*African Entomology* 2024, 32: e19103 (10 pages)
https://doi.org/10.17159/2254-8854/2024/a19103
**RESEARCH ARTICLE**

AFRICAN ENTOMOLOGY
ISSN (online) 2224-8854

# An analysis of the phase status of the red locust, *Nomadacris septemfasciata* (Serville) in KwaZulu-Natal, South Africa

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*Nomadacris septemfasciata* is a true locust species and exhibits phase polymorphism, which can potentially lead to outbreaks and plagues. In a recent outbreak of acridids in sugarcane in South Africa, swarms of *N. septemfasciata* were observed at increasing densities and displaying colouration indicative of the gregarious phase. The aim of this study was to determine the density-dependant phase polyphenism of populations of *N. septemfasciata* occurring in sugarcane study sites, based on traditional and geometric morphometric measurements, eye stripes and field observations of hopper colour specimens of *N. septemfasciata* were collected at three locations from May 2012 to May 2013. Three body characters (length measurements) were measured on 594 individuals and the number of dark vertical stripes on the eyes were counted. Lastly, 100 specimens from two locations (25 males and 25 females from each location) were analysed using geometric morphometrics, based on landmarks on wings. Significant differences in E/F ratios were found between locations and seasons, while wing shape also indicated a significant difference between locations (although small) and wing size (centroid size) showed no significant differences. There was a highly significant difference between wing shape of males and females, and the more gregarious males also exhibited higher E/F ratios in many instances. Eye stripes did not appear to be a reliable character and seemed to contradict the E/F ratio values. To our knowledge, this is the first report of using geometric morphometrics, traditional morphometrics and the number of eye stripes to assess phase polyphenism in adult locusts.

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**DATES**
**Received:** 10 July 2024
**Accepted:** 17 September 2024

**KEYWORDS**
**Orthoptera**
**morphometrics**
**E/F ratios**
**pest management**
**sugarcane**

## INTRODUCTION

*Nomadacris septemfasciata* (Serville) (Orthoptera: Acrididae) is a true locust species (Lecoq et al. 2011a) and consequently exhibits density-dependent phase polyphenism (or phase polymorphism), defined as the ability to form marching hopper bands and/or flying swarms which can potentially lead to outbreaks and plagues (Lecoq et al. 2011a). This form of phenotypic plasticity is in response to changes in local population density and affects the expression of numerous behavioural, physiological and morphological traits (Loher 1990; Simpson and Sword 2006; Sword et al. 2010). Phase polyphenism is limited by two extreme phenotypes, namely, gregaria (swarming, gregarious form) and solitaria (sedentary, isolated form). However, polyphenism occurs on a continuous scale and individuals can occur in an intermediate or transiens phase and are then described by the terms *congregans* or *dissocians*, depending on the direction of the current phase change (Albrecht 1956; Simpson et al. 2006; Sword et al. 2010; Lecoq et al. 2011a). Behavioural change is the most labile of responses to crowded conditions and is mediated by direct physical contact between individuals (Simpson and Sword 2006). These promiscuous encounters provide positive feedback for continued local crowding and subsequent change in behaviour, from avoidance to active aggregation, that can lead to other phenotypic changes such as changes in colouration and morphology, which develop more slowly (Sword et al. 2010). The irregular fluctuations between remission and upsurge periods requires knowledge about the gregarisation process and understanding this process can allow for early detection and prediction of the severity of the locust outbreak (Lecoq et al. 2011a).

A comprehensive, historical review of four species of plague locust, including *N. semptemfasciata*, in southern Africa is provided by Price (2023). This review details three major historical outbreaks, the first documented in 1843 around Cape Town of suspected *N. semptemfasciata*, with later outbreaks in Zululand from 1847 to 1853. The second plague cycle of *N. semptemfasciata* occurred from 1888 to 1907, moving in from Mozambique and Botswana, while the third invasion took place from 1927 to 1945. This invasion led to the northern Natal coastlands becoming the second most important breeding region for new swarms (Price 2023). Further upsurges and sporadic invasions occurred in the 70s, 80s and 90s (Price 2023), with a *N. semptemfasciata* swarm occurring in Swaziland across 90 ha of sugar-cane fields, necessitating aerial insecticide applications (Carnegie 1982). In a recent outbreak of acridids in sugarcane in Empangeni (KwaZulu-Natal, South Africa), incipient swarms of *N. septemfasciata*, rather than the more commonly found individual hoppers and/or adults, were observed at increasing densities. Hopper density and colouration indicated that these populations showed gregarious tendencies, possibly indicating a shift from solitarious individuals to gregarious individuals (Bam 2014). These populations provided the material for this case study on quantifying the phase status of *N. septemfasciata,* as an aid to the prediction of potentially damaging populations of this species occurring.

Three different techniques exist to determine the phase status of *N. septemfasciata*. The first technique uses hopper body colour as a phase determinant. The gregarisation threshold for hoppers is estimated to be 100 000 hoppers/ha, after which individuals start to behave in a gregarious manner and change from a general green body colour to a combination of orange, yellow and black (Faure 1935; Burnett 1951). From initial observations, individuals in the study area were either in the transiens or gregarious phase and very few hoppers matched the description of a true solitarious individual (Figure 1). For adults the phase transformation threshold is estimated at 5000 individuals/ha (Lecoq et al. 2011a). The second technique uses morphological measurements of the adult's legs and wings. Numerous studies have used traditional morphometric ratios to determine phase status, such as in Burnett (1951), Rainey et al. (1957) and Franc et al. (2005). In these studies, the ratio of elytron length (E) to hind femur length (F) was compared, resulting in an E/F ratio which can be compared to other studies. An E/F ratio of approximately 2.0 marks the limit between the two forms (i.e., an E/F value above 2.0 generally means a population is in a gregarious state) (Franc et al. 2005). In morphological terms, the longer the wings and shorter the hind legs (proportionately) the greater the chance that the individual is gregarious and therefore able to migrate farther. The third technique uses adult eye stripes as an indication of phase change. According to Burnett (1951a) adults of the phase solitaria should exhibit eight eye stripes while adults of the phase gregaria should exhibit seven eye stripes.

The use of geometric morphometrics in studying locust species is limited to the investigation of adult male genitalia (Song and Wenzel 2008) and it has not been used to study phase polyphenism. There is potential, however, to use geometric morphometrics as a method of analysing wing shape variation in relation to phase polyphenism. Geometric morphometrics was developed as an alternative way of quantifying and analysing morphological shape variation, using landmark-based data in a two- or three-dimensional coordinate system (Adams et al. 2004).

