Biology of Dubas Bug, *Ommatissus lybicu*s (Homoptera: Tropiduchidae), a Pest on Date Palm During Spring and Summer Seasons in Panjgur, Pakistan

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Abstract.- Dubas bug, *Ommatissus lybicu*s is one of the major sucking pests of date palm. Both nymphs and adults suck the sap from fronds and fruit stalks. Severe infestations cause even death of date palms. Biological parameters of the bug were studied for the four consecutive generations on Kehraba cultivar during spring and summer seasons 2009-2010. The mean fecundity and longevity of male adults of first (spring) generation were significantly lower than that of second (summer) generations 2009-2010. Mean egg laying frequency, adult longevity, incubation and post ovipositional period during 1st and 2nd generation were 4.90, 19.50, 147.60 and 3.60; and 5.30, 21.80, 62.70 and 4.50 days, respectively. The mean nymphal development periods were 46.9 and 49.6 days in spring and summer generations with no significant difference. On the average, females have longer life duration (27.85 days) than males (18.85 days) under the similar climatic conditions and generations. This bivoltine hibernates and aestivates in the egg stage in fronds during winter and summer and on an average completes total life cycle of 1st and 2nd generation in 217.25 and 136.35 days, respectively. Dubas bug passes 61.43 and 38.56 % time of life cycle in eggs stage during spring and summer generations, respectively.

Keywords: Dubas bug, *Ommatissus lybicu*s, date palm.

INTRODUCTION

D ubas bug, *Ommatissus lybicu*s (Deberg) Aschae and Wilson (Homoptera: Tropiduchidae) locally known as “Sherago” is one of the most important sucking pests of date palm in district Panjgur of Pakistan. Infestation of this pest was first reported in 1999 and since then it has become one of the major problems in date palms in Panjgur. It is also considered a major pest of date palm in several countries of Old World (Alfieri, 1933; Klein and Venezian, 1985). It apparently originated in the Tigris-Euphrates river valley (Dowson, 1936). In 1930s, date palm in the Basra regions of Iraq was free of dubas bug (Dowson, 1936) whereas, in recent past it has been ranked as number one among pests of date palm in Iraq (Heil, 2007) causing economic losses upto 50% (Kranz et al., 1978). Whereas according to Gassouma, (2004) in case of heavy infestation, the dubas bug might reduce the crop yield to level less than 50%. Fruits of infested palms are reported to be smaller and to ripen more slowly, with a high percentage of reducing sugar and low percentage of sucrose (Hussain, 1974). In Oman Dubas bug has been considered the most serious pest of date and can even cause the death of tree (Hunter-Jones and Tunstall, 1972). Nymphs (Fig. 1A) and adults (Fig. 1B) of this bivoltine pest cause damage to date palm by sucking the sap from leaflets; midrib of frond and fruit stalks (Hussain, 1963; Lepesme, 1947). In case of heavy infestation, they produce extremely large quantities of honeydew which cover the leaves and support sooty mold that grows on the honeydew and reduces the photosynthetic activities (Mokhtar and Al-Mjeini, 1999; Elwan and Al-Tamiemi, 1999; Gassouma, 2004). Whereas, sooty mold was not observed on palm infested with dubas bug in the Arava valley, Israel (Klein and Venezian, 1985).

Dubas bug has two generations (spring and summer) in a year and it completes whole life cycle of 1st and 2nd generation in frond (Esmaili, 1983; Askari and Bagheri, 2005; Capinera, 2008; Sepanji et al., 2010). In Oman, the emergence of nymphs
of spring and summer generations takes place in the months of February and August, respectively (Thacker et al., 2003). Al-Mahmooli et al. (2005) on the other hand, reported that the emergence of spring generation takes place in the month of January. Total nymphal development period of spring generation on an average lasts for 48.4 days. The duration of adult male and female is 82 and 72 days, during which female deposits 143 eggs. This pest hibernates and aestivates in egg stage for 120 and 95 days during spring and summer generation, respectively (Abd-Allah et al., 1998).

Owing to the isolated pest population prevalent under adverse climatic conditions and disagreement of different investigators on different biological parameters, this study under the agro-ecosystem of district Panjgur was carried out with the objectives to provide basic information regarding development duration of different life forms, which are necessary to devise an effective management programme for this pest in district Panjgur and similar areas.

