INTRODUCTION

The arrowhead scale, *Unaspis yanonensis* Kuwana (Homoptera: Diaspididae) is a major insect pest of citrus trees in Asia including Korea, Japan, and China (Ohkubo, 1980; Blackburn and Miller, 1984). This sessile scale moves only during a short period of time after hatching and primarily feeds on foliage, young stems and fruit of citrus hosts, which sometimes causes tree dieback when the trees are heavily infested (Ohkubo, 1980).

*Unaspis yanonensis* is considered native to China. The arrowhead scale has invaded and spread through much of Japan (Matsumoto et al., 2003), from which it is thought to have been introduced to Korea in 1930s (NPQS, 1999). In Korea, most citrus orchards are in Jeju Island where this pest has not yet made a serious economic impact (Kim D. H. et al., 2000). However, recently the populations of *U. yanonensis* have increased and sometimes caused tree dieback on unsprayed trees, especially in organic citrus orchards.

*Unaspis yanonensis* overwinters primarily as fertilized adult females and they lay eggs beneath their scale covers in the spring (Kuwana, 1923; Okudai et al., 1966). The eggs hatch within a few hours, and crawlers escape from the scale covers and settle down on appropriate sites of citrus trees. Oviposition peaks of *U. yanonensis* are thought to be controlled by temperature and ovovipary.

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Post-diapause development and multimodal oviposition activity of arrowhead scale, *Unaspis yanonensis* (Homoptera: Diaspididae) and its modeling

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Abstract

The longevity and fecundity of overwintered *Unaspis yanonensis* Kuwana (Homoptera: Diaspididae) were examined at constant temperature 24°C, and its periodical oviposition activity was modeled. Adult females collected in early November showed abnormal post-diapause development; prolonged pre-oviposition period, not producing progenies and much lower fecundity. All females collected from early December through early March showed normal post-diapause development and had ~20 d of pre-oviposition period and ~80 d of longevity. Overwintered *U. yanonensis* showed a periodical oviposition activity with a maximum 4 times of oviposition cycle during their life time, and the pattern was flexibly fitted to a 4-peak Gaussian function. The average peak timings (parameter $a$) occurred at 5.5, 25.2, 41.6, and 56.4 d for the 1st, 2nd, 3rd, and 4th peak from the start of oviposition, respectively. The height of the peaks (parameter $b$) gradually decreased from 14.9 for the 1st peak to 5.0 for the 4th peak. The parameter values of the 4-peak equation were successfully converted to degree-days unit with a lower threshold temperature 13°C for field validation. The model predicted the 1st oviposition peak of overwintered *U. yanonensis* very well (~282 DD from 1 January), while showed large discrepancy with actual data in the later peak period. A 3-modal oviposition curve that includes the individual variations of oviposition activity of *U. yanonensis* females with removing the 4th cycle showed a better shape fitting ability in the later peak period. Further, application and improvement of the multi-peak model were discussed.

Key words: Citrus; longevity; fecundity; phenology; forecasting model

INTRODUCTION

The arrowhead scale, *Unaspis yanonensis* Kuwana (Homoptera: Diaspididae) is a major insect pest of citrus trees in Asia including Korea, Japan, and China (Ohkubo, 1980; Blackburn and Miller, 1984). This sessile scale moves only during a short period of time after hatching and primarily feeds on foliage, young stems and fruit of citrus hosts, which sometimes causes tree dieback when the trees are heavily infested (Ohkubo, 1980).

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*Unaspis yanonensis* overwinters primarily as fertilized adult females and they lay eggs beneath their scale covers in the spring (Kuwana, 1923; Okudai et al., 1966). The eggs hatch within a few hours, and crawlers escape from the scale covers and settle down on appropriate sites of citrus trees. Oviposition peaks of *U. yanonensis* are thought to be controlled by temperature and ovovipary.

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Takezawa and Aihara (1962) showed that the eggs of *U. yanonensis* remain in the ovary until near completion of embryonic development, and egg production temporarily stops when a certain capacity is reached, then resumes after oviposition begins.

