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Effect of temperature on the oviposition, longevity and mating of codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae)

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The effect of temperature on the oviposition, longevity and mating of codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) was investigated. The preoviposition development time ranged from 2.54 days at 21 °C to 7.54 days at 15 °C. The lower threshold temperature for the preoviposition period was 11.4 °C with a thermal requirement of 22.8 degree-days. Moths did not mate and few eggs were laid at temperatures below 15 °C or above 27 °C. The mean adult longevity of summer moths, from pupae of larvae leaving fruit in December through to February, was 11.7 days when exposed to fluctuating temperatures (range 14.4–37.5 °C) and 22.5 days at constant temperatures of 15, 17, 19 and 21 ± 1 °C. At constant and fluctuating temperatures longevity decreased with increasing temperature; thus spring moths lived longer than summer moths. Significantly more eggs were laid by summer moths at constant, compared to fluctuating temperatures. At fluctuating temperatures the mean number of eggs per female was 92.6 for spring moths and 121.2 for summer moths.

Key words: *Cydia pomonella*, codling moth, oviposition, longevity, mating, temperature, biology, behaviour.

INTRODUCTION

The codling moth, *Cydia pomonella* (Linnaeus) (Lepidoptera: Tortricidae), is a worldwide pest of apple and pear. Since its introduction around 1885 (Lounsbury 1898; Giliomee & Riedl 1998) codling moth has become a key pest of these fruits in South Africa (Pettey 1925; Pettey & Joubert 1926; Myburgh 1963; Myburgh *et al.* 1973; Blomefield 1989). Under South African climatic conditions there are usually three moth flights between September and April. The first, referred to as the spring flight, occurs from September to end-November. The two flights that occur between December and April are referred to as the summer flights. From each of the three larval generations a progressively greater proportion of the mature fifth instar larvae enter diapause, in response to decreasing seasonal day length, until all the third generation larvae enter diapause. The development of the diapausing larvae is completed the following spring when the larvae transform to pupae from which the spring moths emerge. The summer moths arise from the larvae that do not enter diapause.

Although relative humidity (Shelford 1927), food quality (Hathaway *et al.* 1971), water (Howell

1991), and photoperiod (Riedl & Croft 1978) have been shown to affect the development of codling moth, temperature is considered to be the most important environmental factor (Glenn 1922; Headlee 1930, 1932; Webster 1932; Wilson & Barnett 1983; Higley *et al.* 1986; Kneifl 1992). The relationship between temperature and the development of codling moth was first investigated by Glenn (1922) who proposed the use of day-degrees for the timing of control applications against this insect. Temperature influences longevity of adult moths, which decreases with increasing temperature (Hagley 1972; Howell 1991). The oviposition period of codling moth was reported to be relatively short, particularly at higher temperatures, with 90 % of the eggs being oviposited by the fifth day following mating (Howell 1981). Despite a decrease in longevity with increasing temperature the fecundity of summer moths tended to be higher than that of the spring moths (Hall 1929; Isely 1938; Hagley 1972; Deseö 1973). List & Yetter (1927) obtained equal numbers of oocytes in the ovaries of spring and summer broods and considered the lower fecundity of spring moths to be due to the lower temperatures in spring. However, studies undertaken in Australia showed no significant difference in longevity and fecundity

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between spring and summer moths (Geier 1963). In South Africa codling moths are reported to live from 10 days to four weeks during which a female moth lays an average of 40–60 eggs (Petty 1925; Myburgh 1963; Myburgh *et al.* 1973). Despite the relatively low number of eggs produced by South African female moths compared to other studies (Selkregg & Siegler 1928; Deseö 1973; Ferro *et al.* 1975; Trottier & Hagley 1979) the infestation of codling moth in South Africa is considered to be one of the highest in the world (Myburgh 1980).

Many of the studies on longevity and oviposition have been undertaken with laboratory colonies that may differ from field populations due to adaptation to laboratory conditions and rearing procedures (Proverbs & Newton 1962; Deseö 1971; Hagley 1972; Batiste & Olson 1973; Hathaway *et al.* 1973; Howell 1981). Consequently, there are inconsistencies in relating laboratory observations to field observations (Geier & Briese 1978). In order to avoid the limitations of using laboratory-reared moths, this study was undertaken with moths of the spring and summer generations collected from an apple orchard. The objectives of this study were to investigate the effect of temperature on the oviposition and longevity of *C. pomonella*. Observations are also provided on mating of spring and summer moths at constant and fluctuating temperatures. This study provides a more thorough understanding of codling moth biology and behaviour under South African climatic conditions.

The rate of development of codling moth depends mainly on temperature. Changes in temperature, particularly during spring, can increase or decrease the biotic potential of codling moth during summer when effective control is more difficult. By monitoring temperature conditions and comparing the data to previous years, additional control actions can be implemented under conditions favourable to codling moth development.

MATERIAL AND METHODS

Codling moth material was collected from an apple orchard untreated with insecticides on the Overberg Research Farm (formerly Elgin Experiment Farm), Western Cape Province, South Africa (34°09'S 19°02'E). Spring generation moths (emerging early September to late November) originated from diapausing fifth instar larvae collected weekly between September and April 1988 from corrugated cardboard bands (Cutright

1937; Geier 1964) placed around the trunk and branches of Granny Smith trees the previous season. The diapausing larvae in the cardboard bands were kept in two cylindrical gauze cages suspended from branches in the orchard throughout the summer and winter months. During September 1989 the gauze cages were removed from the orchard and transported to the laboratory where the bands were inspected for pupae. Summer generation moths originated from pupae of mature larvae leaving fruit in December to February 1989. Bands were collected weekly and inspected for pupae. Pupae from the spring and summer periods were placed in plastic Petri dishes and maintained in a laboratory at $22 \pm 3^\circ\text{C}$ and RH of $70 \pm 10\%$.

Longevity, preoviposition and oviposition periods of spring and summer generation moths were observed at constant temperatures of 15, 17, 19 and $21 \pm 1^\circ\text{C}$ and $70 \pm 10\%$ RH. Aspects of oviposition studied were the oviposition period and time from mating to 50 % and 80 % and peak oviposition. Observations at each temperature were replicated 12–13 times, except for spring generation moths where only seven replications were used at 15°C . Newly emerged virgin moth pairs were each placed in a cylindrical nylon mesh cage (80 × 90 mm) with a mesh diameter of 2 mm. The top and bottom of each cage was open. Rigidity was obtained by gluing the nylon at the top and bottom of the cage to thin circular plastic bands 6 mm in width, the top and bottom bands being attached to each other by two 6 mm plastic strips. Black Velcro® material was used to discourage moths from ovipositing on the plastic. The bottom of the cage was placed on wax paper and the top covered with wax paper pressed down with a clear plastic lid. A wad of cotton wool, moistened twice daily with water, was pressed against the side of each cage. The cages were placed in desiccators, in which a relative humidity of 70 % was maintained using a potassium hydroxide solution, following the method of Solomon (1951). The desiccators were placed in incubators that were fitted with an outer metal and inner glass door. The laboratories in which the incubators were kept had one double-layered glass wall. Incubators facing the glass wall with the outer metal door of the incubator left open and the inner glass door closed exposed moths to natural light and dark conditions. Laboratories were maintained at the same temperature and humidity to ensure mini-

mum disruption when desiccators were opened.

Sufficient successful matings in the desiccators, particularly at 15 °C, were not obtained. Therefore, moths that emerged during the day were placed in nylon net cages (30 × 30 cm). While *in copula* mating pairs were gently coaxied into a test tube (150 × 12.5 mm). Immediately after they completed mating, the pair were carefully transferred to an oviposition cage in the desiccators. Each oviposition cage contained one mated pair and three cages were placed in each desiccator. The wax paper was changed daily between 08:00 and 09:00 and maintained in a laboratory at 22 ± 3 °C and 70 ± 10 % RH. All eggs oviposited by each female were kept separate and the numbers of hatched and unhatched eggs were recorded.

Oviposition and longevity of the spring and summer moths were also observed at fluctuating temperatures in an open insectary. The insectary consisted of a wooden framed structure 3 × 2 × 3 m with a peaked corrugated Perspex roof, wooden floor and slatted sides covered with gauze. Between 18 and 26 October 1988, 5 and 8 pairs of moths, respectively, that had mated on the same evening, were kept in cages as described for constant temperature conditions. The oviposition period and longevity of 17 individual pairs of moths that had mated on different evenings, between 3 and 16 October, were also observed. Similarly, during the summer months between 24 January and 19 February 1989, 8–13 pairs of moths that had mated on the same evening were observed. Wax paper was replaced hourly after 13:00 to determine the initiation and pattern of oviposition. A wad of cotton wool, moistened twice daily with water, was pressed against the side of each container to avoid desiccation of the moths. The egg totals and daily egg production per female were determined. For the oviposition studies under fluctuating temperatures, daily maximum and minimum, as well as hourly recordings, were obtained from a weather station site 85 m from the insectary.

