs per nut	Time lag (week)	Mean % nuts with damaged husks
Eggs numbers	5	0.525	4	0.769	5	0.549				
	6	0.720			6	0.652				
Mean nr. of larvae per nut	3	0.695	1	0.583	3	0.734	–2	0.585		
			4	0.607	4	0.569	–1	0.661		
							0	0.793		
Mean % nuts with damaged husks	6	0.532	3	0.522	3	0.514	–1	0.685		
			4	0.699	4	0.611	0	0.914		
					5	0.504	1	0.579		
Mean % nuts with damaged shells	2	0.548	0	0.516	2	0.590	–3	0.609	–3	0.589
	3	0.589	3	0.552	3	0.656	–2	0.634	–2	0.558
							–1	0.691	–1	0.725
									0	0.702
cv. 816	Time lag (week)	Mean nr. of FCM moths per week	Time lag (week)	Mean nr. of MNB moths per week	Time lag (week)	Mean total number of moths	Time lag (week)	Mean number of eggs per nut	Time lag (week)	Mean % nuts with damaged husks
Egg numbers	5	0.734	-1	0.506	4	0.542				
			0	0.759	5	0.731				
Mean nr. of larvae per nut	2	0.653	0	0.546	1	0.587	–3	0.592		
					2	0.731	–2	0.636		
					3	0.558	–1	0.724		
Mean % nuts with damaged husks	2	0.539	0	0.583	2	0.640	–2	0.666		
	3	0.535			3	0.640	–1	0.798		
	4	0.537			4	0.598	0	0.889		
							1	0.573		
Mean % nuts with damaged shells	2	0.541	0	0.580	2	0.642	–3	0.504	–2	0.616
	3	0.528			3	0.631	–2	0.674	–1	0.834
	4	0.530			4	0.588	–1	0.803	0	0.999
							0	0.880	1	0.811
							1	0.560	2	0.586

its pest status in the area was low. However, MNB made up the majority of larval numbers in the first five weeks of the season, even when moth abundance was low. These results are further supported by the small contribution (between 8–33%) of MNB larvae to the community composition from week 48 onwards.

The dynamic nature of pest populations within macadamia orchards necessitates continuous monitoring to tailor control strategies to specific pests that are present and dominant (Smith et al. 2022). These results are useful for evaluating the timing of chemical control. Growers in South Africa usually commence insecticide applications immediately after the flowering period (September/October), despite reports by Waite et al. (1999) and Schoeman (2009) that the nut borer complex is primarily pests of larger, older nuts. Knowledge of changing species dominance and infestation patterns are therefore critical for efficient control. These results highlight the importance of long term and regional monitoring to determine the species composition of the nut borer complex.

The proportion of each of the four species that were sampled varied depending on the monitoring method. Discrepancies were observed between the numbers of moths collected in pheromone traps and larvae retrieved from nuts for both FCM and MNB. While weekly FCM moth numbers over the first 10 weeks of trapping (week 36–46) were higher than those of MNB, higher numbers of MNB larvae were recorded inside nuts during the first four weeks (weeks 43–46) of sampling. Although no CM moths were found in pheromone traps for the duration of the study, larvae were recovered from inside nuts for most of the sampling period.

Pheromone traps may provide useful information on pest dynamics. For example, in Malawi the maximum incidence of larval damage was reported to occur approximately four weeks after the influx of moths into macadamia orchards (La Croix and Thindwa 1986). Our results confirm that data from pheromone traps are, however, not always a reliable source of information to reflect damage caused by larvae to macadamia nuts (Jones 1995). Using pheromone trap catches as the only source of information in pest control decision making may therefore not generate sufficiently accurate results for macadamia pest management. In contrast, sampling larvae within nuts may provide a more accurate representation of damage. One of the limitations of this monitoring method is that although correct identification of the larval specimen observed is crucial (Venette et al. 2003), it is often impossible to identify younger instars and challenging to identify older instars based on morphology alone. Although molecular markers can be used to identify species and overcome some of the limitations of morphological identification (Hebert et al. 2004; Timm et al. 2007; Smith et al. 2022), such methods are not yet available at a farm level and farmers are mostly guided by moth numbers in pheromone traps.