The arrowhead scale typically shows bimodal oviposition activities per generation separated by a resting period, resulting in two distinct peaks in appearance of hatched nymphs (crawlers) in the field (Murakami, 1970; Adachi and Korenaga, 1991). Adachi and Korenaga (1991) developed a bimodal fertility model to predict the occurrence of *U. yanonensis* crawlers in the field. As this model was developed from empirical observations and under arbitrarily selected temperature threshold in Japan, it is expected for the model to have limitations in application to a field with different environmental conditions, i.e., citrus orchards in Jeju, Korea.

Petroleum oil is an alternative to synthetic insecticides in control of scale insects in the organic citrus farms. It suffocates the pest of a specific target stage (Tomlin, 2003). Application of petroleum oil to *U. yanonensis* nymphs (crawlers) would successfully control them in organic citrus orchards. Better understanding of oviposition activity and the related parameters of *U. yanonensis* would be required to predict the crawler phenology in the field. Thus, the objectives of this study were to illustrate the oviposition behavior and periodicity of overwintered *U. yanonensis* and model the general pattern of the oviposition activity to understand further the crawler emergence pattern in the field. Additionally, the post-diapause development of *U. yanonensis* females was described in relation to their pre-oviposition period and fecundity.

**MATERIALS AND METHODS**

**Laboratory experiments.** Citrus leaves infested with overwintered *U. yanonensis* females were collected from an unsprayed orchard in Jeju Korea during the period from late December to late April at 20 d intervals; 28 December in 2005, and 19 January, 10 February, 4 March, 25 March, and 25 April in 2006. The leaves were cut into squares of 1×1 cm with single female. The leaf squares were placed on cotton wool supported by a sponge block saturated with water in a rearing cage (dia. 95 mm, depth 40 mm). The cover of rearing cage has a mesh hole of dia. 40 mm for air circulation. Twenty to 25 leaf squares were placed in a rearing cage, and held at 24±1°C, 50 to 70% RH and a photoperiod of 16:8 (L:D) in the laboratory. Adult *U. yanonensis* females lay eggs beneath their scale covers (Okudai et al., 1966), and the eggs hatch within few hours or as soon as they are laid (Korenaga, 1983). Thus, the emergence of crawlers (hatched young nymphs) from the scale cover of adult females was regarded as oviposition. Twenty five to 40 females at each collection date were chosen and observed daily until the first appearance of crawlers under a binocular microscope with 10 to 40×. After the first oviposition, the overwintered females were observed three times a week. From the sample of February 10 in 2006, males and females were recorded separately. The sexes were distinguished by the morphological characteristics between males and female crawlers of *U. yanonensis*. Female crawlers had a deep yellow body color during the period from their hatching to the early settlement state, while pale yellow for male crawlers. Also, the female nymphs produced a two long waxy filament on their head end within a few hours after settlement. Whereas, settled male nymphs made a short curled dense waxy filament on the dorsum. Hatched crawlers were removed from the leaf squares and counted whenever observations were made.

Since all *U. yanonensis* females underwent normal post-diapause development without a diapause symptom in the experiments above, additional two samples of November 7 and December 4 in 2006 were collected to investigate if those females were in diapause. Twenty five females at each additional sampling date were observed as the method described above.

Overwintering adult female longevity in this study was the period from the collection to the last oviposition as deaths of female adults under the protective cover could not be examined.

**Data analyses.**

**Statistical analyses.** Oviposition period, fecundity, and sex ratio data were analyzed using SAS GLM and their means were separated by Tukey test at *p*=0.05 (SAS Institute, 1999). The sex ratio data were transformed to a natural logarithm before analysis. Also, comparisons of the periods up to the 1st emergence between female and male crawlers were analyzed using a two sample *t*-test.
**Pattern of oviposition activity.** To get rid of a variation caused by different pre-oviposition periods among females, the first emergence day of any crawlers was set to ‘1’ in each adult female and then, age and the frequencies of crawler emergence were arranged on the new age scale in all cases. The frequency data were subjected to a series of smoothing procedure to make the location of peaks more distinct and to remove a juggling noisy on the peaks. At the first step, the data points with 2 to 3 d intervals were changed to constant-spaced data at 1d intervals by rearranging the numbers of crawlers between two points equally. And then 3 moving average was applied to make a smooth sequence. Finally the sequences were smoothed by Gauss convolution method at <4.5% (Jandel Scientific, 1996). To model the smoothed data, a 4-peak equation which has a form of serial connections of Gaussian function was developed using the matched-asymptotic method (Vollset et al., 1991; Kim, D. S. et al., 2000):