Under natural weather conditions (*viz.* fluctuating temperatures) mating was observed on a pear tree. Ten branches approximately 50 cm in length were individually enclosed in a nylon bag with a mesh diameter of 2 mm. A pair of adults that had emerged during the day was released into each bag and observed at 5–10 minute intervals until the ambient temperature had dropped below 15 °C (when reproductive activity ceases) to record the time of day and temperature at which mating

took place. Between 1 and 30 October 1988, 35 pairs of mating moths were observed and 25 pairs between 10 and 23 November 1988.

Statistical analysis

The development time of the preoviposition stage, duration of the oviposition period, number of days from mating to peak, 50 % and 80 % oviposition and longevity of the spring and summer moths was estimated by linear regression, using the model $1/y = a + bx$, where x = temperature, y = time in days required to complete development, and a and b are regression constants. The number of eggs per female and daily oviposition (eggs/day) were estimated by linear regression ($y = a + bx$). The lower threshold temperature for development of the preoviposition stage was obtained by solving for x in $1/y = 0 = a + bx$ (Arnold 1959). The thermal constant for development of the preoviposition stage was calculated as the reciprocal of the slope of the regression equation. The thermal constant was compared to the mean degree-days (°D) required for duration of the preoviposition stage at each constant temperature. The mean °D for development was estimated using the method of Jackson & Elliott (1988). Intercepts and slopes for longevity and oviposition (dependent variables) of moths of the spring and summer generations for constant temperatures (independent variables) were compared using standard deviations. The means of longevity and oviposition of moths of the spring and summer periods for fluctuating temperatures were compared using pairwise *t*-tests at the 5 % level of significance.

RESULTS

Preoviposition period

The preoviposition period decreased as temperature increased, the means ranging from 2.54 days at 21 °C to 7.54 days at 15 °C (Table 1). The estimated lower threshold temperature for preoviposition was 11.4 °C and the mean °D estimate was 22.8 °D. Although there was a linear relationship between the reciprocal of the duration of the preoviposition stage and temperature, only 50 % of the variability in rates could be explained by changes in temperature ($P < 0.05$) (Fig. 1).

Oviposition period

There was no difference between the intercepts and slopes for the duration of the oviposition

Table 1. Mean development time and degree-days ($^{\circ}\text{D}$) of *Cydia pomonella* preoviposition period at five constant temperatures.

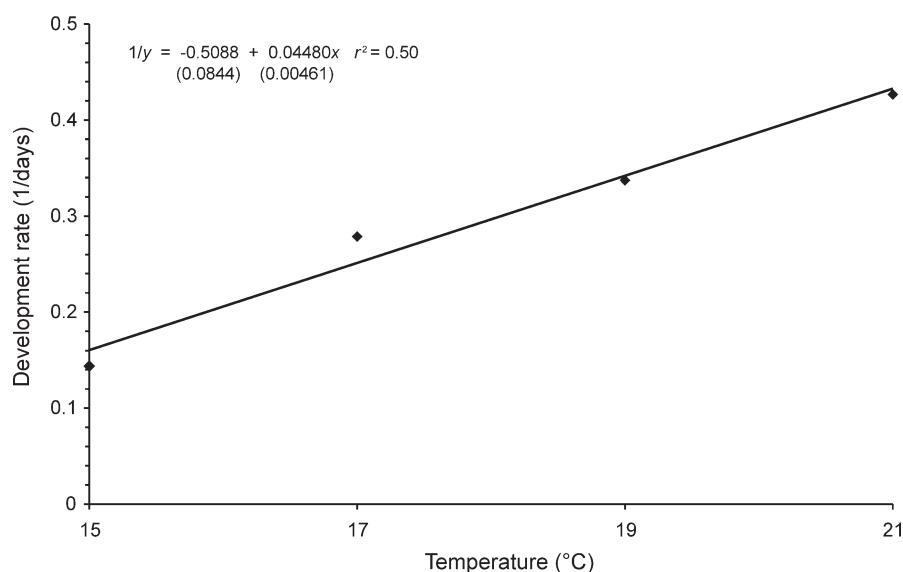
Temperature ($^{\circ}\text{C}$)	<i>n</i>	Development time (mean days \pm S.D.)	Range (days)	($^{\circ}\text{D} \pm$ S.D.)
15	20	7.54 \pm 2.85	3.0–14.0	27.14 \pm 10.20
17	25	4.31 \pm 1.11	3.0–6.0	24.12 \pm 6.20
19	25	3.23 \pm 0.93	2.0–5.0	24.55 \pm 7.00
21	25	2.54 \pm 0.44	2.0–4.0	24.37 \pm 6.30

period of moths of the spring and summer generations (Fig. 2) held at constant temperatures and therefore the data were combined. The estimated mean duration of the oviposition period at 15, 17, 19 and 21 $^{\circ}\text{C}$ was 20.6, 14.7, 9.6 and 10.6 days, respectively. The oviposition period at 21 $^{\circ}\text{C}$ was almost half of that at 15 $^{\circ}\text{C}$. The longest oviposition period for a moth of the spring generation was 30 days at 15 $^{\circ}\text{C}$, while that for a moth of the summer generation was 40 days at 15 $^{\circ}\text{C}$.

At fluctuating temperatures the duration of the oviposition period of spring moths (11.7 days) was significantly longer than that of the summer moths (7.4 days) (Table 2) ($t_{40} = 3.416$, $P = 0.001$). Even with the short oviposition periods there were females of both the spring and summer generations whose oviposition period extended beyond 20 days.

Time to peak, 50% and 80% oviposition

There were no differences between either the intercepts or slopes for the seasonal generations in the number of days to peak oviposition at constant temperatures (Fig. 3), the data were therefore pooled. The estimated mean number of days to peak oviposition at 15, 17, 19 and 21 $^{\circ}\text{C}$ was 13.3, 6.2, 5.1 and 4.1 days, respectively. There was a strong positive relationship between the reciprocal of the time to peak oviposition and temperature ($r^2 = 0.89$). This suggests that peak oviposition would be enhanced by the summer temperature conditions in pome fruit orchards. The number of days from mating to peak oviposition increased more than threefold when temperatures were reduced from 21 $^{\circ}\text{C}$ to 15 $^{\circ}\text{C}$. There were no differences between either the intercepts and slopes in the inverse mean number of days to 50 % ovi-

**Fig. 1.** Rate of *Cydia pomonella* preoviposition development at four constant temperatures (standard errors in brackets).

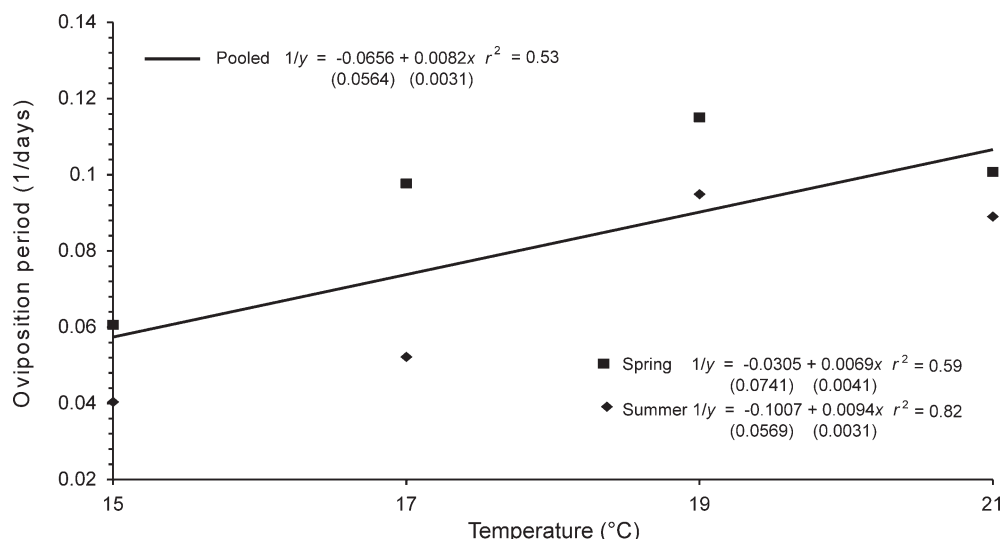


Fig. 2. Relationship between temperature and oviposition period of *Cydia pomonella* females of the spring and summer generations at four constant temperatures (standard errors in brackets).

position for spring and summer moths (Table 3). The estimated mean number of days to 50 % oviposition at 15, 17, 19 and 21 °C were 15.3, 7.5, 6.9 and 5.2 days, respectively. The number of days from mating to 50 % oviposition at 21 °C was also almost a third of that at 15 °C. There was a strong positive relationship between the reciprocal to 50 % oviposition and temperature. There were no differences between either the intercepts and slopes in the inverse mean number of days to 80 % ovi-

position for spring and summer moths (Table 3). The mean number of days to 80 % oviposition at 15, 17, 19 and 21 °C were 22.2, 11.7, 9.5 and 8.1 days, respectively. The number of days from mating to 80 % oviposition at 15 °C was 2.7 times more than that at 21 °C. There was a strong positive relationship between the reciprocal to 80 % oviposition and temperature.