The aim of this study was to determine the density-dependant phase polyphenism of populations of *N. septemfasciata* occurring in sugarcane study sites, based on traditional and geometric morphometric measurements, eye stripes and field observations of hopper colour. This will provide information determining the potential of these populations forming swarms and outbreaks.

## MATERIALS AND METHODS

### Traditional morphometric measurements

For traditional morphometrics, *N. septemfasciata* specimens were collected at three locations, Jengro (28°37′30.84″ S, 32°00′52.68″ E), Kelly Farm (28°41′29.75″ S, 31°54′26.92″ E) and GSA farms (28°40′54.94″ S, 31°54′51.98″ E) in the Empangeni region of KwaZulu-Natal, South Africa from May 2012 to May 2013. Three body characters were measured on 594 individuals using a digital Vernier caliper (Tolsen 150 mm, Marshal Tools, Durban, South Africa) to the nearest 0.05 mm. Body length, from frons to the end of the forewings when folded over the abdomen (LTOT), length of left forewing (elytra) (E) and length of right hind femur (F) were measured. These characters are ideal for morphometric measurements as they do not change after the insect dies or is dried (Bazelet 2011). Measurements were made according to the method as stipulated at the 4th International Locust Conference in Cairo, Egypt (Anonymous 1936).

**Table 1.** Comparison of the E/F ratios of *Nomadacris septemfasciata* from various studies in Africa and Madagascar. In all countries where the E/F ratio exceeded 2, gregarious populations were reported by the referenced authors.

| Location | Sex | E\F Ratio | Reference |
|---|---|---|---|
| D.R. Congo | M | 2.02 | Bredo (1938) |
| | F | 2.14 | |
| Zimbabwe | M | 2.11 | Michelmore and Allan (1934) |
| | F | 2.11 | |
| Chad | M | 1.85 | Tetefort and Wintrebert (1967) |
| | F | 1.82 | |
| Madagascar | M | 1.88 | Tetefort and Wintrebert (1967) |
| | F | 1.84 | |
| Tanzania | M | 1.84 | Burnett (1951) |
| | F | 1.82 | |
| Madagascar | M | 2.06 | Franc et al. (2005) |
| | F | 2.03 | |
| Empangeni | M | 2.02 | Present study |
| | F | 1.99 | |

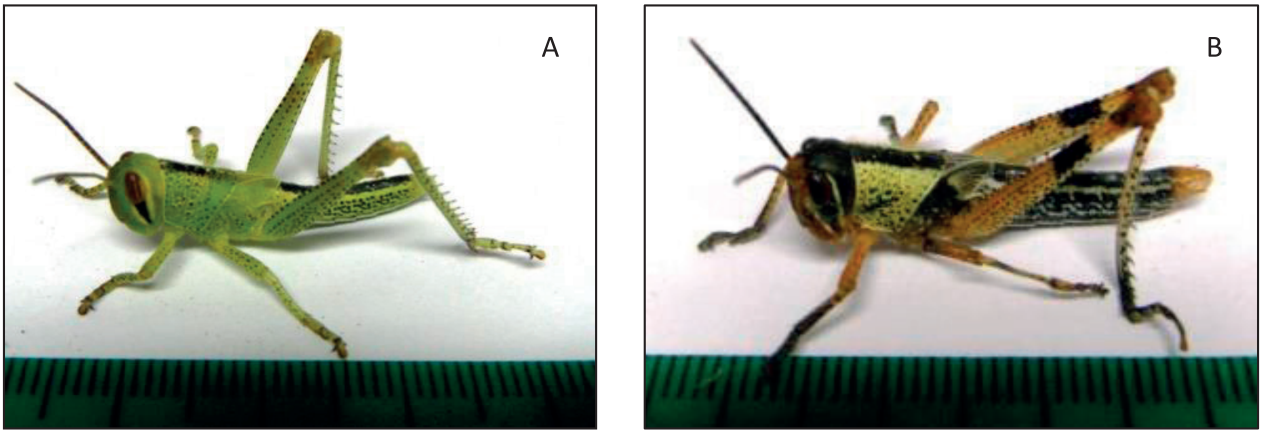

**Figure 1.** An example of a solitarious (A) and gregarious (B) hopper of *Nomadacris septemfasciata* found in Empangeni sugarcane.

Specimens were sorted according to gender using the description of the reproductive organs by Faure (1935). A summary of morphometric measurements from literature is given in Table 1.

### Eye stripes

Individuals collected for morphometric measurements were also observed under a dissecting microscope (Zeiss; 2.5× magnification) to count the dark vertical stripes present on the eye. Eye stripes of the left eye were counted wherever possible and recorded as seven or eight eye stripes (Figure 2). The nymphal instar was determined according to Lecoq et al. (2011b), and was based on overall size, size and orientation of the wing pads, and the number of eye stripes, with seven stripes indicating the gregarious phase (nymphs undergoing six instars) and eight stripes indicating the solitarious phase (nymphs undergoing 7 instars).

### Geometric morphometric measurements

For geometric morphometrics, 100 specimens from two locations (25 males and 25 females from each location) were collected within 1 week of each other in May 2013. The two locations were Jengro farm (28°37′30.84″ S, 32°00′52.68″ E) and Kelly Farm (28°41′29.75″ S, 31°54′26.92″ E). These two farms were selected because they were a considerable distance apart (12.8 km), reducing the chance of immigration and emigration between the two populations. Left and right forewings of the 100 specimens were removed at the base using fine scissors. Individual wings were mounted between two standard microscope slides (25.4 × 76.2 mm, 1.0–1.2 mm thick), which were taped together and labelled according to replicate number, locality, gender and side (left or right wing). Images were taken of each wing between the slides (to account for imaging error), using a tripod mounted Canon 50D, with 100 mm macro lens (f2.8L), positioned inside a photographic light box (FalconEyes® Model #: FLB 416AB). The tps utility programmes (Rohlf 2008) were used to prepare files for data analysis (Stonybrook morphometrics). To generate files in the correct format, tpsUtil 1.52 was used. From the individual images, nine common landmarks (Figure 3) were selected and positioned on specific vein intersections or terminations of the wing using tpsDIG 2.16. Vein intersections were selected based on prominence and to obtain the best coverage over the entire wing. Lastly, tpsRelw 1.11 was used to generate a consensus file of x–y coordinates for each wing.