**MATERIALS AND METHODS**

Biology of dubas bug (*Ommatissus lybicu*s) for four consecutive generations (spring and summer) was studied in district Panjgur (N 26°59.165 E 064°05.880, Alt., 3200ft) Balochistan, Pakistan during the years 2009 and 2010.

**Plant materials**

“Kehraba” which is one of the major (in term of area) and most susceptible cultivar (against dubas bug) in this area was selected for this study. Kehraba sucker and mature plant leaflets were used for stock population and fecundity study, respectively. The suckers were grown in earthen pots with a dimension of 2’x 2’x 4’ and covered with a muslin cloth, while leaflets were covered in locally made cages at egg laying stage of dubas bug one season earlier. Suckers were about 4-5 years old at the time of planting. Same suckers were used for the four generations. The suckers were irrigated at weekly intervals and no chemical fertilizer and farm yard manure were applied during the course of experiment.

**Insect culture**

After emergence, a number of first instar dubas bug nymphs were collected from date palm cv. Kehraba and maintained in caged potted plant suckers for mass culture (stock population). In order to note the fecundity (number of eggs/female), a single pair (♀ and ♂) of dubas bug, at 5th nymphal instar were collected from stock population with the help of aspirator and released in a locally made...
micro cage of the size of 28 x 305 mm in diameter and length, respectively. In each cage, single leaflet of about two years old (free from eggs infestation) were caged and remained intact with tree during the course of study. Dubas bug pairs were kept in the same cage for the whole adult period. To study the pre-ovipositional, ovipositional and post-ovipositional periods and egg laying frequency (eggs per female/day), a single pair of dubas bug was confined in circular micro cages of the size 19 x 13 mm diameter containing about two years old leaflets. Each day the circular cages containing dubas bug pairs were dragged on the same leaflet and circled/marked the caged area with marker to facilitate eggs, counting. After completion of egg deposition and on the death of adults, micro cages were removed from leaflets. Confined leaflets (with eggs) caged in both cages were cut with sharp cutter from frond at base and put into paper envelops and brought to laboratory for counting the above parameters. Some of the infested leaflets remained caged for the purpose to note the hatching time (date/month) and incubation period (days) of first and second generations. During first year, in order to note the emergence of nymphs of spring and summer generations, caged leaflets were observed regularly. Number and duration (days) of each nymphal instar were recorded by caging 0 day old nymphs in circular micro cage. Caged nymphs were monitored daily and exuvae (shaded skin) was recorded for counting number and duration of instars /moults. Adult longevity (both of male and female) was recorded by caging them separately at 5th nymphal instar.

Meteorological data
The mean temperature (maximum and minimum) and relative humidity data recorded from January to December in 2009-2010 are shown in Figure 4.

Statistical analysis
The data recorded were analysed using one way ANOVA followed by Duncan’s (1955) multiple range test for significance of differences at 5 %. Graphic work was done using Microsoft Excel programme.

RESULTS

Fecundity
Mean fecundity (no. of eggs/female) in spring (1st generation) 2009 was lower (104.60) than summer (2nd generation) (116.60) 2009, and the same trend continued during spring (106.20) and summer (117.40) during 2010 respectively (Table I). Data further showed that average fecundity of both, the spring generation (2009-10) was also lower (105.40) than summer 2009-10 (117.00) (Fig.2). However, no significant difference was observed in the mean number of eggs (fecundity) in 1st and 2nd year (Table II).

Eggs laying frequency
Difference between number of eggs laid/female/day was non significant during spring (4.80 days) and summer 2009 (5.60 days) generations. The same pattern was observed in spring (5.00 days) and summer (5.00 days) generations 2010. The mean eggs laying frequency for four generations (2 years) in 21.60 days (oviposition periods) was 5.1 eggs per days (Table I). Overall egg laying frequency was high (5.30 eggs) in summer than spring (4.90 eggs) generation during 2009-2010 (Fig. 2). In both the years it was non significant however numerically it was more (5.20 eggs) in the 1st year than 2nd year (5.00 eggs /female/day) (Table II).