At fluctuating temperatures there were significant differences between moths from the spring and

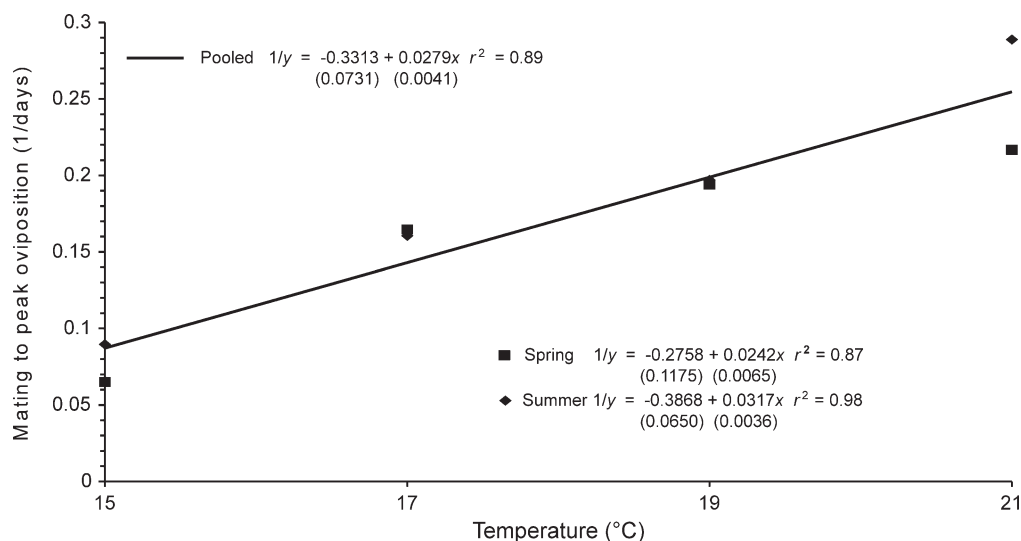


Fig. 3. Relationship between temperatures and mean number of days after mating to peak oviposition of *Cydia pomonella* of the spring and summer generations at four constant temperatures (standard errors in brackets).

Table 2. Mean longevity (days) and oviposition of *Cydia pomonella* of the spring (September to November) and summer (January to February) generations at fluctuating temperatures.

Period	Longevity (days \pm S.D.) (range) [n]		Mean duration of oviposition period (days \pm S.D.) (range) [n]	Mean daily number of eggs/female (days \pm S.D.) (range) [n]	Mean number of eggs/female (eggs \pm S.D.) (range) [n]	Mean number of days after mating to:		
	Male	Female				Peak oviposition (\pm S.D.) (range) [n]	50% of eggs laid (\pm S.D.) (range) [n]	80% of eggs laid (\pm S.D.) (range) [n]
Spring	17.1 \pm 6.82 (5–38) [40]	21.5 \pm 6.91 (11–39) [40]	11.7 \pm 6.26 (1–25) [40]	7.7 \pm 11.24 (0–72) [470]	92.6 \pm 62.21 (7–222) [40]	5.1 \pm 3.7 (1–17) [40]	7.0 \pm 4.2 (3–22) [40]	10.7 \pm 5.1 (3–25) [40]
Summer	11.4 \pm 6.47 (3–38) [34]	11.9 \pm 4.67 (4–23) [40]	7.4 \pm 4.92 (1–21) [40]	16.5 \pm 18.80 (0–111) [293]	121.2 \pm 77.99 (1–303) [40]	2.2 \pm 1.21 (1–5) [40]	3.3 \pm 2.23 (1–12) [40]	5.3 \pm 3.29 (1–14) [40]

Spring: the duration of the nightly oviposition period (hours) was 2.0 (S.D. = ± 1.21) with a range of 1–6 h ($n = 196$).Summer: the duration of the nightly oviposition period (hours) was 2.7 (S.D. = ± 1.65) with a range of 1–9 h ($n = 167$).

summer periods in the mean number of days at which peak ($t_{40} = 4.712$, $P < 0.001$), 50 % ($t_{40} = 5.187$, $P < 0.001$) and 80 % ($t_{40} = 5.627$, $P < 0.001$) oviposition occurred. The number of days at which peak, 50 % and 80 % oviposition occurred for the summer generations was approximately half that of the spring moths (Table 2).

In two oviposition trials initiated on 18 and 26 October 1988, oviposition commenced 1–4 days after mating. Oviposition was erratic due to fluctuating temperature conditions (Fig. 4), with very few eggs being oviposited below 15 °C. Of the total eggs (3409) oviposited by spring moths under fluctuating temperature conditions between 3 October and 18 November 1988 only four (0.1 %) were laid below 15 °C (Fig. 5). Oviposition commenced at 14:00 and ended at 22:00, with peak oviposition occurring at 17:00 for spring generation moths (Fig. 6). In the oviposition trial commencing on 18 November 1988 the temperature remained above 20 °C for the first 21 days of the oviposition period, resulting in a daily oviposition rate similar to that obtained for the oviposition trials undertaken during the summer months (Fig. 4).

In the four oviposition trials conducted between 24 January and 12 February 1989 peak oviposition occurred on the first night following mating on two occasions (Fig. 7). In all trials 50 % of the eggs were laid within 3–4 days after mating and 80 % within 4–9 days of mating. In these trials the temperature between 16:00 and 24:00 never dropped below 15 °C (Fig. 7), with few eggs being oviposited below 18 °C (Fig. 5). Oviposition decreased sharply above 27 °C, 0.9 % of the eggs being oviposited above 30 °C. Oviposition commenced at 16:00 with most eggs being laid between 18:00 and 22:00 (Fig. 6).

Eggs oviposited per female

Significant differences were recorded between the intercepts and slopes for number of eggs per female ($P < 0.001$) for spring and summer moths at constant temperatures (Fig. 8). Significantly more eggs were produced per female for summer moths compared with spring moths and a significant increase was recorded in the number of eggs for spring and summer moths with increasing temperature. The estimated mean number of eggs per female for summer moths at 15, 17, 19, and 21 °C was 153.1, 149.4, 163.3 and 188.1, respectively, compared with

Table 3. Linear regression functions of time from mating to 50 % and 80 % oviposition at four constant temperatures of 15, 17, 19 and 21 °C.

Mating to:	Seasons	Regression function (S.E.)
50 % oviposition	Spring	$1/y = -0.2153 + 0.0193x$ $r^2 = 0.82$ (0.1168) (0.0064)
	Summer	$1/y = -0.2170 + 0.0197x$ $r^2 = 0.99$ (0.0194) (0.0011)
	Pooled	$1/y = -0.2161 + 0.0195x$ $r^2 = 0.90$ (0.0489) (0.0027)
80 % oviposition	Spring	$1/y = -0.1175 + 0.0118x$ $r^2 = 0.80$ (0.0755) (0.0042)
	Summer	$1/y = -0.1569 + 0.0136x$ $r^2 = 0.98$ (0.0230) (0.0013)
	Pooled	$1/y = -0.1372 + 0.0127x$ $r^2 = 0.88$ (0.0348) (0.0019)

71.8, 80.2, 105.6 and 105.8 at the same temperatures for the spring moths. The highest number of eggs (308) was oviposited by a female from the summer generation at 21 °C, whilst the most eggs produced by a female from the spring generation was 226 at 19 °C.

At fluctuating temperatures there was no significant difference between the number of eggs oviposited by spring moths (92.6 eggs/female) and summer moths (121.2 eggs/female) ($t_{40} = 1.775$, $P = 0.084$) (Table 2). The highest number of eggs produced (303) was by a female moth of the summer generation. The average temperatures for the periods during October/November and January/February when oviposition studies were undertaken was 16.0 °C and 23.1 °C, respectively, while the average temperature between 13:00 and 18:00 for the two periods was 20.3 °C and 27.7 °C, respectively.