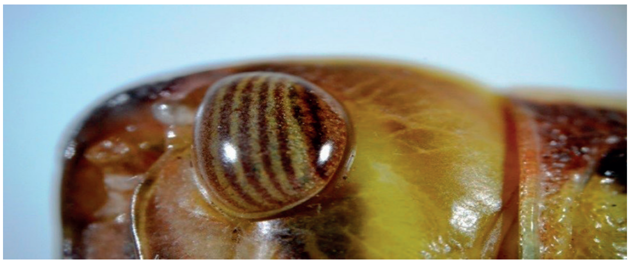

**Figure 2.** Dark vertical eye stripes present in adult *Nomadacris septemfasciata* eyes which are used to determine the number of instars an individual passed through and therefore the phase status of the specimen.

### Data analysis

For traditional morphometrics, analyses were performed using Genstat 15.0 (VSN International Ltd, UK). Data were tested for normality of frequency distribution using the Shapiro-Wilks test. The data were found to be homoscedastic. Univariate General Linear Model (GLM) analysis of variance (ANOVA) was used to test the interactions between populations in terms of location and time. Where the interactions were found to be significant, Tukey's post-hoc test was used to separate means.

A discriminant function analysis (DFA) was conducted to determine the major differences between groups (i.e. phases: solitarious, transiens and gregarious) relative to the variation within these groups (Fisher 1936). The E/F values were divided into three groups based on the criteria from Rainey et al. (1957) as follows: solitarious: 1.8–1.87; transiens: 1.88–2.05; and gregarious: 2.06–2.15. For the analysis, the grouping variable selected was phase, while the independent variables were the morphometric measurements (LTOT, E, F and E/F) of each specimen, with a stepwise analysis selected. The analysis was performed in Statistica version 14.0.0.15 (StatSoft Inc., Tulsa, USA).

For geometric morphometric analysis, MorphoJ version 1.05c (Klingenberg 2011) was used. From the *x–y* coordinates, shape information was extracted with a full procrustes fit, aligned by principal axes, which removes information for size, position and orientation, leaving only centroid size and shape information for each specimen (Rohlf and Slice 1990). To ensure that the potential error, as a result of the imaging and digitising processes, was within acceptable limits, a Procrustes ANOVA {$2k - 4$, where $k$ = number of landmarks in two dimensions (*x–y* coordinates) minus four degrees of freedom (two are lost during translation for position, one for scaling to a standard size and one for rotating to a standard position) (Klingenberg and McIntyre 1998)}, was performed on a subset (40 specimens) of the complete data in a separate analysis. For this subset, each specimen was imaged twice (to account for imaging error) and then each image copied and digitised twice (to account for digitising error).

On the total dataset, a new procrustes fit was performed, again aligned by principal axes. This was followed by a discriminant function analysis (DFA), to determine whether group differences existed between the populations at Jengro and Kelly (solitarious and gregarious, respectively). In MorphoJ, Fisher's classification rule is used for the DFA, which sets the cut-off point at zero (Fisher 1936). Left and right wings were averaged to exclude asymmetry. Differences of shape caused by the two locations and gender were determined using a Canonical Variate Analysis (CVA) with 1000 permutations. Data points for log centroid size were exported from MorphoJ and analysed in Statistica version 14.0.0.15 (StatSoft Inc., Tulsa, USA) using the non-parametric Kruskal-Wallis ANOVA, as data were not normally distributed.

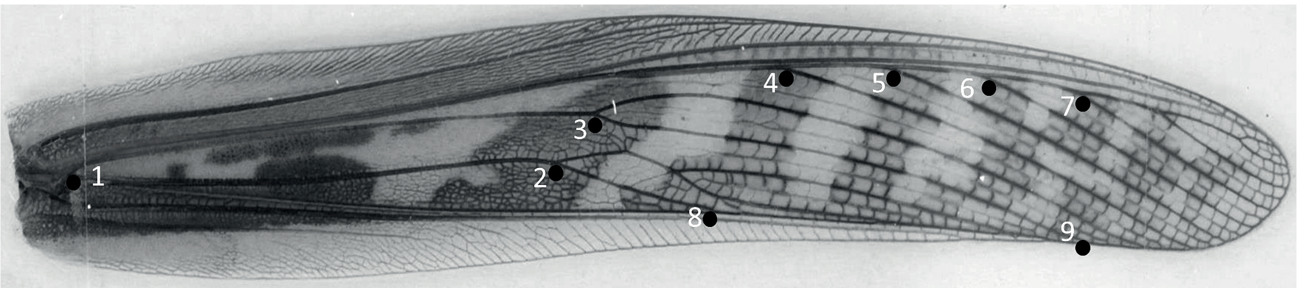

**Figure 3.** Nine landmarks used in geometric morphometric studies on the forewing of adult *Nomadacris septemfasciata.*

## RESULTS

### Traditional morphometric measurements

Table 2 displays morphometric measurements and associated sample variance (the average of the squared differences from the mean) of the different populations separated by location and year. Females were larger (79.4 to 79.9 mm) than males (68.7 to 70.1 mm). Kelly and GSA harboured more gregarious populations, as indicated by their E/F ratio's being greater than 2, than Jengro. Furthermore, at the former 2 farms, in the summed ratios between the two years, males had a higher E/F ratio compared to females. The mean E/F value (males and females combined) for GSA was 2.024 and for Kelly farm it was 2.0165. The mean E/F value of the Jengro population was 1.9851. The E/F ratio varied significantly according to site ($F_{(2,\ 513)} = 17.77$; $p < 0.001$) and year ($F_{(1,\ 513)} = 23.84$; $p < 0.001$) (Figure 4). Observations indicated that each female lays three egg packets on average with each containing between 20 and 100 eggs, which explains why populations can increase so markedly. Egg laying was observed to take place between October and December of each year.