\[ f(x) = \sum_{i=1}^{4} a_i \exp\left[-\frac{1}{2}\frac{(x-b_i)^2}{c}\right] \]

where, \( f(x) \) is number of crawlers at time \( x \), \( a_1 \) to \( a_4 \) indicate the height of each peak, \( b_1 \) to \( b_4 \) are the center of each peak, and \( c \) is a common parameter controlling the width of peaks. In all cases, individual-based adjustment was conducted. The equation with the nine-parameters describes a frequency distribution with 4-peak situation. But this equation can be easily modified to account for situations with reduced peaks, by substituting any parameter of \( b \) series as an extremely large value. So, if full parameter model (4-peak model) was failed to convergence, \( b \) series parameters were set to 10,000 from the last peak parameter until getting successful estimation of parameters. Thus, 3-peak or 2-peak model was successively applied. The values of the parameters were estimated using TableCurve (Jandel Scientific, 1996).

**Model validation.**

**Field phenology data.** Field phenology data of *U. yanonensis* for model validation were obtained from the report of Kim et al. (2007), which were investigated in a citrus orchard in Jeju island, South Korea in 2005 and 2006. The orchard was 0.3 ha with about 15 y old trees (spacing 4×3 m), and un-sprayed abandoned orchard. Each 5 to 10 leaves per tree were picked from randomly selected 6 trees, resulting in total 30 to 60 leaves at weekly interval. The numbers of the 1st nymphs of *U. yanonensis* on the collected leaves were examined under a binocular-microscope with 15 to 30×. For the purpose of comparison with 4-peak model outputs, the nymph numbers were scaled to a ratio against the peak numbers.

**Parameter change and model simulation.** Estimated parameters, \( b_i \) and \( c \) were converted from Julian date to day-degree unit by a method which calculates effective accumulative temperature, to validate the multi-Gaussian model in fields under variable temperatures. A lower threshold temperature 13°C reported by Sakagami and Korenaga (1982) was applied for the conversion. The 4-peak full model was applied to compare clearly the discrepancy between model outputs and actual field situations, and to deliberate a further improvement of the model. The parameter values of \( b_i \) through \( b_4 \) that positioned each peak center were changed to 58.3, 276.1, 457.6, and 620.4, respectively (original parameter values×daily effective temperature 11°C; the 11°C was calculated by 24–13°C). Then, additional 223.3 DDs were added to each changed parameter, which were compensating the degree-days required for the completion of pre-oviposition period (average pre-oviposition period 20.3 d×daily effective temperature 11°C). The parameter values of \( a_1 \) through \( a_4 \) that indicated each peak height were scaled to a ratio against the maximum peak height (parameter \( a_4 \)) resulting in 1.00, 0.66, 0.44, and 0.34, respectively. Parameter \( c \), a common parameter controlling the width of peaks, was subjected to change as 48.4 (original parameter value 4.4×daily effective temperature 11.0°C).

**Meteorological data.** Daily average air temperatures were obtained from Jeju weather station located 4 km away from the orchards where the phenological data were collected.

**RESULTS**

**Post-diapause development**

The pre-oviposition periods (from the collection to the first appearance of hatched crawlers) and longevities of overwintered *U. yanonensis* females are shown in Table 1. The pre-oviposition periods were significantly different by the sampling dates
Table 1. Pre-oviposition period and longevity (mean±SE) of overwintered *U. yanonensis* adult females at 24°C