Eggs per day

There were no differences between intercepts or slopes for the daily oviposition rate of spring and summer moths at constant temperatures (Fig. 9) therefore the data were pooled. Mean oviposition at 15, 17, 19 and 21 °C was 6.4, 8.3, 14.8 and 14.2 eggs/day, respectively. Although the mean daily oviposition at 21 °C was 14.2 eggs, the highest number of eggs oviposited in an evening (90) was by a female from the summer generation at 19 °C. The highest number of eggs produced in an evening by a female moth from the spring generation was 68 at 21 °C. For the summer generation moths maintained at 15 °C, periods of

oviposition were frequently followed by intervals when no oviposition occurred (Fig. 10). At this temperature no oviposition occurred on 41.6 % of the days of the oviposition period, while at 17 °C, 19 °C and 21 °C the percentage of days when no oviposition occurred was 26.8, 11.6 and 11.0, respectively. It is evident that with increasing temperature there was a decrease in the number of days when no eggs were deposited (Fig. 10). This pattern was not observed for spring moths. Moths maintained at 15 °C (34.3 %), 17 °C (28.8 %) and 21 °C (30.6 %) all had a similar percentage of days when oviposition did not occur, only at 19 °C (6.1 %) were fewer days observed when no oviposition took place.

At fluctuating temperatures the mean daily oviposition of summer moths (16.5 eggs/day) was significantly higher than that of the spring moths (7.7 eggs/day, $t_{293} = 7.246$, $P < 0.001$) (Table 2). The maximum number of eggs produced by a female of the summer generation in a single evening was 111, while that for a female of the spring generation was 72. The number of evenings during which more than 24 eggs were laid by a single female was greater for the summer generation (25.6 %) than the spring generation (8.1 %). During the spring period there were more evenings when no oviposition occurred (38.3 %) compared to the summer period (11.0 %).

Adult longevity

Details of the longevity of males and females of *C. pomonella* of the spring and summer moths are given in Fig. 11. There were no differences between

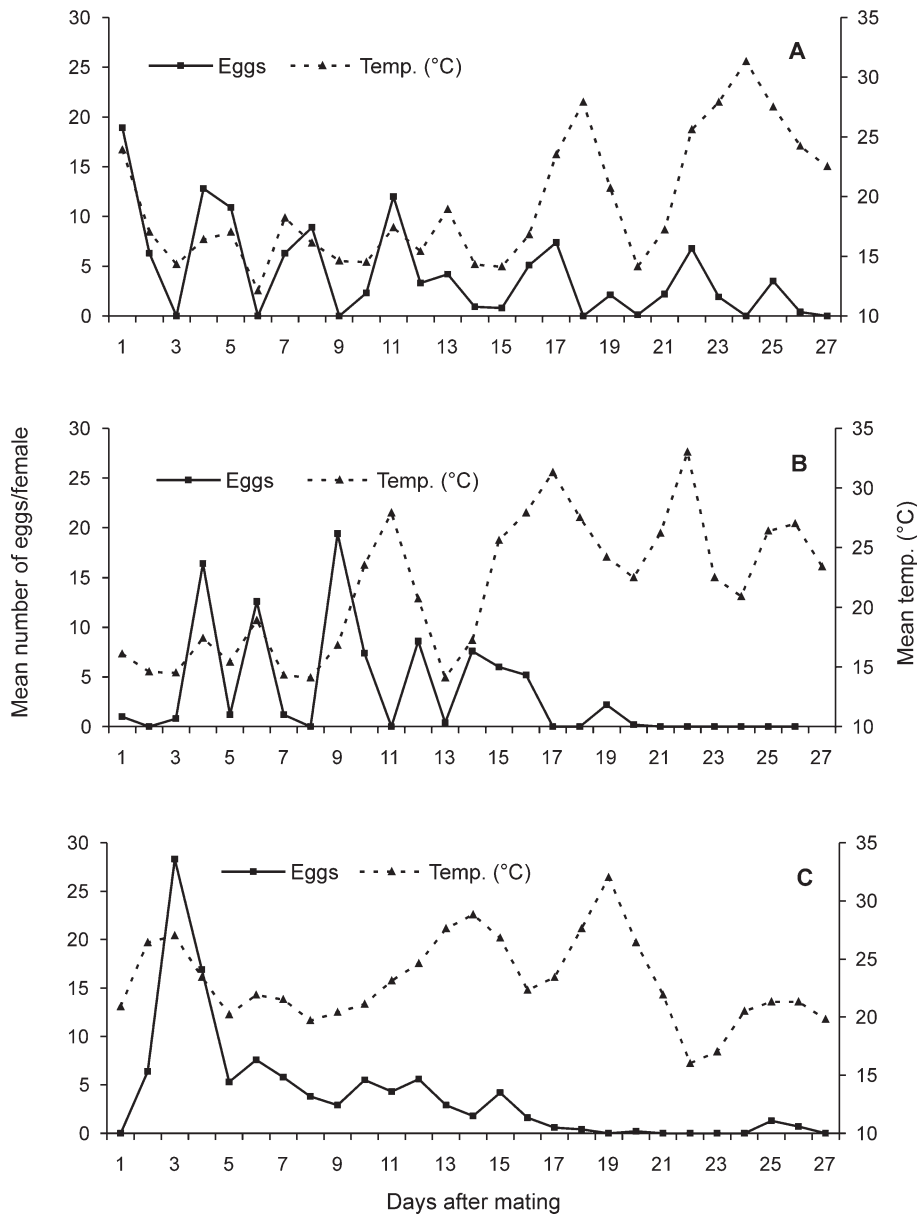


Fig. 4. Mean daily oviposition of *Cydia pomonella* of the spring generation at fluctuating temperatures with mean temperature of hourly recordings between 15:00 and 20:00. Mating occurred on (A) 18 October, (B) 26 October and (C) 18 November.

either the intercepts and slopes for male and female moths of the seasonal generations therefore the data were pooled. The estimated mean longevity at 15, 17, 19 and 21 °C was 35.4, 23.4, 19.0 and 17.1 days, respectively. Longevity decreased by approximately 50 % at 21 °C compared to 15 °C. The reciprocal of adult longevity and temperature

was positively correlated ($r^2 = 0.81$). It was inferred from this finding that longevity would be shortened by summer temperatures under natural weather conditions in the orchard. The longest life span was 51 days for a male moth of the spring period at 15 °C and 49 days for a female of the summer period maintained at 15 °C

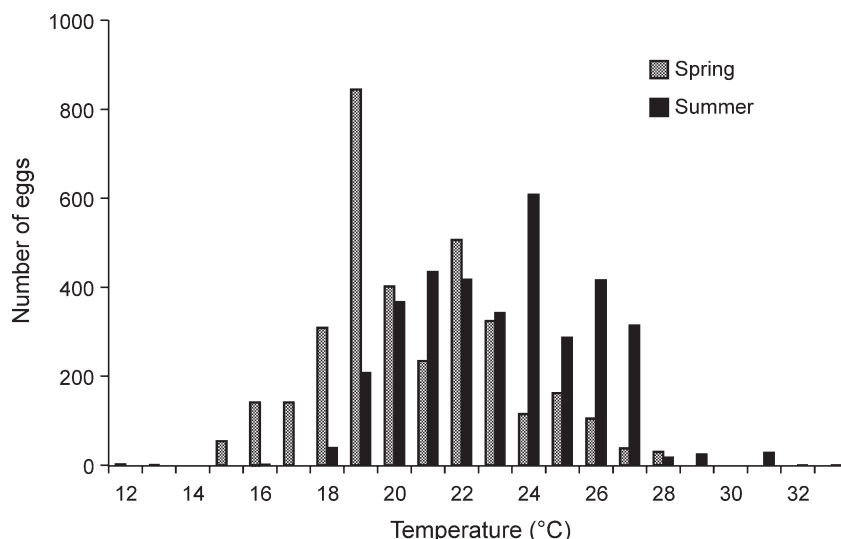


Fig. 5. Oviposition of *Cydia pomonella* of the spring ($n = 29$) and summer ($n = 40$) generations in relation to fluctuating temperature.

At fluctuating temperatures moths lived 3–39 days (Table 2). There was a significant difference ($t_{40} = 2.867$, $P = 0.007$) in longevity between males and females of the spring generation with the latter living longer. No difference was found in the longevity between the two sexes of the summer generation ($t_{40} = 0.375$, $P = 0.710$). Males of the spring generation lived significantly longer than males ($t_{40} = 3.684$, $P = 0.001$) and females ($t_{40} = 3.979$, $P = 0.003$) of the summer generation. Similarly, females of the spring generation lived significantly

longer than males ($t_{40} = 6.486$, $P < 0.001$) and females ($t_{40} = 7.280$, $P < 0.001$) of the summer generation.