### Discriminant function analysis (DFA)

The following E/F values, as found in Rainey et al. (1957), were used to delimit specimens into their respective categories: Solitaria: 1.8–1.87, Transiens: 1.88–2.05 and Gregarious: 2.06–2.15 for the DFA. The stepwise-forward analysis was completed in one step and removed LTOT, E and F as variables (Table 3). Overall, the discrimination of E/F was highly significant (Wilks' lambda = 1.0000; $F_{(2,\ 478)} = 302.85$; $p < 0.0000$). The classification functions are given in Table 4. With these functions, the transiens and solitary phases were classified correctly in 100% of cases, while the gregarious phase was classified correctly in 92% of cases. Of the total specimens measured, 359 were of the transiens phase, which was over-predicted by 2.7%, 119 were of

**Table 2.** Morphometric measurements of *Nomadacris septemfasciata* samples collected from the study sites in the Empangeni region showing the mean total length, elytron length, femur length and the elytron/femur (E/F) ratio as an indication of the phase status of each population.

| | Total Length (mm) | | | | Elytron length (mm) | | | | Femur length (mm) | | | | E/F Ratio | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♂ | | ♀ | | ♂ | | ♀ | | ♂ | | ♀ | | ♂ | | ♀ | |
| | Mean | Var. | Mean | Var. | Mean | Var. | Mean | Var. | Mean | Var. | Mean | Var. | Mean | Var. | Mean | Var. |
| Kelly (*n* = 136) | 70 | 7.56 | 79.7 | 4.29 | 57.6 | 2.5 | 66.1 | 3.43 | 28.3 | 0.55 | 33.1 | 1.22 | 2.0318 | 0.0028 | 1.9969 | 0.0028 |
| GSA (*n* = 82) | 69.8 | 3.14 | 79.4 | 5.29 | 57.6 | 2.5 | 66 | 3.16 | 28.3 | 0.77 | 32.8 | 1.08 | 2.0341 | 0.0026 | 2.0104 | 0.0029 |
| Jengro (*n* = 108) | 68.7 | 2.68 | 79.5 | 6.22 | 56.5 | 2 | 65.8 | 4.31 | 28.3 | 0.78 | 33.5 | 1.6 | 1.999 | 0.0022 | 1.9656 | 0.0016 |
| 2012 (*n* = 216) | 70.1 | 3.66 | 79.9 | 4.81 | 57.3 | 2.8 | 66.1 | 3.42 | 28.5 | 0.63 | 33.3 | 1.37 | 2.007 | 0.003 | 1.9875 | 0.0032 |
| 2013 (*n* = 378) | 69.4 | 2.92 | 79.5 | 4.69 | 57.3 | 2.4 | 66 | 3.4 | 28.3 | 0.63 | 33 | 1.3 | 2.0265 | 0.0026 | 1.9998 | 0.0027 |

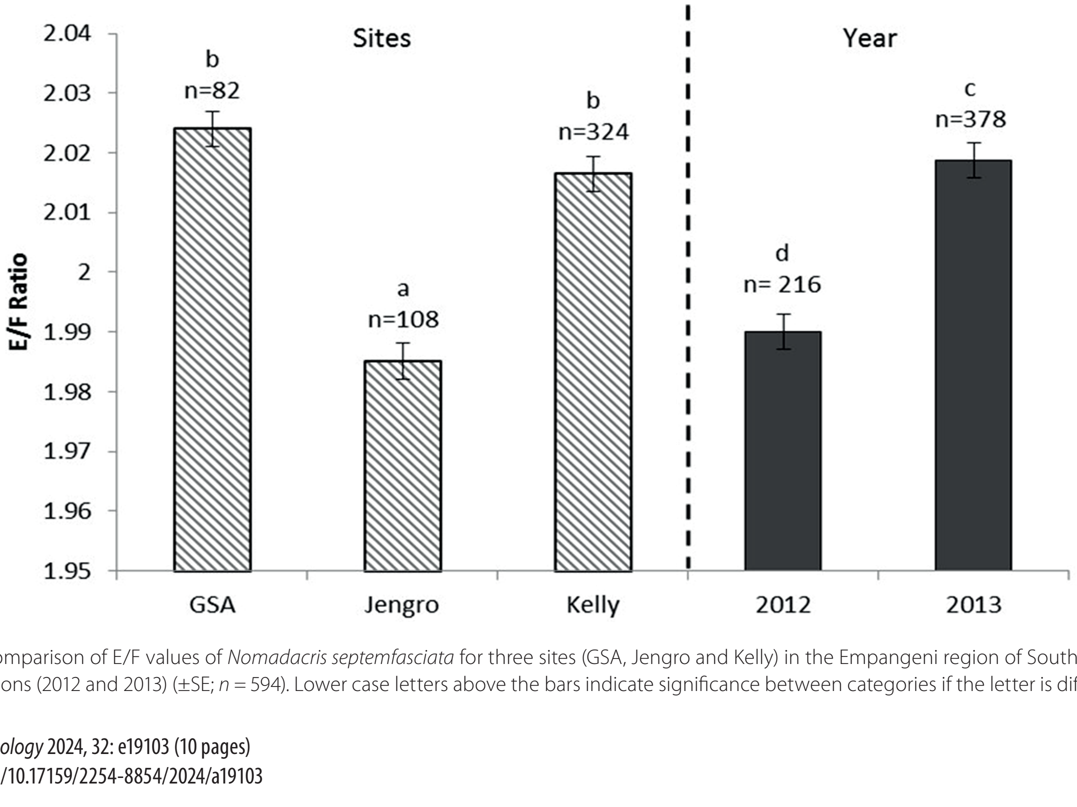

**Figure 4.** Comparison of E/F values of *Nomadacris septemfasciata* for three sites (GSA, Jengro and Kelly) in the Empangeni region of South Africa over two generations (2012 and 2013) (±SE; *n* = 594). Lower case letters above the bars indicate significance between categories if the letter is different.

the gregarious phase, which was under-predicted by 8.4% and 3 were of the solitarious phase, which was correctly predicted, based on E/F ratios alone. Means of E/F ratios of observed values for each phase were 1.85 (solitarious), 1.99 (transiens) and 2.08 (gregarious). The DFA confirms that the E/F ratio is the best trait to use in separating specimens according to phase in these grasshoppers.

## Eye stripes

According to this method, most specimens observed were in the gregarious phase (Table 5), with 90.2% of specimens having seven eye stripes (meaning they underwent six nymphal instars) while 8.5% had eight eye stripes (meaning they underwent seven nymphal instars).

The results further suggest that Kelly farm held the most gregarious population and Jengro had the least gregarious population (Table 5), which compliment morphometric data from individuals collected from the two farms (Figure 4). In 2012, no individuals were found with eight eye stripes, while in 2013 about 10% had eight eye stripes. This result conflicts with the morphometric E/F data which indicated that the 2013 generation was more gregarious than the 2012 generation. However, it should be noted that roughly four times more specimens were measured in 2013 compared to 2012.