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>n</th>
<th>Pre-oviposition period</th>
<th>n</th>
<th>Oviposition period</th>
<th>Total longevity</th>
<th>Days to the 1st emergence for each sex</th>
</tr>
</thead>
<tbody>
<tr>
<td>7 Nov</td>
<td>22</td>
<td>30.6±3.56 a,b</td>
<td>21</td>
<td>71.3±7.54</td>
<td>102.3±5.66</td>
<td>21</td>
</tr>
<tr>
<td>4 Dec</td>
<td>24</td>
<td>20.3±0.51 bc</td>
<td>19</td>
<td>53.1±3.10</td>
<td>73.4±3.22</td>
<td>23</td>
</tr>
<tr>
<td>28 Dec</td>
<td>29</td>
<td>21.1±0.22 b</td>
<td>13</td>
<td>62.1±3.74</td>
<td>82.7±3.75</td>
<td>—</td>
</tr>
<tr>
<td>19 Jan</td>
<td>34</td>
<td>20.4±0.18 bc</td>
<td>26</td>
<td>58.3±2.51</td>
<td>78.2±2.55</td>
<td>—</td>
</tr>
<tr>
<td>10 Feb</td>
<td>35</td>
<td>19.7±0.17 bc</td>
<td>23</td>
<td>60.4±3.18</td>
<td>80.1±3.23</td>
<td>33</td>
</tr>
<tr>
<td>4 Mar</td>
<td>34</td>
<td>20.1±0.17 bc</td>
<td>26</td>
<td>59.8±2.73</td>
<td>79.8±2.66</td>
<td>33</td>
</tr>
<tr>
<td>25 Mar</td>
<td>36</td>
<td>17.9±0.23 c</td>
<td>12</td>
<td>50.6±2.41</td>
<td>68.3±2.59</td>
<td>32</td>
</tr>
<tr>
<td>24 Apr</td>
<td>20</td>
<td>13.7±0.23 d</td>
<td>12</td>
<td>49.8±0.97</td>
<td>63.4±0.99</td>
<td>18</td>
</tr>
</tbody>
</table>

a All samples were collected in 2006 except the sample of 28 December in 2005.
b Means followed by same letters are not significantly different (p=0.05, Tukey test).
c A two sample t-test was applied for the comparison of days required to the 1st emergence between female and male (ns, not significant; *p<0.05; **p<0.01).
d Not examined.

Table 2. Mean fecundity and sex ratio (mean±SE) of overwintered *U. yanonensis* adult females at 24°C

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>n</th>
<th>Total</th>
<th>Female crawler</th>
<th>Male crawler</th>
<th>Sex ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>7 Nov</td>
<td>21</td>
<td>168.5±27.13 e,b</td>
<td>53.1±8.44</td>
<td>133.2±25.88</td>
<td>3.3±0.69 d</td>
</tr>
<tr>
<td>4 Dec</td>
<td>19</td>
<td>293.7±20.94 b</td>
<td>110.2±11.43</td>
<td>183.5±23.5</td>
<td>3.3±1.30 cd</td>
</tr>
<tr>
<td>28 Dec</td>
<td>13</td>
<td>396.9±26.49 a</td>
<td>—</td>
<td>283.3±19.19</td>
<td>3.4±0.36 bcd</td>
</tr>
<tr>
<td>19 Jan</td>
<td>26</td>
<td>391.5±17.88 a</td>
<td>—</td>
<td>275.2±15.53</td>
<td>4.8±0.63 abc</td>
</tr>
<tr>
<td>10 Feb</td>
<td>23</td>
<td>384.7±18.89 a</td>
<td>101.3±8.78</td>
<td>267.5±15.30</td>
<td>9.5±1.46 a</td>
</tr>
<tr>
<td>4 Mar</td>
<td>26</td>
<td>355.6±13.75 ab</td>
<td>84.0±9.95</td>
<td>251.6±15.05</td>
<td>26.4±2.42 ab</td>
</tr>
<tr>
<td>25 Mar</td>
<td>12</td>
<td>353.3±22.59 ab</td>
<td>46.3±10.20</td>
<td>310.7±23.84</td>
<td>—</td>
</tr>
<tr>
<td>24 Apr</td>
<td>12</td>
<td>335.8±18.22 ab</td>
<td>48.9±10.65</td>
<td>286.8±21.84</td>
<td>—</td>
</tr>
</tbody>
</table>

a All samples were collected in 2006 except the sample of 28 December in 2005.
b Means followed by same letters are not significantly different (p=0.05, Tukey test).
c Not examined.