Pre-oviposition period
Data in Table I showed that the mean pre-oviposition period of spring and summer generations were non significant among all four generations. It was 2.4 and 2.6 days in spring and summer generations, respectively during 2009. Pre-ovipositional duration in spring (2009-2010) and summer (2009-2010) were 2.5 and 2.6 days, respectively and with no significant difference (Fig. 2). Pre-oviposition period was more (2.6 days) in 2nd year as compared to first year (2.5 days) but no statistical difference was observed (Table II).

Oviposition period
Data in Table I revealed that the oviposition period was 21.00 and 21.80 days during spring and summer generations 2009 with no significant
Table 1.- Means duration of different life forms of Dubas bug (*Ommatissus lybicus*) in spring and summer seasons (2009-10).

<table>
<thead>
<tr>
<th>Generation/season</th>
<th>Eggs</th>
<th>Ovipositional period</th>
<th>Adult longevity (days)</th>
<th>Incubation days</th>
<th>Nymphal period (days)</th>
<th>Life cycle (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>LF</td>
<td>Pre</td>
<td>Oviposition</td>
<td>Post</td>
<td>Male</td>
</tr>
<tr>
<td>Sp. 2009</td>
<td>104.60b</td>
<td>4.80 a</td>
<td>2.40 a</td>
<td>21.00 a</td>
<td>3.80 a</td>
<td>17.20 a</td>
</tr>
<tr>
<td>Su. 2009</td>
<td>116.60a</td>
<td>5.60 a</td>
<td>2.60 a</td>
<td>21.80 a</td>
<td>4.60 a</td>
<td>19.80 a</td>
</tr>
<tr>
<td>Sp. 2010</td>
<td>106.20b</td>
<td>5.00 a</td>
<td>2.60 a</td>
<td>21.60 a</td>
<td>3.40 a</td>
<td>18.00ab</td>
</tr>
<tr>
<td>Su. 2010</td>
<td>117.40a</td>
<td>5.00 a</td>
<td>2.60 a</td>
<td>22.00 a</td>
<td>4.40 a</td>
<td>20.40 a</td>
</tr>
<tr>
<td>Mean</td>
<td>111.2</td>
<td>5.1</td>
<td>2.55</td>
<td>21.6</td>
<td>4.05</td>
<td>18.85</td>
</tr>
<tr>
<td>LSD 5%</td>
<td>4.24</td>
<td>17.17</td>
<td>16.41</td>
<td>12.15</td>
<td>19.78</td>
<td>9.5</td>
</tr>
<tr>
<td>LSD 1%</td>
<td>6.49</td>
<td>1.2</td>
<td>0.57</td>
<td>3.61</td>
<td>1.5</td>
<td>2.46</td>
</tr>
<tr>
<td>Sig.</td>
<td>9.1074</td>
<td>1.69</td>
<td>0.8</td>
<td>5.07</td>
<td>1.95</td>
<td>3.46</td>
</tr>
</tbody>
</table>

Means in columns followed by the same letters are not significantly different (P=0.05).

Sp, spring; Su, summer; LF, laying frequency; M&F, male & female.

A non significant difference was observed in the mean duration of post-oviposition period in the mean duration of post-oviposition period.

**Fig. 2.** Mean seasonal fecundity, eggs frequency, pre-oviposition, oviposition, post-oviposition, male, female duration of dubas bug (*Ommatissus lybicus*) of both spring and summer (2009-2010).

A deviation in spring and summer 2010 it was 21.60 and 22.00 days, respectively. Cumulative result of both spring and summer 2009-2010 showed that it was high (21.9 days) in summer than spring (21.3 days) generations (Fig. 2).
Table II.- Mean duration (yearly) of different life forms of Dubas bug (*Ommatissus lybicus*) during the year 2009 and 2010.