Mating

The time of day and temperature at which mating took place under fluctuating temperatures are given in Figs 12 and 13. The earliest mating of spring generation moths observed during October took place at 16:45, with most matings (68.6 %) occurring between 18:00 and 19:00 (Fig. 12). In

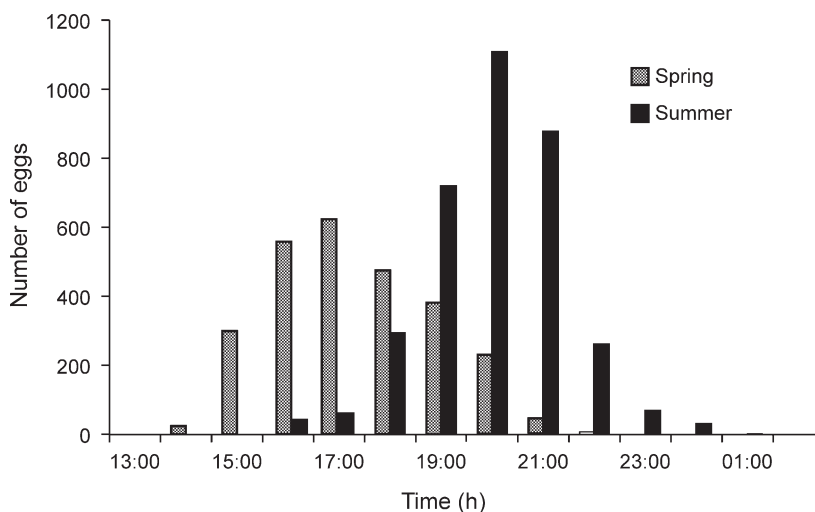


Fig. 6. Oviposition of *Cydia pomonella* of the spring ($n = 29$) and summer ($n = 40$) generations recorded hourly at fluctuating temperatures.

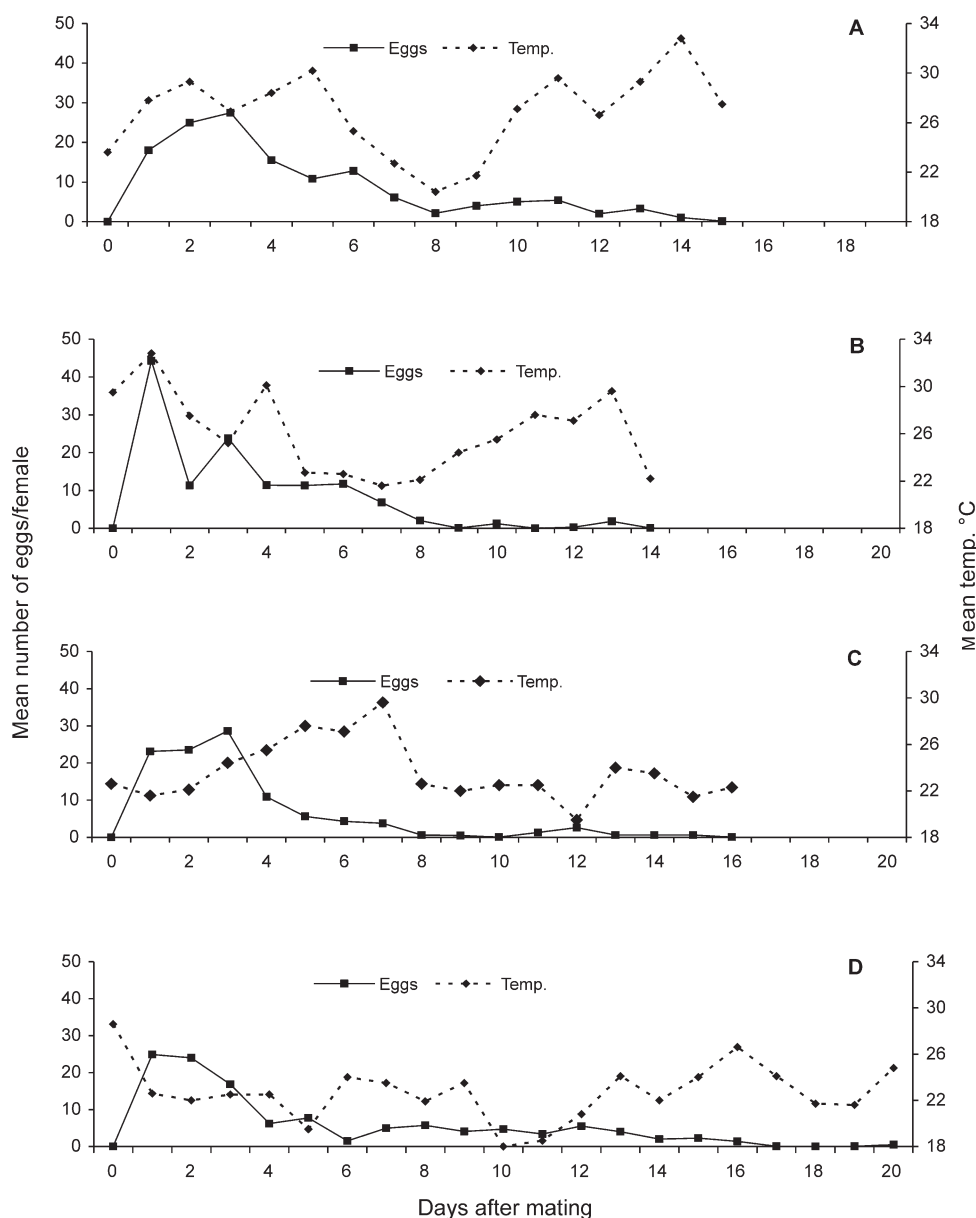


Fig. 7. Mean daily oviposition of *Cydia pomonella* of the summer generations at fluctuating temperatures with mean temperature of hourly recordings between 17:00 and 20:00. Mating occurred on (A) 24 January, (B) 6 February, (C) 12 February and (D) 19 February.

November most matings (88 %) occurred slightly later, between 19:00 and 20:00. In October mating took place between 15 °C and 20 °C with female activity noticeably decreasing below 16 °C and no mating observed below 15 °C. In November most matings (84 %) took between 18 °C and 22 °C (Fig. 13).

DISCUSSION

Preoviposition period

Although the temperature range selected varied by only 6 °C there was almost a threefold difference in the preoviposition period between 15 and 21 °C. However, the overall °D estimate of 22.8

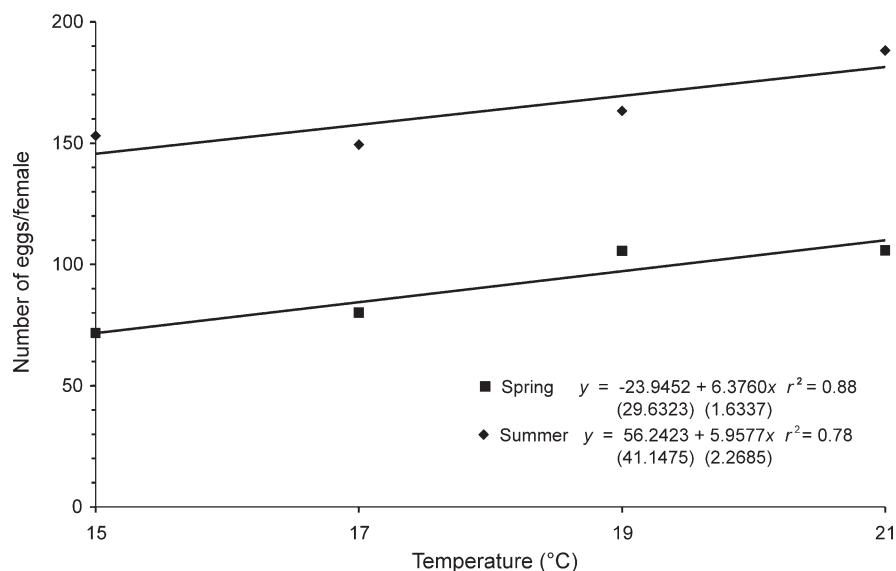


Fig. 8. Relationship between temperature and number of eggs per female of *Cydia pomonella* of the spring and summer generations at four constant temperatures (standard errors in brackets).

is comparable with the mean °D values given at each temperature. Although only 50 % of the variability in oviposition rates could be explained by changes in temperature it can provide a guide to the preoviposition period that could be expected during the spring and summer months. Mean °D for September, October and November between 1980 and 1990 on the

Overberg Research Farm was 3.2, 4.7 and 6.8 °D, respectively. Based on the mean °D of each month the mean preoviposition period expected during September, October and November would be 6.9, 4.7 and 3.2 days, respectively. Based on mean degree days for January and February the mean preoviposition period expected would be 2.3 and 2.2 days.