Table 6 displays the number of nymphal instars passed through by *N. septemfasciata* under laboratory conditions (± 27 $^{0}$C, 60% RH). Eggs collected from the field hatched in the laboratory on 20 November 2012. Hoppers and eventually adults were kept in cages at low densities (three individuals per cage). The progeny of these eggs would inherit the phase which their parents experienced because the effect of parental crowding is passed on through a chemical agent introduced into the foam surrounding the eggs (Simpson and Sword 2006). This laboratory data confirmed that *N. septemfasciata* in Empangeni can exhibit the "six larval instar" phase type typical of swarming *N. septemfasciata* (Burnett et al. 1951a; Albrecht 1957).

## Geometric morphometrics

The Procrustes ANOVA indicated that the mean square (MS) and *F* values for imaging error and digitising error were much smaller than the individual*side interaction, which indicates that the variation present in the data because of imaging and digitising is negligible (Table 7). No significant difference existed between left and right wings (side) therefore these data were combined for all further analyses.

For the CVA, canonical variate 1 (CV1) quantified the differences occurring due to gender, which was most of the variance (82.7%), while CV2 accounted for 12.5% of the variation,

**Table 3.** Discriminant Function Analysis of variables (morphometric measurements of *Nomadacris septemfasciata*) not used in the model.

| Variable | Wilks' lambda | Partial Wilks' lambda | $F_{(2, 477)}$ | *p*-value | Tolerance |
|---|---|---|---|---|---|
| Total length (LTOT) | 0.441082 | 0.999998 | 0.000569 | 0.999432 | 0.993073 |
| Elytron length (E) | 0.440935 | 0.999664 | 0.080275 | 0.922875 | 0.993958 |
| Femur length (F) | 0.440808 | 0.999377 | 0.148661 | 0.861901 | 0.905586 |

**Table 4.** Classification functions for the character E/F ratio required to classify *Nomadacris septemfasciata* into solitary, transiens or gregarious phases.

| Measurement | Solitary | Transiens | Gregarious |
|---|---|---|---|
| E/F ratio | 1382.9 | 1488.81 | 1556.37 |
| Constant | –1284.13 | –1482.76 | –1621.45 |

**Table 5.** Results of adult eye stripe counts per locality and over two years for *Nomadacris septemfasciata* in the Empangeni region of South Africa. These results illustrate the spatial and temporal variation in number of instars, indicated by the number of eye stripes undergone between different populations.

| Site/Year | Sex | 8 eye stripes (%) | 7 eye stripes (%) |
|---|---|---|---|
| Kelly (*n* = 196) | ♂ (*n* = 113) | 3.5 | 98.2 |
| | ♀ (*n* = 83) | 2.4 | 95.2 |
| GSA (*n* = 18) | ♂ (*n* = 8) | 12.5 | 87.5 |
| | ♀ (*n* = 10) | 10.0 | 90.0 |
| Jengro (*n* = 109) | ♂ (*n* = 58) | 19.0 | 81.0 |
| | ♀ (*n* = 51) | 17.6 | 70.6 |
| 2012 (*n* = 67) | ♂ (*n* = 34) | 0.0 | 100.0 |
| | ♀ (*n* = 33) | 0.0 | 100.0 |
| 2013 (*n* = 257) | ♂ (*n* = 155) | 8.4 | 91.6 |
| | ♀ (*n* = 102) | 11.8 | 88.2 |
| Mean (%) | | 8.5 | 90.2 |

**Table 6.** Laboratory rearing of *Nomadacris septemfasciata* from field collected eggs indicating the number of instars undergone by one individual from November 2012 until reaching the adult stage.

| | Instar | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Hatched | 1 | 2 | 3 | 4 | 5 | 6 | 7(Adult) |
| Date | 20-Nov | 27-Nov | 05-Dec | 13-Dec | 24-Dec | 15-Jan | 26-Jan | 08-Feb |
| Duration (Days) | | 7 | 3 | 8 | 11 | 22 | 16 | 13 |

which represented location. The shape changes associated with the CVs represent specific shifts of landmarks in various regions of the wing (Figure 5). The wireframe graph of PC1 (gender) indicates that the shape change resulted in a shorter, broader wing, while for PC2 (location) the change resulted in a slightly narrower, shorter wing, relative to the mean shape (Figure 5). The $p$-values from permutation tests (1000 rounds) for the Mahalanobis distances (within group variation) and Procrustes distances (between group variation) are shown in Table 8.

Differences between males and females of each location were highly significant (Table 8), resulting mostly from the gender differences, as observed also by the CVA (Figure 5). Location differences were less pronounced, but still significant, except for the between group variation between Jengro and Kelly males (Table 8).

Differences between populations according to location were also significant according to the DFA, however, separation of groups was not very precise, although significant at the 5% level (Table 9). The separation of samples of the original scores seems to be somewhat inflated compared to the cross-validation scores. It was found that 70% of transiens individuals were correctly classified, whereas 68% of gregarious individuals were correctly classified. The eigenvalue was 0.261, accounting for much less variation than the discriminant function using gender as classification variable (Table 9).

According to the results of the DFA, a significant difference existed between wing shape of males and females, as also indicated by group allocation (Table 10). The discriminant analysis illustrates very clearly the good separation of groups in terms of gender and cross-validation scores were more like the original scores than the case with separation according to location. The eigenvalue was 1.634, accounting for a relatively large part of the variance.

No significant differences in log centroid size were found between either gender ($H_{(1, 200)} = 0.066$; $p = 0.796$) nor location (Jengro and Kelly farms) ($H_{(1,200)} = 3.129$; $p = 0.0769$). As centroid size is a measure of size in morphometrics (square root of the sum of squared distances of all landmarks from their centroid), this can be used to approximate the wing size of *N. septemfasciata*.