<table>
<thead>
<tr>
<th>Year</th>
<th>Eggs Number</th>
<th>Eggs LF</th>
<th>Pre.Ov.</th>
<th>Post.Ov.</th>
<th>Incubation(days)</th>
<th>Nymph(days)</th>
<th>Adult(days)</th>
<th>Life cycle(days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st year</td>
<td>110.60 a</td>
<td>5.20 a</td>
<td>2.50 a</td>
<td>4.20 a</td>
<td>103.70 a</td>
<td>47.70 a</td>
<td>23.05 a</td>
<td>176.15a</td>
</tr>
<tr>
<td>2nd year</td>
<td>111.80 a</td>
<td>5.00 a</td>
<td>2.6 a</td>
<td>3.90 a</td>
<td>106.70 a</td>
<td>48.80 a</td>
<td>23.65 a</td>
<td>177.35a</td>
</tr>
<tr>
<td>Mean</td>
<td>111.2</td>
<td>5.1</td>
<td>2.55</td>
<td>4.05</td>
<td>105.15</td>
<td>48.25</td>
<td>23.35</td>
<td>176.75</td>
</tr>
<tr>
<td>CV</td>
<td>3.64</td>
<td>11.6</td>
<td>11.6</td>
<td>13.24</td>
<td>2.87</td>
<td>4.93</td>
<td>8.04</td>
<td>3.36</td>
</tr>
<tr>
<td>LSD 5%</td>
<td>7.11</td>
<td>1.03</td>
<td>0.51</td>
<td>0.94</td>
<td>5.29</td>
<td>4.17</td>
<td>3.3</td>
<td>10.45</td>
</tr>
<tr>
<td>Sig.</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>

Ov. (Oviposition), LF (laying frequency).
Means in columns followed by the same letters are not significantly (P=0.05).

during spring and summer generations 2009-2010. It was 3.8 and 4.60 days in spring and summer 2009, respectively. Cumulative result of both spring and summer (2009-10) showed that it was lower (3.6 days) in spring than summer (4.5 days) (Fig. 2). Comparatively it was more (4.2 days) in the 2nd year than first year (3.9 days) (Table II).

**Adult life longevity**
Results of adult (male and female) longevity showed a non significant difference in spring and summer 2009-2010. In all four generations, maximum value (24.20 days) and minimum value (22.20 days) for adult life period was recorded during summer 2010 and spring 2009, respectively with an average of 23.35 days. Male adult longevity ranged 17.20 to 20.40 days with an average of 18.85 days. On an average, female had more (27.85 days) life longevity than male (18.85 days) (Table I). Comparatively adult longevity was more in both summers (21.80 days) than spring (19.50 days) generations 2009-10 (Fig.2). Difference in adult longevity of 1st year (23.05) and 2nd year (23.65 days) during 2009-10 was non significant (Table II).

**Incubation period**
Highly significant difference was observed in the mean incubation period of spring and summer generations 2009-2010. Incubation period of eggs during spring generation were higher (149.00 days) than summer generation (64.20 days) of 2009. A similar trend was followed in spring (146.20 days) and summer (61.20 days) generations of 2010. (Table I). Incubation period of both spring and summer (2009-2010) were 147.6 and 62.70 days, respectively and with highly significant difference (Fig. 4). There is no significant difference in the means incubation period in 1st and 2nd year (Table II).

**Nymphal period**
Nymphs of dubas bug pass through five nymphal instars to reach adult stage. During this study an increasing trend was observed in the mean development duration as nymph aged. Mean duration of first, second, third, fourth and fifth nymphal instar was 4.00, 7.40, 9.20, 12.40 and 12.40 days for the first (spring) generation 2009 and the mean interval of the same instars was 4.8, 7.40, 8.60, 13.40 and 15.80 days in the 2nd (summer) generation 2009, respectively with no significant difference except the 5th instar. The same trend was observed in spring and summer generation 2010 (Table I). In both the years (four generations) maximum nymphal period (50 days) was observed during summer 2009 followed by (49.20 days) in summer 2010 (Table I). Mean seasonal duration of five instars was high (49.20 days) during summer 2009-2010 but with a non significant difference with spring 2009-10 generation (47.30 days) (Fig. 2B). Difference in mean nymphal period of both the years was non significant and it was numerically high (48.80 days) in 2nd year as compared to 1st year (47.70 days) (Table II).