of females (F=26.4; df=7, 225; p<0.001). However, there were no statistical difference in pre-oviposition periods among samples collected between early December and early March, and its mean preoviposition period was 20.3 d at 24°C. Adult females of *U. yanonensis* collected during the same period produced progeny for about 60 d, and lived for ≈80 d (longevity). Mean pre-oviposition period was longer in the samples collected on 7 November than the period in the females collected on 25 March and 24 April. In the first emergence of crawlers, females appeared later than males (7 November, T=3.53; df=20; p<0.01; 4 March, T=4.54; df=32; p<0.01; 25 March, T=2.65; df=31; p<0.05), although there were no significant differences in some cases (on 4 December, 10 February, and 24 April). Female fecundity was significantly different among sampling dates (Table 2, F=14.9; df=7, 147; p<0.001). A maximum mean fecundity of 396.9 per female was observed in the samples collected on 28 December. Much lower fecundity was observed in the samples on 7 November, and slightly lower fecundity on 4 December. There was no statistical difference in fecundity of the samples collected between 28 December and 24 April. All females collected on 4 December and thereafter produced higher numbers of progeny crawlers than
those collected before 4 December. In the females collected on 7 November and survived longer than 80 d after the collection, 28% of them generated crawlers of \(U. yanonensis\) progeny populations were significantly different with the sampling dates of the parent females, ranging from 3.3 to 9.5 males per female (\(F=7.60; \text{df}=5, 107; p<0.001\)). And, the ratio was much higher when the parent females were collected in the spring (March and April) than in the winter (November, December, and February).

Total 102 data sets were obtained from the samples collected between 28 December and 25 March and applied individually for the parameter estimation of the 4-peak equation. The frequency distributions of crawler emergences were well described by the 4-peak equation. An example of the oviposition cycle of single \(U. yanonensis\) that has an oviposition activity up to the 4th cycle is seen in Fig. 1. Thirty seven females (36.3% of total) survived to the 4th peak period, and were successfully fitted to the 4-peak model. Also, 30 females (29.4% of total) lived till the 3rd peak period, and they showed a successful convergence with 3-peak model. Thus, 67 females (65.7% of total) survived up to the 3rd cycle or more. Consequently, all, 65.7%, and 36.3% of the females contributed to the estimation of parameters associated with 2-peak, 3-peak, and 4-peak model, respectively.

The estimated parameters of the 4-peak Gaussian model are presented in Table 3. Parameters of \(b\) series that indicate the center of each peak were not variable much among the sampling dates in each corresponding peak: average 5.5, 25.2, 41.6, and 56.4 for the 1st, 2nd, 3rd, and 4th peak, respectively. The average peak intervals were 19.7 d for the 1st to 2nd peak, 16.4 d for the 2nd to 3rd peak, and 14.8 d for the 3rd to 4th peak. The height of peaks (parameter \(a\) series) gradually decreased from the 1st peak to the 4th peak, averaging 14.9 for the 1st peak, 9.9 for the 2nd peak, 6.6 for the 3rd peak, and 5.0 for the 4th peak.

Figure 2 shows two types of the multimodal

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**Fig. 1.** An example of the periodical oviposition activity of overwintered \(U. yanonensis\). This example obtained from single \(U. yanonensis\) female. Dotted line (-----), interpolated to daily frequency; solid line with open circles (-○-), 3 d moving average; dashed line (-----), smoothed by Gauss convolution; and solid line (--), estimated by 4-peak Gaussian model.

**Table 3.** Estimated parameter values (mean±SE) of 4-peak equation for the periodical oviposition activity of overwintered \(U. yanonensis\) adult females

<table>
<thead>
<tr>
<th>Sampling date(a)</th>
<th>(a_1)</th>
<th>(a_2)</th>
<th>(a_3)</th>
<th>(a_4)</th>
<th>(b_1)</th>
<th>(b_2)</th>
<th>(b_3)</th>
<th>(b_4)</th>
<th>(c)</th>
<th>(r^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>28 Dec</td>
<td>13.9±0.69</td>
<td>10.0±0.64</td>
<td>7.3±0.85</td>
<td>5.5±0.49</td>
<td>6.1±0.47</td>
<td>26.9±0.57</td>
<td>44.0±0.78</td>
<td>59.0±1.70</td>
<td>4.5±0.12</td>
<td>0.94</td>
</tr>
<tr>
<td>19 Jan</td>
<td>15.9±0.91</td>
<td>10.7±0.47</td>
<td>6.9±0.48</td>
<td>5.6±0.59</td>
<td>5.1±0.15</td>
<td>25.6±0.35</td>
<td>42.0±0.47</td>
<td>57.2±2.02</td>
<td>4.6±0.09</td>
<td>0.91</td>
</tr>
<tr>
<td>10 Feb</td>
<td>15.7±0.59</td>
<td>10.7±0.35</td>
<td>7.3±0.67</td>
<td>5.4±0.29</td>
<td>5.1±0.20</td>
<td>25.1±0.26</td>
<td>42.0±0.59</td>
<td>58.5±1.62</td>
<td>4.2±0.11</td>
<td>0.88</td>
</tr>
<tr>
<td>4 Mar</td>
<td>15.4±0.70</td>
<td>9.8±0.35</td>
<td>6.2±0.39</td>
<td>5.3±0.49</td>
<td>4.8±0.15</td>
<td>24.6±0.28</td>
<td>40.2±0.43</td>
<td>53.5±1.00</td>
<td>4.2±0.13</td>
<td>0.87</td>
</tr>
<tr>
<td>25 Mar</td>
<td>12.6±0.68</td>
<td>8.2±0.51</td>
<td>5.1±0.75</td>
<td>5.2±1.26</td>
<td>5.4±0.37</td>
<td>23.4±0.50</td>
<td>39.9±1.67</td>
<td>53.8±4.59</td>
<td>4.2±0.16</td>
<td>0.89</td>
</tr>
</tbody>
</table>