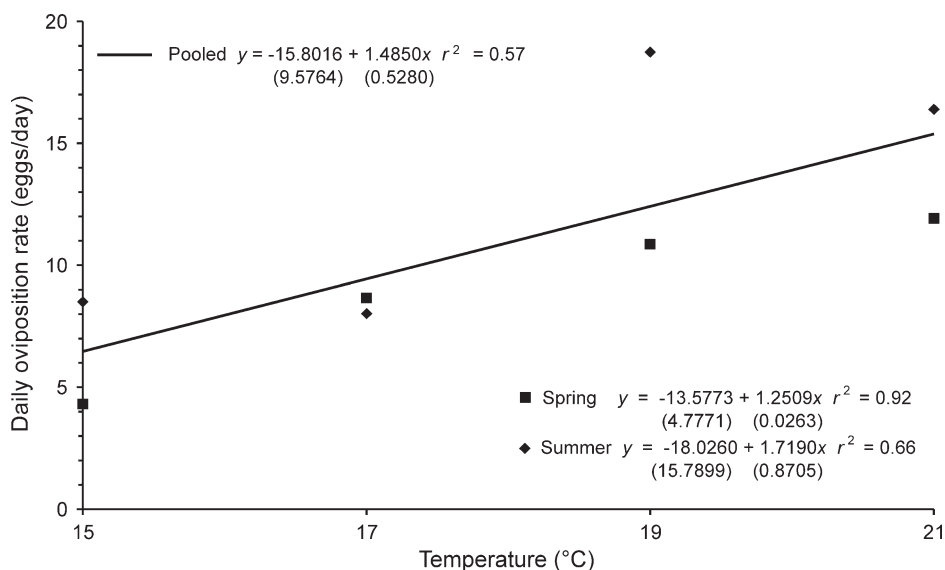


Fig. 9. Relationship between temperature and daily oviposition of *Cydia pomonella* of the spring and summer generations at four constant temperatures (standard errors in brackets).

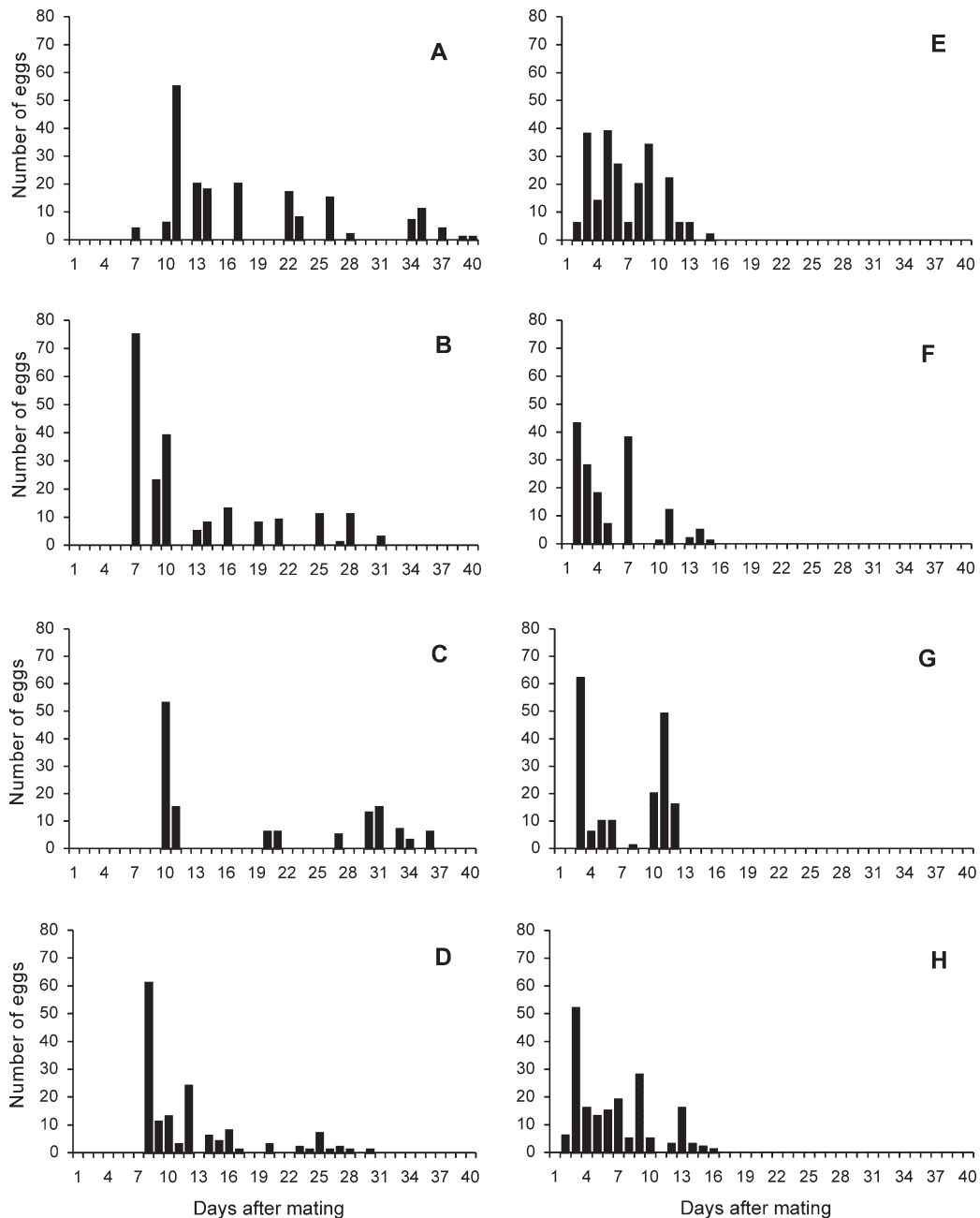


Fig. 10. Daily oviposition of four *Cydia pomonella* moths each confined individually in oviposition cages at constant temperatures of 15 °C (A, B, C, D) and 21 °C (E, F, G, H).

Oviposition period

There was no difference in the duration of the oviposition period of spring and summer generation moths at constant temperatures. This is contrary to the findings at fluctuating temperatures, where

the mean duration of the oviposition period of the spring adults was significantly longer than that of the summer moths. The results obtained under constant temperature and humidity conditions suggest that there is no difference in the quality (as

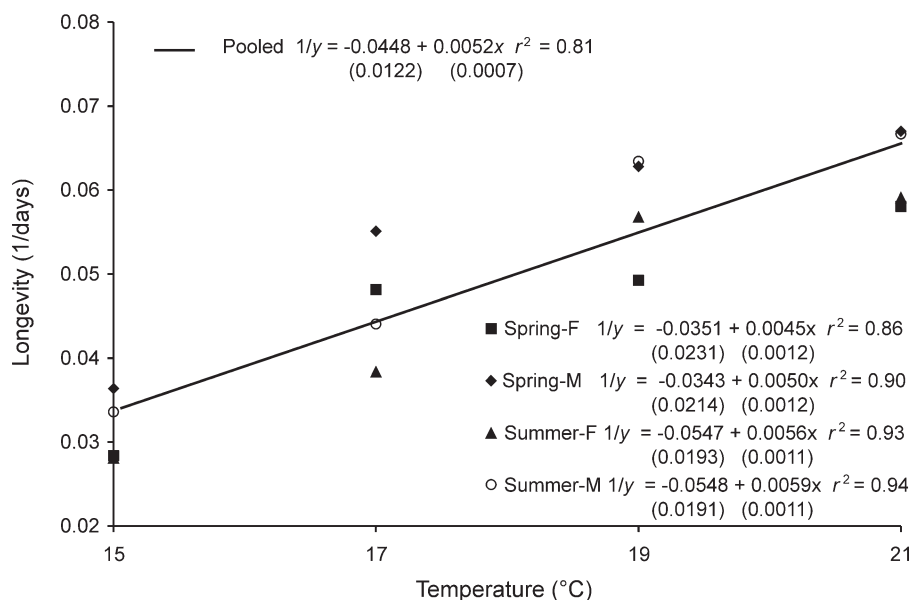


Fig. 11. Relationship between temperature and longevity of males (M) and females (F) of *Cydia pomonella* of the spring and summer generations at four constant temperatures (Standard errors in brackets).

measured by longevity and fecundity) of spring and summer females. This is unexpected as the spring generation females originated from mature larvae overwintering in the orchard from end-December–September/October, a period of 9–10 months, while the summer generation moths arose from mature larvae that immediately pupated after leaving the fruit from mid-December to end-March. At fluctuating temperatures the higher temperatures during the summer observation

period compared with those during the spring observation period, may have reduced the duration of the oviposition period of the summer moths. It is probable that humidity is lower during the summer months and this might have had a negative impact on the oviposition period of moths during the summer period.