Monitoring the presence of tortricid eggs on fallen nuts can easily be done but pest management decisions should also be supported by data on egg load of nuts on trees. In this study, strong positive correlations between egg and larval numbers per nut were recorded, followed by similarly strong correlations between egg numbers per nut and the incidence of nuts with damaged husks and kernels. Positive correlations between egg numbers and damage have previously been reported but the

presence of eggs may not be a good indicator of damage (Jones 1995). For example, even when the mean number of eggs per nut was three or higher, fewer than 60% of the nuts contained larvae or exhibited larval damage symptoms. In the latter study the presence of eggs on nuts coincided with larval presence (or larval damage) in < 50.5% of the cases.

Although the relative seasonal abundance of larvae of these tortricid moths followed a similar pattern to that observed by Daiber (1976), Newton and Crause (1990) and Schwartz (1981) in peaches, litchi and citrus orchards respectively, our results show that it is important to integrate monitoring information (moth trap catches, egg and larval numbers) with aspects such as crop phenology before decisions regarding pest control are made. Cross correlation analyses indicated that weekly moth numbers provided some prediction of egg numbers that could be expected at a later interval. These correlations were, however, poor and only significant at much later time periods (4–5 weeks). For example, weekly FCM moth numbers correlated with egg numbers only 5–6 weeks later in the two different orchards. Weekly MNB moth numbers correlated strongly with egg numbers on cv. 816 nuts, even when there was no time lag between variables. Egg numbers per nut, on the other hand, correlated strongly with larval numbers and damage, and therefore provide valuable information on what to expect at subsequent time intervals. Monitoring of egg numbers on developing nuts was previously reported to provide general information on the time of pest infestation in macadamia. However, it was not considered to be a suitable predictor of damage (Jones 1994b), with the presence of eggs on nuts coinciding with larval presence (or larval damage) < 50.5% (Jones 1995). Our results, however, show that this might always be the case and that egg numbers per nut may be useful to predict larval numbers and subsequent damage.

In this study, very few eggs were detected on nuts with a diameter < 5 mm. Egg numbers only started to increase from week 49 onwards when nuts reached a mean diameter of 18 mm and peaked when nuts reached their maximum size (32 mm diameter; week 6). Egg numbers started to increase from week 50 onwards and peaked during week 5 (early February). The mean numbers of eggs per nut recorded in this study were similar to those reported by Schoeman et al. (2016) on another macadamia cultivar (Nelmak D) in the same region. In this study, however, higher numbers of eggs were recorded on Beaumont nuts throughout the season, supporting previous findings (Schoeman 2009).

The strong positive correlation between nut diameter and egg numbers per nut, and the near-exclusive occurrence of eggs only on nuts of > 18 mm implies that scouting and monitoring of infestation levels do not have to be implemented until nuts are at least 18 mm in diameter. *Thaumatotibia* females oviposit only to a very limited extent on macadamia and litchi fruit that are smaller than 15 mm (Jones 1995). Nuts < 20 mm in diameter are seldomly selected as oviposition sites, and nuts > 30 mm generally have a hardened shell, which protects the kernel from larval feeding (Jones 1994a). Nut size usually correlates strongly with nut age, with the preferred size being reached approximately nine weeks after full bloom. Joubert (1986) identified this as a very important period in crop phenology since the premature abortion period (November dump in South Africa, Julian weeks 45–48) occurs during the first nine weeks post anthesis. It is therefore suspected that moths do not lay eggs on nuts that are predestined to drop. Schoeman (2009) also noted that nuts may only become attractive to gravid female moths after the period of natural drop.

The rate of shell hardening influences the incidence of direct damage to kernels, which is reduced in cultivars whose shell hardens quicker. Studies in Hawaii showed that nuts are most susceptible to direct kernel damage when they are between 20–30 mm in diameter (Jones 1994b). When nut diameter is < 20 mm they are still developing and susceptible to direct kernel damage. Tunnelling by *Thaumatotibia* spp. larvae inside nuts causes direct kernel damage if it occurs before shell formation (Namba 1957; Jones and Caprio 1992).