**Life cycle**
This bivoltine pest completes total life cycle
of spring and summer generations (2009) in 216.80 and 138.10 days, respectively and the same trend was observed during spring (217.70 days) and summer (134.60) generations 2010 with high significant difference (Table I). Mean duration of life cycle in both spring and summer 2009-10 was 217.25 (61.43%) and 136.55 (38.56%) days, respectively (Fig. 2B). And no significant difference was observed in the mean duration of life cycle in 1\textsuperscript{st} (177.35 days) and 2\textsuperscript{nd} (176.45 days) year (Table II). Out of the total period of life cycle, dubas bug passed 61.31%, 39.06%, 61.57% and 38.07% time ‘in egg stage during spring and summer generations 2009-10, respectively (Fig. 3).

**DISCUSSION**

Results of present study with regard to mean fecundity showed that in both the years (2009-2010) the mean fecundity of 1\textsuperscript{st} generation (2009-2010) was lower than that of 2\textsuperscript{nd} generation (2009-2010). The disparity in the mean fecundity of present study in spring and summer generations was attributed to dissimilarity in food quality, quantity at developmental stage of dubas bug in spring and summer generations. Mattson (1980) found that numbers of eggs laid by female are affected both by various plants and insect factors. Similarly, Wheeler et al. (1998) reported that quality of food at developmental stage might have influence on potential fecundity of an insect. Irrespective of numbers of eggs per female overall trend of our result are in accordance as previously reported (Hussain, 1963; Gharib, 1966; Payandeh et al., 2010). However, in other study, Bassim (2003) recorded more number of eggs in summer generation than scored in the present study. And we assumed that this may be due to difference in quality and quantity of food, life duration of female and mean temperature and relative humidity of the area which can affect the fecundity. It was also found that Lepidopterous adults developed from larvae fed on relatively high quality diets have comparatively more fecundity (Taylor, 1984; Taylor and Sands, 1986; Taylor and Forno, 1987).

In this study, it was found that the egg laying frequency of spring 2009 (1\textsuperscript{st} generation) was lower (4.8 eggs) than of summer 2009 (5.60 eggs) and there was no difference in spring and summer values of 2010. But the average frequency of spring (4.9 eggs) was lower than summer (5.3 eggs) in 2009-2010 Owing to little information on this aspect, the results of current findings in spring 2009 generation were found at par with the results of Payandeh et al. (2010). While the higher eggs laying frequency (5.60) in summer 2009 in current results, it can be attributed to favourable nutritional and environmental availability during development time of female.
On maturity the female mate, get fertilized and most of the insects remained in pre-oviposition state for some period. This period vary from species to species, availability of food and prevalent environmental conditions. Our results regarding the mean duration of pre-oviposition and post-oviposition period are at par with Sepanji et al. (2010). However our results disagree with Sepanji et al. (2010) regarding the oviposition period (15.93 days) of 1st generation and 2nd (18.00 days) generation. Possible reasons for this may be due to variation in plants, environment (temperature and relative humidity) and insect factors.

Insects which are poikilotherms are mainly depending on surrounding temperature of area for the development of various life forms (Dent and Walton, 1997). Results of mean duration (days) of nymphal development had no statistical differences during spring and summer generations 2009 and 2010, in exception with 5th instar. On an average the total nymphal period (49.20 days) of summer generation was numerically higher than spring (47.30 days) generations. Our finding regarding total nymphal development period confirmed the findings of Hussain (1963), Bassim (2003) and Sepanji et al. (2010). However, Payendah et al. (2010) reported that mean development of nymphal stage was 54.07, 44.82 and 54.71 days at 25, 30 and 35 °C under laboratory condition. The difference in the developmental period of each instar as reported above attributes to differences in temperature, quality of food and some other environmental factors which have obvious effect on the development of insect.

The results obtained from an earliest work transpire that food quality at developmental stage may have influence on the adult longevity (Wheeler et al., 1998). Sepanji et al. (2010), reported that adult life duration of male longevity in 1st and 2nd generation was 16.56 and 17.64 days, respectively. Irrespective of sex the mean duration of adult in overwintering (1st) and summer (2nd) was 15 and 13 days, respectively (Hussain, 1963). Overall results of present work are in consonant with the reported work. While these studies disagree with the findings of Bassim (2003), who found that on an average the adult longevity of male/female during the first (spring) and 2nd (summer) generation were 33.5/58.05 and 82.35/89.75 days, respectively. Under laboratory conditions the male and female (in bracket) adult longevity at three constant temperatures (25, 30 and 35°C) was 18.80 (24.17), 15.61 (19.78) and 3.28 (5.14) days, respectively (Payendah et al., 2010).