## DISCUSSION

### Hopper colouration

The majority of hoppers observed exhibited colours matching the description of gregarious or transiens individuals. A semi quantitative method, as used by Lecoq et al. (2011a), was used as

**Table 7.** Procrustes ANOVA for shape effects quantifying measurement error at two levels for *Nomadacris septemfasciata* forewings.

| Effect | SS | MS | df | F | p |
|---|---|---|---|---|---|
| Side | 0.00029446 | 0.0000210330 | 14 | 0.0002 | 0.9473 |
| Individual*Side | 0.03409083 | 0.0002705621 | 126 | 28.87 | <0.0001 |
| Imaging error | 0.00262392 | 0.0000093711 | 280 | 2.43 | <0.0001 |
| Digitizing error | 0.00216062 | 0.0000038582 | 560 | | |

**Table 8.** Mahalanobis and (Procrustes) distances for location and gender for *Nomadacris septemfasciata* wings. Significant differences are indicated by ** ($p < 0.0001$) and * ($p < 0.05$).

| | Jengro (F) | Jengro (M) | Kelly (F) |
|---|---|---|---|
| Jengro (M) | 3.03** (0.03**) | | |
| Kelly (F) | 1.24* (0.13*) | 2.46** (0.02**) | |
| Kelly (M) | 3.10** (0.34**) | 1.37** (0.1) | 2.36** (0.03**) |

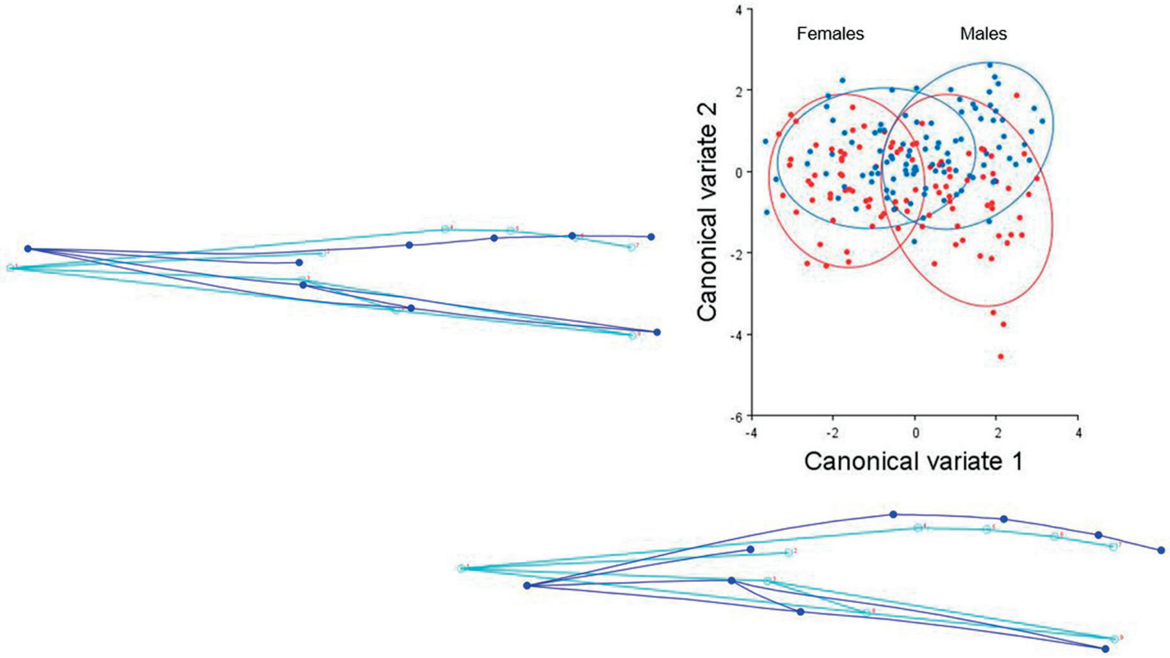

**Figure 5.** Canonical variate analysis quantifying the shape differences for *Nomadacris septemfasciata* collected from Jengro (red) and Kelly (blue). Equal frequency ellipses were used with a 0.9 probability. Wireframe graphs show changes in wing shape associated with gender (CV1) and the two locations (CV2), exaggerated by a factor of 20. The light blue outline represents the mean shape of the sample, while the dark blue outline represents the shape change of interest.

a guideline in this study when relating hopper colour to phase status. Observations indicated that highly melanised orange/yellow hoppers with the black spot on the hind femur (Figure 1) were seen very often, indicating that the transiens/gregarious phase hoppers were, by far, in the majority. Gregarisation of first-generation hoppers seems to have taken place quickly, which led to transient/gregarious traits, typical for this species (Lecoq et al. 2011a).

### Traditional Morphometrics

The close similarity in the mean E/F value between GSA and Kelly farms is most likely because they are situated within 2 km of each other. The environmental conditions would be similar and the possibility of individuals migrating from one farm to another is large. It is well known that *N. septemfasciata* adults are highly mobile (Faure 1935). The E/F ratio for GSA and Kelly were significantly higher compared to Jengro indicating that *N. septemfasciata* populations at GSA and Kelly were more gregarious than at Jengro. E/F ratio was higher in 2013 compared to 2012 indicating that overall, the F1 generation were more gregarious than the parent populations.

Rainey et al. (1957) and Franc et al. (2005) both found that E/F ratios are higher in males than in females, as is the case in our study. Rainey et al. (1957) also found that low variances in E/F ratio are typical of either of the extreme phases (gregarious or solitarious). Regarding this study, variances were equal or lower compared to the findings of Rainey et al. (1957), which strengthens the argument for gregariousness in the Empangeni *N. septemfasciata* populations. It must be mentioned though that present measurement techniques may be more accurate than in 1957, which may have contributed to the low observed variances. Burnett (1951b), in the Rukwa valley, Tanzania, compared populations of *N. septemfasciata* over two generations and concluded that they were becoming more solitary due to the decreasing E/F ratio. By comparing the E/F ratio over two seasons (2012 vs. 2013) in Empangeni, it is evident that the 2013 generation of *N. septemfasciata* was becoming more gregarious than the previous generation, meaning they may exhibit a higher propensity for swarming and further outbreaks. According to the classification functions used by Rainey et al. (1957) most specimens measured in this study were in the transiens phase. The classification functions used can be considered conservative considering that Franc et al. (2005) used an E/F ratio of 2.0 to separate gregarious forms from solitarious forms, while in the present study a value of 1.87 was used as the limit between solitarious and transiens and 2.05 was the limit between transiens and gregarious. Generally, the E/F ratio if higher than 2, corresponds to reports of swarming *N. septemfasciata* (Table 11).