\(a\) All samples were collected in 2006 except the sample of 28 December in 2005.
oviposition curve of overwintered *U. yanonensis* with the different contribution of female and male crawlers on its overall pattern. A majority of the overwintered females produced much more male crawlers than the females in all ovipositions they had (Fig. 2A). However, about 15% of them, in the first oviposition, produced predominantly more females than males but in the following ovipositions, generated more male crawlers than the females (Fig. 2B).

**Model validation**

Observed and model predicted *U. yanonensis* nymph (1st instar) population patterns in 2005 and 2006 are shown in Fig. 3. The model outputs were almost same with the actual in the 1st peak period. Also, the relative rates of the 2nd peak height were not different between the model results and the actual. During the peak periods after the 1st peak in the model, however, the actual nymph population did not show multimodal peaks. The actual 2nd peak was spread and consisted of the 2nd and the 3rd peak or a partial the 3rd peak of the model. The 4th peak in the model outputs did not contribute to the actual nymph population.

![Fig. 2. Two types of oviposition curve of overwintered *U. yanonensis* comparing the emergence of female and male progeny crawlers. Thick dotted line (· · ·), female crawlers; dotted line (.....), male crawlers; and solid line (—), total crawlers. A: The multimodal pattern were produced by prevailing male crawlers with no specific female peak, B: The 1st peak period was formed by females with few male crawlers, and the remaining peaks were made by most male crawlers.](image)

![Fig. 3. Comparison of model outputs (—, solid line) with actual (dotted line with open circles, · · ·) *U. yanonensis* nymph population in citrus orchards in 2005 (A) and 2006 (B). The actual data were obtained from Kim et al. (2007). The nymph numbers were scaled to a ratio against the peak nymph number.](image)

**DISCUSSION**

**Post-diapause development**

In general, most insects that have once entered diapause cannot leave this state instantly in re-
sponse to favorable conditions (Tauber et al., 1986). Overwintering diapause of most insects ends in mid-winter rather than in the spring (Tauber and Tauber, 1976). All *U. yanonensis* females collected after November and held at 24°C in the laboratory produced crawlers. Some *U. yanonensis* females collected in the early winter, 7 November, and held in the laboratory did not produce crawlers or only produce a few crawlers (Table 2). This indicates that at least a portion of *U. yanonensis* females probably have not yet completed diapause by the collection date, 7 November. Also, longer mean pre-oviposition period and its large variation (see larger standard error) indicate that not all females in the group are at the same physiological state to start post-diapause development. Our observations correspond to the findings of Okudai et al. (1971) in Japan. They reported that *U. yanonensis* females were in a diapause state between mid-September and late November, while females could start post-diapause development from December when met favorable condition. Also, they found prolonged pre-oviposition periods when *U. yanonensis* females received heating-treatment before diapause termination. In Jeju Island, Korea, *U. yanonensis* females are considered in a post-diapause state from early December, since all females collected from December appeared to go through normal post-diapause development and produced their progenies when they were exposed to a favorable environment. Also, fairly constant mean pre-oviposition periods with reduced variations (see smaller standard errors in Table 1) strongly indicate that *U. yanonensis* females between early December and early March are at almost identical physiological state, and are ready for post-diapause development. The big decrease of pre-oviposition period in the population of late April must be caused by warmer outside temperatures above the lower threshold temperature of *U. yanonensis*. Sakagami and Korenaga (1982) reported a developmental threshold temperature of 13°C for egg development (embryogenesis) within ovaries of overwintering females. Average ambient temperatures in Jeju Island frequently exceeded 13°C from early March (KMA, 2006).