Hagley (1972) reported a correlation between longevity, and duration of the oviposition period which varied from 4–15 days at a constant temper-

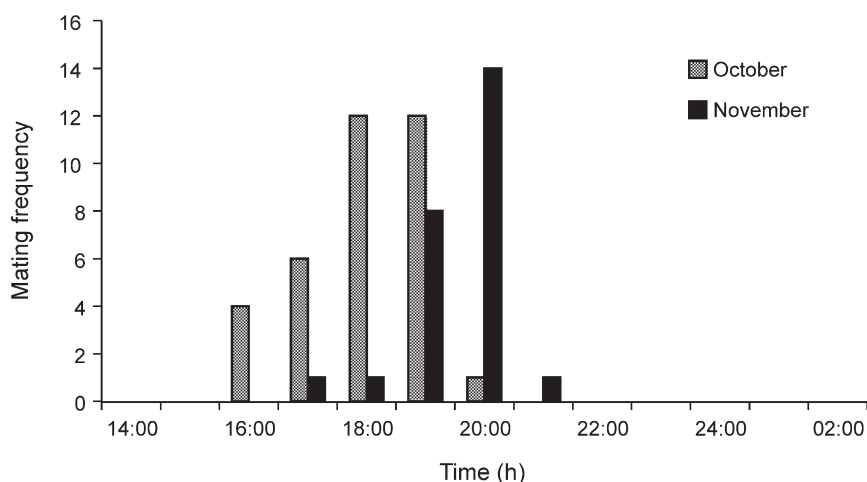


Fig. 12. Time of mating of *Cydia pomonella* of the spring generation in October and November at fluctuating temperatures. Sunset occurred at 16:30.

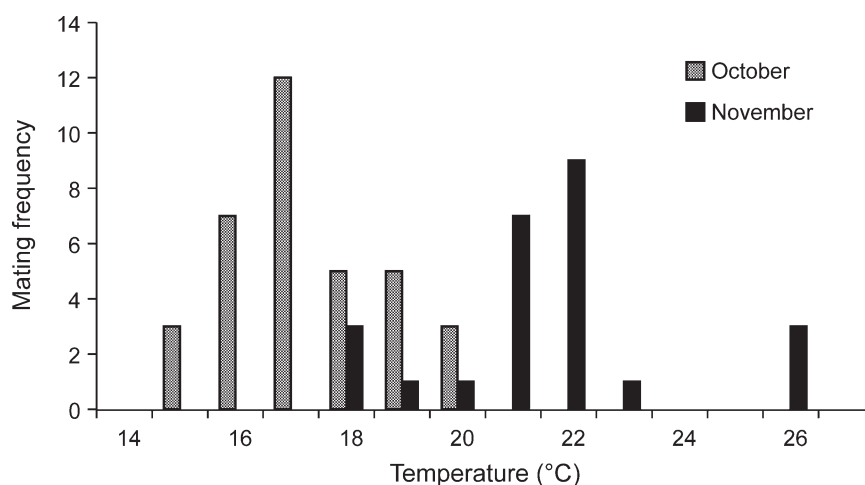


Fig. 13. Mating of *Cydia pomonella* adults of the spring generation in October and November in relation to fluctuating temperatures. Sunset occurred at 16:30.

ature of 24 °C. Isely (1938) showed that at fluctuating summer temperatures over a mean temperature range of 21–33 °C, the oviposition period was approximately seven days, although individual moths oviposited for up to 20 days. Selkregg & Siegler (1928) reported similar results with a mean oviposition period of between seven and eight days for both spring and summer moths with a maximum period of 17 days.

Time to peak, 50 % and 80 % oviposition

In this study there were no significant differences in the mean number of days from mating to peak, 50 % and 80 % of total eggs laid for the spring and summer moths at constant temperatures but at fluctuating temperatures there were significant differences. The difference in results obtained with constant and fluctuating temperatures was attributed to the moths being exposed to a greater daily range and higher temperatures under fluctuating temperatures. During the spring period there were numerous evenings when the temperature was about 15 °C which may have impacted on number of eggs oviposited. The mean duration of the nightly oviposition period in spring was 2 h (S.D. = ± 1.21) with a range of 1–6 h ($n = 196$), while in summer the oviposition period was 2.7 h (S.D. = ± 1.65) with a range of 1–9 h ($n = 167$). Previous researchers have also reported very short periods between peak, 50 % and 80 % oviposition, particularly at high temperatures. Howell (1981) found that oviposition was greatest on the second and third day of the adult stage and 90 % com-

pleted by the fifth day at 26.7 °C. Riedl & Loher (1980) recorded peak oviposition on the first day, 50 % eggs produced by the third day and 90 % completed by the ninth day at constant temperatures. At fluctuating temperatures, Isely (1938) reported summer oviposition being highest on the first day and 90 % completed by the seventh day. In spring 16 % of eggs were deposited on the first day and 90 % completed by day 12.

Eggs per female

The mean fecundity of the spring moths at constant and fluctuating temperatures (90.9 and 92.6 eggs/female, respectively) was very similar, suggesting a similar range of temperatures to which the moths were exposed. Although summer generation moths (163.5) produced significantly more eggs per female than the spring moths (90.9) at constant temperatures, there were no seasonal differences in fecundity at fluctuating temperatures. This is probably a reflection of the consistently high temperatures recorded during summer compared to the spring period. The high temperatures had an impact on longevity resulting in a wide variation in the number of eggs laid per female. Fecundity studies using branches, enclosed in nylon netting, in the orchard (Blomefield, pers. obs.) produced higher mean fecundity levels than were obtained at fluctuating temperatures in the open insectary.

The figures for the fecundity of codling moth cited in the literature are highly variable as studies have involved both feral females and females from

Table 4. Recorded* fecundity of feral codling moth, *Cydia pomonella* (L).

Reference	Region	Generation	Mean fecundity
Blomefield (present study)	Western Cape, S.A.	Spring	92.6
		Summer	121.2
Isley & Ackerman (1923)	Arkansas, U.S.A.	Spring	8
		Summer	52
Allman (1928)	Bathurst, NSW	Spring	22
		Summer	26
Hall (1929)	Ontario, Canada	Spring	64
		Summer	83
Miller (1943)	Victoria, Australia	Spring	5
		Summer	7
		Late summer	15
Tadic (1957)	Yugoslavia	Spring	39
		Summer	37
Chang <i>et al.</i> (1960)	Sinkiang, China	Spring	33
		Summer	39
Proverbs & Newton (1962)	Canada	Summer	33
Geier (1963)	Australia	Spring	44
		Summer	44
Arias & Nieto (1972)	Spain	Spring	33
		Summer	63
Deseö (1973)	Hungary	Spring	16.8
		Summer (1st brood)	88.3
		Summer (2nd brood)	36.6
Esteban-Duran (1975)	Spain	Spring	47
		Summer	78
Ferro <i>et al.</i> (1975)	Washington State, U.S.A.	Summer	42
		Summer	37
1973			
1974			
Trottier & Hagley (1979)	Ontario, Canada	Spring	9.7–32.9

*From Geier (1963), Ferro *et al.* (1975) and Howell (1991).

laboratory colonies reared on artificial medium or immature apples. The present study was concerned with the oviposition of feral females and the findings suggest that the fecundity of codling moth in South African orchards is one of the highest in the world (Table 4) and higher than that recorded previously for South African populations (Petty 1925; Myburgh 1963; Myburgh *et al.* 1973). Where the fecundity of seasonal generations has been researched separately, the summer generations have been shown to have the highest fecundity. However, in many of the studies there was very little difference in fecundity between the seasonal generations (Hall 1929; Geier 1963; Howell 1981). However, Hall (1929) and Deseö (1973) reported

that females of the spring generation produced up to 80 % fewer eggs than the summer female moths. Where fecundity has been found to vary between and within seasons this variation has been attributed to variations in climatic factors, such as either unfavourable temperatures (Isely 1938; Geier 1963; Wearing & Ferguson 1971) or snowfall (Trottier & Hagley 1979), rather than food quality which has also been cited as a reason for variation in fecundity (Wearing & Ferguson 1971). Deseö (1971) found a positive correlation between adult weight and fecundity, while Hathaway *et al.* (1973) found no relationship between pupal weight and fecundity. Geier (1963) reported a significant difference between the mean body weights of the

spring, early summer and late summer moths, but the differences were considered too slight to affect fecundity. In the present study significant differences could be found between the female pupal weights of the spring period and those of the early summer and late summer periods. Little oviposition took place at or below 16 °C and above 27 °C.