### Eye stripes

Eye stripe data indicates that most specimens observed were of the 'seven stripe gregarious type' as in Burnett (1951a). In 2013, more specimens were found with the extra eye stripe, typical of the solitarious individual compared to 2012, which therefore seem to contradict the E/F ratio results. This difference, however, was small. Current literature searches reveal that no studies have used eye stripes as an indicator of phase since the 1950's (Burnett 1951; Albrecht 1957) which may suggest that it is not a very reliable indicator of phase status. According to this literature, eye stripes are only indicative of the gregarious and solitary phase,

**Table 9.** Classification matrix from Discriminant Function Analysis comparing two *Nomadacris septemfasciata* populations by location with gender excluded as a variable.

| Discriminant Function Analysis | | | |
|---|---|---|---|
| Comparison: | Location | | |
| *T*-square: | 34.3183 | | |
| *p*-value: | 0.0179 | | |
| Discriminant function scores | | | |
| | Jengro (transiens) | Kelly (gregarious) | Total |
| Transiens | 35 | 15 | 50 |
| Gregarious | 16 | 34 | 50 |
| Cross-validation scores | | | |
| | Jengro (transiens) | Kelly (gregarious) | Total |
| Transiens | 27 | 23 | 50 |
| Gregarious | 23 | 27 | 50 |

**Table 10.** Classification matrix from Discriminant Function Analysis comparing two *Nomadacris septemfasciata* populations by gender with location excluded as a variable.

| Discriminant Function Analysis | | | |
|---|---|---|---|
| Comparison: | Gender | | |
| T-square | 180.4715 | | |
| *p*-value | <0.0001 | | |
| Discriminant function scores | | | |
| | Male | Female | Total |
| Male | 46 | 4 | 50 |
| Female | 5 | 45 | 50 |
| Cross-validation scores | | | |
| | Male | Female | Total |
| Male | 42 | 8 | 50 |
| Female | 9 | 41 | 50 |

the present E/F ratios indicate that most specimens measured are in the transiens phase, which results in this method being fairly limited in its ability to accurately determine the phase status of *N. septemfasciata*.

### Geometric morphometrics

There was a highly significant separation in wing shape between males and females according to the DFA and CVA, but not centroid size. This indicates that sexual dimorphism (in shape) is prominent in this species, supported also by the similar cross-validation scores to the original analysis. *Nomadacris septemfasciata* males tend to be more gregarious than females, often exhibiting higher E/F ratios than their female counterparts (Michelmore and Allan 1934; Bredo 1938; Burnett 1951; Rainey et al. 1957; Franc et al. 2005). This could possibly be the reason why males and females showed such a large disparity in wing shape. Very little research has been conducted on the use of geometric morphometrics in Orthoptera and even less on gender differences (see Klingenberg et al. 2010; Beasley et al. 2012) working on cricket and grasshopper wings, respectively). However, in stingless bees (Apidae: Meliponini), it is known that males and workers have different behaviours and flight activities during their lifespan which could lead to differentiation in the patterns of wing venation (Francoy et al. 2009). Similarly, Glanville fritillary butterfly's *Melitaea cinxia* Linneaus (Lepidoptera: Nymphalidae) dispersal ability and forewing shape is associated with the different life-history traits of the sexes (males may need to fly further than females), resulting in different selection pressures being enforced on wing shape in each of the sexes (Breuker et al. 2007).

Differences in wing shape when comparing individuals from Jengro and Kelly locations were investigated, with the predetermined assumption that any shape differences observed would be due to the different phase status of the populations at the Jengro and Kelly farms. A significant difference did exist (although small) between the two locations. Kelly harboured more gregarious populations while Jengro harboured a more solitarious population. The cross-validation results were very different from the original analysis, which indicates that the separation is not that clear, either due to the actual separation between gregarious and transiens phases not being that clear-cut between the farms, or due to sample size not being large enough (100 specimens). The results, however, clearly indicate that between Jengro and Kelly populations, a statistically significant difference in the E/F ratio (from traditional morphometrics) and wing shape (from geometric morphometrics) does exist. The potential for long distance dispersal in this species is high, given their highly mobile nature and therefore it could be presumed that an appreciable amount of dispersion occurs between these populations. The results, however, seem to indicate that these populations are quite separate in terms of immigration and emigration due to their significantly different E/F ratios, even though they are only separated by a few kilometres. It was observed that *N. septemfasciata* populations at all survey sites were quite sedentary, with minimal overall movement throughout the season, a phenomenon also noted by Rainey et al. (1957) who 'observed the often-static nature of populations' in the Rukwa valley, Tanzania. Lea (1935) also noted that in 1934, 'a large *N. septemfasciata* swarm originating from the north settled on a 3 000-acre sugar estate in Entumeni, Zululand, and spent at least six weeks confined to this area, which was in stark contrast to the mobility of swarms in uncultivated bush country further north. Therefore, it is proposed that the current behaviour of swarms and the geographical separation of these two populations are far enough to ensure that they develop in relative isolation to one another and therefore are likely to show differences in terms of their E/F ratios and wing shape. Population densities at Kelly farm were a lot higher than at Jengro farm (Bam 2014).

### Resource quality and distribution in relation to swarming and phase change

It is well known that favourable weather plays a key role in promoting crowding and subsequent population increases, swarming and plagues (Camuffo and Enzi 1991) in locusts. Habitat structure is also a critical factor which initially promotes behavioural gregarisation and ultimately leads to local crowding and population increases (Sword et al. 2010). A heterogeneous habitat with patchily distributed host plants tends to concentrate populations and this promotes crowding (Simpson and Sword 2006). Michelmore (1947) found that *N. septemfasciata* adults showed a marked preference for tall dense grass while hoppers preferred shorter grass, but upon being disturbed they immediately made for tall clumps of vegetation for shelter, which may act as concentrating factors. On individual field scales, sugarcane can be considered a homogenous habitat, as here it consists of one variety, all at a certain stage of development. However, on farm and/or regional scales, the sugarcane environment becomes heterogenous in terms of sugarcane age. On commercial sugarcane farms, not all the sugarcane is cut at any one time. Harvesting is scheduled throughout the yearly milling season, to optimise sucrose production from different varieties growing in different soils on the farms. This would provide taller sugarcane preferred by *N. septemfasciata* adults and hoppers seeking refuge, and areas of shorter younger sugarcane providing the more open habitat preferred by hoppers, as described by Michelmore (1947) and noted from own observations. Own observations further indicated that hopper bands moved through vegetation as dense bands and roosted as masses, which were observed in the mornings.