This pest hibernates and aestivates in the egg stage. Incubation period of eggs of 1st and 2nd generation was 178.24 and 59.40 days, respectively Sepanji et al. (2010) and Bassim (2003) reported that the incubation period of eggs during spring (1st) and autumn (2nd) generations was 150.00 and 57.83 days, respectively. It was 141 and 50 days during 1st and 2nd generation under the agro-climatic conditions of Iraq (Hussain, 1963). The findings of present investigation regarding incubation period of 1st (147.60 days) and 2nd (62.70 days) generations are in fair correlation with the findings as reported above. While in other study Klein and Venizian (1985) reported that eggs of 2nd generation hatched within 18-21 days. This is the lowest reported duration of eggs incubation period and attributes to fairly high temperature which can fulfil the degree days requirement of this stage and shorter the incubation period. However, Payendah et al. (2010) reported that egg development at 25, 30 and 35°C was 32.41, 30.88 and 35.10 days; it indicated that each development stage of dubas bug have specific optimum temperature for development.

Dubas bug has two distinct generations (spring and summer) in a year. In 2009 nymphs of 1st and 2nd generations emerged in end of March and 1st week of April, respectively while in both of the years, nymphs of 2nd generation emerged in mid and last week of August, respectively. Results of present work regarding number of generations per year are in line with Hussain (1963), Klein and Venizian (1985) and Sepanji et al. (2010). However, according to present study results, time of emergence disagree with that of the authors reported above. Differences in time of emergence attributed to difference in the mean temperature of area. Hussain (1963) reported that dubas bug completed the 1st and 2nd generations in 203 and 113 days, respectively. Sapanji (2010) reported that the duration of 1st and 2nd life cycles was 221.13 and 110.96, respectively. Finding of this research are in line with the findings reported above. Slight
differences can be attributed to variation in the mean temperature of the area.

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REFERENCES


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Table I: Means duration of different life forms of Dubas bug (*Ommatissus lybicus*) in spring and summer seasons (2009-10).

<table>
<thead>
<tr>
<th>Generation/season</th>
<th>Eggs No.</th>
<th>LF</th>
<th>Pre (days)</th>
<th>Oviposition (days)</th>
<th>Post (days)</th>
<th>Adult life longevity (days)</th>
<th>Incubation days</th>
<th>Nymphal period (days)</th>
<th>Life cycle (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Male</td>
<td>Female</td>
<td>Adult</td>
<td>1st</td>
<td>2nd</td>
<td>3rd</td>
<td>4th</td>
</tr>
<tr>
<td>Sp. 2009</td>
<td>104.60b</td>
<td>4.80a</td>
<td>2.40a</td>
<td>17.20b</td>
<td>7.20a</td>
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<td>23.90a</td>
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<tr>
<td>Mean</td>
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<td>2.55</td>
<td>18.85</td>
<td>27.85</td>
<td>23.35</td>
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<td>7.45</td>
</tr>
<tr>
<td>CV</td>
<td>4.24</td>
<td>1.77</td>
<td>1.5</td>
<td>9.5</td>
<td>19.95</td>
<td>13.27</td>
<td>5.11</td>
<td>18.92</td>
<td>16.49</td>
</tr>
<tr>
<td>LSD 5%</td>
<td>6.49</td>
<td>1.2</td>
<td>0.57</td>
<td>2.46</td>
<td>7.65</td>
<td>4.26</td>
<td>7.41</td>
<td>1.17</td>
<td>1.69</td>
</tr>
<tr>
<td>LSD 1%</td>
<td>9.1074</td>
<td>1.69</td>
<td>0.8</td>
<td>3.46</td>
<td>10.73</td>
<td>5.98</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Sig.</td>
<td>** ns</td>
<td>ns</td>
<td>Ns</td>
<td>* ns</td>
<td>ns</td>
<td>** ns</td>
<td>ns ns</td>
<td>ns ns</td>
<td>ns ns</td>
</tr>
</tbody>
</table>

Means in columns followed by the same letters are not significantly different (P=0.05).
Sp, spring; Su, summer; LF, laying frequency; M&F, male & female.