Eggs per day

Although summer moths laid more eggs than spring moths at the lower constant temperatures, there was no significant difference in the mean daily egg production between the spring and summer moths. At fluctuating temperatures, the mean daily egg production per female in summer (16.5) was almost double that in spring (7.7), but the difference was also not statistically significant, probably due to the wide variation in the number of eggs laid per day. Isely (1938) found that mean daily egg production per female of summer moths was highest at 27 °C (19.2) and lowest at 33 °C (7.0) and 22 °C (6.7). He also found that periods of high temperatures (heat waves) during the final stages of pupal development had an adverse effect on fecundity. According to Newcomer & Whitecomb (1924), as reported by Howell (1991), daily oviposition was 5–8 eggs. The high number of eggs (111) that was produced by one female in an evening in this study, and the number of evenings when more than 24 eggs per female were oviposited suggest that under optimum conditions a considerable number of eggs can be laid in an evening, particularly if adverse conditions have delayed oviposition for a number of days. Isely (1938) and Riedl & Loher (1980) also observed days of high oviposition/egg production followed by days of low egg production. In the present study periods of high egg production were often followed by periods of low or no egg production at constant temperatures. This phenomenon was more evident at 15 °C than at 21 °C, particularly for the summer generation moths. The periods of no egg production extended from 1–10 days at 15 °C and 1–3 days at 21 °C. The number of days when no eggs were laid at 15 °C and 21 °C was 135 (out of 324 oviposition evenings) and 15 (out of 131), respectively. The oviposition trend for the spring and summer moths, at fluctuating temperatures, was similar. For the spring and summer moths periods of no egg production also extended from 1–10 days and 1–3 days, respectively. The extended periods of

no oviposition often occurred toward the end of the oviposition period. These observations suggest that daily egg production will be more extended and erratic during the spring than during the summer period.

Longevity

Constant and fluctuating temperatures were used independently in studies to determine the longevity of adults of the spring and summer generations. This provided a more complete understanding of this aspect of the biology of codling moth than studies at either constant or fluctuating temperature could have given on their own. From our observations, as well as those of other authors, it is evident that temperature is an important parameter in the longevity of codling moth adults, longevity decreasing with increasing temperature. With a temperature increase of 6 °C (from 15 to 21 °C) there was a decrease in mean longevity of 18.3 days at constant temperatures. The longevity of adults exposed to fluctuating temperatures also showed a similar trend, *i.e.* decreasing with increasing temperature.

The mean longevity of spring generation adults exposed to constant temperatures of 19 °C and 21 °C was similar to the longevity of spring adults exposed to fluctuating spring temperatures. This similarity was probably due to the fluctuating temperatures during the spring observation period being comparable to the exposure of spring adults to 19 °C and 21 °C at constant temperatures. There were no differences in longevity between spring and summer generation moths at constant temperatures. However, at fluctuating temperatures the spring generation adults lived significantly longer than summer adults. There was also no significant difference between the longevity of the sexes of the summer adults, both living for between 11 and 12 days. Furthermore, the overall mean adult longevity of summer adults (11.7 days) exposed to fluctuating summer temperatures was almost half the overall mean adult longevity (22.5 days) at constant temperatures. This difference can be attributed to temperatures in excess of 30 °C that adults were exposed to during the summer observation period. It would appear that high temperatures during summer had a considerable negative impact on the longevity of summer moths. These findings differ to some extent from those of other researchers. Hagley (1972) also observed a decrease in longevity with an increase

in temperature at constant temperatures, using moths reared on immature green apples. However, there was little variation in longevity between adults of different sexes. Geier (1963) reported a mean female longevity of 12 days under fluctuating spring and summer temperatures, there being no difference in longevity between spring and summer adults despite the use of field collected moths. Selkregg & Siegler (1928) also found little seasonal variation in longevity. The average longevity of spring and summer adults was between 8 and 9 days and 7 and 8 days, respectively. Hathway *et al.* (1971) reported a much lower average adult longevity that varied between 5.4 and 7.0 days for females and between 6.1 and 9.5 days for males reared on different artificial diets or immature green apples at 26.7 °C. Moffitt & Albano (1972) obtained similar results for adults from larvae reared on immature green apples. Howell (1981) found that at a high constant temperature of 26.7 °C laboratory reared moths lived significantly longer when provided with water (12.9 days) compared to no water (4.7 days). Jones & Wiman (2008) reported a mean longevity for females of 13.7 days when fed on honey-water and maintained at 22 °C and $\pm 70\%$ RH. In the present study the moths were provided with water twice daily and the mean longevity of summer moths (11.7 days) was similar to the findings of Howell (1981). During the dry hot summer months the availability of free water in the form of dew or rain will be scarce and this may have a negative impact on longevity.

Although the longest recorded survival of a female moth at constant temperatures was 49 days, it is unlikely that this would ever be achieved under natural conditions. The results under fluctuating temperatures suggest that adults in the earlier and cooler part of the season will live the longest. Based on the mean longevity and standard deviation obtained under fluctuating temperatures, the female moth will probably live 14–24 days in spring and 7–17 days in summer.

Mating

Most matings took place between 18:00 and 22:00, and none below 15 °C. On one of the occasions that mating did take place between 15 °C and 16 °C the moths were found *in copula* the following morning. The highest temperature at which moths were observed mating was 26 °C. Van Leeuwen (1929) observed that most matings

occurred between 19:00 and 21:00. Based on the assumption that pheromone trap catches and mating period are synchronous (Howell 1991), Wong *et al.* (1971) showed that peak sexual activity was during the hour immediately after sunset. Borden (1931) and Cutright (1937) also reported peak mating shortly after sunset. However, contrary to these findings, Castroville & Carde (1979) found that most female calling was confined to darkness, although periodically females called prior to and shortly after the scotophase. Maximum calling was one hour after sunset and lasted for 1.5 h. Thereafter it declined and terminated at sunrise. In the present study most of the matings observed in October occurred prior to and just after sunset (18:30), suggesting that under the cool spring conditions most matings will occur prior and after sunset. During November, 56 % of the matings took place during darkness and at higher temperatures than during October. This is in accord with the findings of Batiste *et al.* (1973), *i.e.* that flight activity and subsequent mating is advanced under cool conditions.

CONCLUSION

Despite its economic importance as a major pest in South Africa, little was previously known about codling moth biology in pome fruits, particularly with regard to the effect of temperature on longevity and oviposition. Effective management of this pest can only be improved by a thorough understanding of its biology and behaviour under South African climatic conditions. An obvious limitation of the caged studies on longevity and oviposition is that the moths are confined to small spaces. This may have created abnormal behaviour such as excessive movement in attempts to escape confinement. This may have had a negative effect on longevity and oviposition, particularly for those studies undertaken during the hot summer months in an outdoor insectary exposed to fluctuating temperatures. Although laboratory studies under constant conditions can be viewed as artificial, they provide a means of comparing differences between spring and summer moths under controlled conditions. These differences would not be as evident with moths in an outdoor insectary exposed to fluctuating temperatures. Furthermore, extrinsic mortality factors are excluded. However, despite the limitations, this study has provided useful information that permits comparison with

similar studies done by researchers in other apple producing areas of the world. It also provides a guide as to the biotic potential of codling moth in South Africa and what can be expected under certain climatic conditions. This information can be used to increase a producer's understanding of the biology of codling moth, improve the control strategy against codling moth and reduce or prevent control failures under certain climatic conditions. The short interval between peak oviposition and 80 % of the total eggs laid by a summer moth, as well as the short incubation period in summer, a period of 5–6 days, highlights the danger of delaying or exceeding the spray interval during critical periods of the pest's life cycle. Periods of cool weather conditions followed by optimum mating and oviposition conditions can lead to a period of high egg production and egg hatch over a limited time period. This can lead to fruit infestation if effective monitoring systems are not in place. This will be especially important if moths are trapped on the night that the traps were inspected and the week's count was zero, indicating that no sprays are required. Under such conditions peak oviposition could be reached by the third night after mating and larvae penetrating the fruit a day after the traps are again inspected. If a spray application

is delayed for any reason, unnecessary infestation may occur.

Oviposition studies at constant temperatures have also shown that the fecundity of summer moths was significantly higher than spring moths and this should be taken into account in the control strategy against codling moth during the spring to early summer period. A low second flight could have as much potential as a high spring flight, particularly as spraying conditions become less optimal during the summer months due the increase in surface area of the tree, increased oviposition on fruit and higher temperatures. It is therefore imperative to strive for optimum control of the larvae of the spring moth flight to ensure that as few larvae as possible complete development to form the second flight.

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