Features of a habitat influence the distribution of populations in terms of finding food and microclimate for basking and shelter (Sword et al. 2010). Duranton (1997) noted that agriculturally induced environmental modifications lead to better ecological conditions for *N. septemfasciata* and could result in more frequent gregarisation in the future, while clumping of resources such as food plants, roosting/basking sites or areas of favourable microclimate encourages solitarious locusts to come together and behaviourally gregarise (BouaÏchi et al. 1996). It has been observed in Empangeni on numerous occasions that sugarcane breaks (the roads intersecting blocks of sugarcane) seem to be acting as an attractant to individuals for basking purposes. *Nomadacris septemfasciata* swarms will typically descend from the sugarcane plants at dawn and sit on the road flanking the sun until the temperature has increased enough to allow them to fly. Similar behaviour was observed in the Rukwa valley by Rainey et al. (1957) in natural grasslands. The reason for this occurrence is presumably because sugarcane growth in fields is very dense and does not provide an optimal basking site and therefore, they move onto the road which often gives 100% exposure to the sun from early in the morning. Basking locusts were commonly found in the early morning on three sugarcane breaks at Jengro, Kelly and GSA farms, all roughly facing north-east, which received the sun the earliest as it rose in the east. Gregarisation potential depends critically on the fine scale distribution and quality of resources (Simpson et al. 2006), therefore it is possible that cane breaks are adding to the 'heterogeneous' aggregating factor which *N. septemfasciata* require within this environment to start to gregarise. Lea (1935) regards the sugarcane fields of Zululand 'as grassland habitats comparable in general facies with the long grass stands of the Rukwa valley.'

An empirical rule which has been repeatedly proven to be correct (see Golding 1934; Michelmore 1947) is that *N. septemfasciata* swarms are more active in short grasslands and bush compared to long grassland habitat. This possibly explains why *N. septemfasciata* populations in Empangeni seem to be quite sedentary and no significant migrations have been observed. We can thus assume that populations of this species in sugarcane fields are likely to remain confined to the areas where they are initially observed. The International Red Locust Control Service (1937) (presently the IRLCOCSA) considers that 'the movement of a swarm out of long grass and into surrounding short grass, very often precedes movement on a much larger scale, out of the general area. Opinions such as these should be noted, and incorporated into monitoring protocols in the Empangeni region, especially if larger areas than normal are harvested at a particular time, because of climatic factors such as drought, heavy wind (causing sugarcane lodging) or floods, and/or unplanned fires, thus providing suitable habitat for hopper aggregations. The relationship between hopper colour and hopper density is also very important as it indicates when a population may reach the gregarisation threshold and start to swarm, therefore this factor should also be incorporated into future survey protocols for this species.

### Harvesting regime and oviposition sites

Related to the above, sugarcane burning prior to harvesting is common in the Empangeni growing region, and this normally occurs from April through to late November/early December. Symmons and Carnegie (1959) found that *N. septemfasciata* significantly preferred areas of burnt grass over unburnt grass in terms of oviposition preference. Lea (1935) found that ground covered by an accumulation of trash was not favoured for oviposition. Faure (1935), Whellan (1968) and Lea (1935) all found that the *N. septemfasciata* females will lay eggs in practically any type of soil. Therefore, it is probable that burning is the critical factor in this region, especially if larger areas of sugarcane must be harvested because of unforeseen factors, providing exposed areas of soil, and thus ideal oviposition sites for *N. septemfasciata* females in sugarcane fields. The oviposition period of *N. septemfasciata* from October to December (Bam 2014) coincides with the peak harvesting (and thus burning) season in Empangeni, which exacerbates the problem. Although it seems that fire will not kill *N. septemfasciata* (Lea and Webb 1939), it may influence their distribution by breaking up swarms (Burnett 1951b) or possibly causing widely distributed populations to come together on unburnt sugarcane areas (personal observations). The possibility of both scenarios occurring is likely, given the vastly different situations on different farms in terms of harvesting scheduling and geography of the farm.

## CONCLUSION AND RECOMMENDATIONS

*Nomadacris septemfasciata* populations in the 2012–2013 seasons in Empangeni sugarcane exhibited characters closer to the gregarious phase in terms of morphometric data, eye stripes and hopper colour, although population densities and adult behaviour tended to indicate a lower degree of gregariousness. Nevertheless, the data indicating a high degree of gregariousness was based on quantitative measurements, and therefore should be regarded as more reliable than that given on the basis of an expert, but on a qualitative opinion (Lecoq et al. 2011a). This subjectivity can be problematic as populations can be miscategorised purely on the basis that they exhibit gregarious tendencies. It is thus important that quantitative data is captured, ensuring the validity of the observations made. This study provides a technique offering the relevant quantitative data collection and analysis for phase analysis – geometric morphometrics. This analysis can therefore combine both measurements and therefore provide more accurate recommendations. Flight ability studies would be beneficial to explain the potential effect that wing shape changes have on migration in both males and females.

Because environmental and physical factors which promote gregariousness and swarming are already present in Empangeni, as demonstrated by the study of Bam (2014), it is important that methodical population and phase status monitoring continues. This will ensure that population, and more importantly, phase changes and upsurges can be recognised as soon as possible, to allow for effective mitigating actions to be implemented in a timeous manner.

## ACKNOWLEDGEMENTS

Funding for the study was provided by the South African Sugarcane Research Institute (SASRI), Mount Edgecombe and Stellenbosch University. The Entomology staff of SASRI, especially Angela Walton, Denise Gillespie, Nelson Muthusamy and the rest of the Insect Rearing Unit. Mike Way is posthumously thanked for constructive project suggestions and specimen photography. Other staff of SASRI instrumental in the success of the project: Sanele Ntonbela for mounting many wings of grasshoppers; Graeme Leslie for insightful conversations on the project. Francois Bekker and Janina Von Deist from the Department of Conservation Ecology and Entomology at Stellenbosch University for imaging and digitising many grasshopper wings. Tom Fortmann for setting up and progressing the project. The managers and owners of GSA, Jengro and Kelly Farms.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the correspondence author upon reasonable request.

## CONTRIBUTOR ROLES

Adrian Bam: Data curation, formal analysis, investigation, writing – original draft.
Desmond Conlong: Conceptualisation, formal analysis, funding acquisition, methodology, project administration, resources, supervision, writing – review and editing.
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