The larval infestation patterns were similar for the two cultivars although the number of larvae per nut was generally higher for Beaumont for most of the sampling period. There was, however, a notable difference in the spatial distribution of larvae inside nuts. While the number of larvae that occurred within the husk tissue was higher for Beaumont nuts, the numbers within the shells (kernels) were similar at peak infestation levels, after which it was higher for cv. 816. This could probably be ascribed to cv. 816 having thinner shells and larger kernels than the Beaumont cultivar, leaving a longer window of opportunity for the larvae to bore through the shell as it hardens.

The incidence of damaged nuts was higher in cv. 816 than Beaumont throughout the season, which could suggest that kernels of Beaumont also remain largely undamaged. Overall, Beaumont is considered by the macadamia industry to suffer less damage than other cultivars and pest control strategies for this cultivar often differ from that of other cultivars. According to Schoeman (2009), Beaumont is less prone to nut borer damage than other cultivars (e.g., cv. 816). However, similar to what was observed in this study, Schoeman (2009) also reported nut damage in pure stands of Beaumont trees.

Egg parasitism was < 7% throughout most of the season and only increased to 13% during the last week of sampling. The negligible levels of egg parasitism (< 5%) during the first 13 weeks can most likely be ascribed to near weekly applications of insecticides that were made during the first six weeks (Julian weeks 41–47). Since egg parasitism beyond this period was low, our results show that egg parasitism probably does not contribute significantly to suppression of pest numbers in the orchards sampled in this study and confirmed those of various other studies. Mlanjeni et al. (2002) also suggested that natural enemies do not seem to suppress nut borer populations since the abundance of parasitic wasps was very low. Although La Croix and Thindwa (1986) reported that the egg parasitoid, *Trichogrammatoidea cryptophlebiae* Nagaraja (Hymenoptera: Trichogrammatidae) parasitises *Cryptophlebia* spp. in Malawi, they also found that pest levels were not suppressed sufficiently. Contrasting results have also been reported for parasitoids associated with species in the macadamia nut borer complex, although not on this crop. High parasitism levels (63%) of *Thaumatotibia* spp. by *Trichogrammatoidea* sp. were reported late in the season on litchi in South Africa (Newton and Crause 1990). Very high FCM egg parasitism levels (80–100%) by *T. cryptophlebiae* in Navel oranges in South Africa were observed if no pesticide applications were made (Moore and Hattingh 2012).

The shortcomings of this study were that only one season of monitoring was done, on two adjacent orchards. Furthermore, several insecticide applications were done during the season which must have influenced the observed moth flight patterns and larval infestation levels. Despite weekly insecticide applications over the first six weeks after commencement of flowering, larval numbers per nut increased over time, and it was not possible to establish potential differential effects of the insecticide applications on the different pest species.

CONCLUSIONS

This study showed that FCM and not MNB was the most abundant species in the nut borer complex in the study area. Although this study was only conducted over a single season at one locality, it highlights the importance of monitoring and the predictive value that such data may have. However, long term monitoring in different geographical regions, followed by modelling of data will be required before such data can be used to support the decision making processes that supports IPM.

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AUTHOR CONTRIBUTIONS

PS Schoeman conceived the study. PS Schoeman, M Enslin designed the study. M Enslin conducted all field work, data curation and basic statistical analyses. M Enslin, J van den Berg and H du Plessis wrote the manuscript. A Timm did all molecular analyses and reviewed the final version of the manuscript. H du Plessis did statistical analyses and contributed to writing and preparation of the manuscript for submission. J van den Berg prepared the manuscript for submission. All authors read and approved the final manuscript.

ORCIDS

M Enslin: https://orcid.org/0000-0003-0484-895X
PS Schoeman: https://orcid.org/0000-0002-8244-4814
AE Timm: https://orcid.org/0000-0002-5800-5512
MJ du Plessis: https://orcid.org/0000-0003-1163-1468
J van den Berg: https://orcid.org/0000-0002-6831-3180

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