Korenaga and Sakagami (1978) showed that average number of eggs produced varied by generation in Shizuoka Prefecture, Japan. The mean number of ovarian eggs was 134.3 and 109.4 for overwintering and the first generation, respectively. In Nagasaki, Japan, the average number of eggs produced by females of the overwintering, the first, and the second generation were 196, 177, and 133, respectively (Kuwana, 1923). The previous studies in Japan indicate that control of progeny produced by overwintered females would have great impact on *U. yanonensis* populations in the growing season. A little information is available on fecundity of overwintering females. Adachi and Korenaga (1991) reported variable fecundities of 150 to 334 crawlers per overwintering female in Shizuoka Prefecture, Japan. The total fecundity of most overwintered females in our study was much higher than those in the previous studies in Japan where the results were obtained either by direct field observations (Adachi and Korenaga, 1991) or by estimations from a regression model between ovarian egg numbers and body lengths (Korenaga and Sakagami, 1978). Our study exploited laboratory observations of individual *U. yanonensis* females and their progeny. It is also possible that *U. yanonensis* strain in Korea may have a higher fecundity than those in Japan. Even though the discrepancy might be attributed to the strain differences of the arrowhead scale between two countries, our results from the laboratory observations are likely to better represent reproductive potentials of overwintered *U. yanonensis*.

The sex ratio of *U. yanonensis* varies in each generation and is not well understood since the laboratory rearing studies have showed variable results. Kohno et al. (cited in Murakami, 1970) showed that male to female sex ratios varied with generations: males were 5.5 and 1.5 times more than females in the first and second generations, respectively, however, the sex ratio was reversed in the third generation that females were more than males at a ratio of 3 to 2. The sex ratios in this study are quite different from the report of Khono et al. The present study found that male to female sex ratios ranged from 3.3 to 9.5 in the progeny of overwintered females and the ratios varied with the time when the overwintered parent females were collected. In addition, the proportion of males increased as the sampling dates were closer to the spring (Table 2). In fact, most of female progeny were produced in the first oviposition of the overwintered females (Fig. 2). Sex-determination system in *U. yanonensis* is not well understood. Sex-
ual dichronism, or the production of male and female progeny at different times, is known in some scale insects and is suggested to play a role in reducing chances of inbreeding or providing higher chances for females to feed quality of food (Gullan and Kosztarab, 1997). Production of more male than female offspring by overwintered females and even more male progeny by the females exposed to longer winter conditions in Jeju, Korea is likely to be an adaptation of *U. yanonensis* to local conditions for better population survival and growth for this sessile scale. It would be interesting to see what environmental factors determine sexual dichroism and the underlying sex-determination system in this sessile insect.

The multi-Gaussian model developed in this study was fitted flexibly to the variable oviposition cycle of *U. yanonensis*. The oviposition data from each female were manipulated in three ways before analysis: first interpolated to daily values, then running-averaged then smoothed. The smoothing processes may generate cycles in random number series resulting in an artificial cyclical pattern. However, the original cyclical pattern was maintained without large losses (Fig. 1). The model would fit a lot better if parameter *c* was peak-specific to the same extent as the other two parameters (*a* and *b*). So, there is some limitation in fitting ability on the peak width. Although the equation and parameters are not based on biological background, the values can be estimated using actual data observed in laboratory experiments. Consequently, the parameter values could be transformed easily to the physiological age (degree-days) of overwintered *U. yanonensis* females, for applying under variable temperatures.

**Field validation**

The 4-peak Gaussian model well predicted the 1st oviposition peak of overwintered *U. yanonensis* in the field, while it showed large discrepancy when compared with the actual in the later peak period (Fig. 3). Unlike the model prediction, there were no specific 4th oviposition peak and no distinctive later peaks in the actual fields. Although the oviposition activity of overwintered *U. yanonensis* females has a typical multimodal form (a distinct 4-peak in many cases) when it is measured on individual level in the laboratory, its overall pattern on population level in the field can be different from the typical form. Figure 4 shows a representative oviposition activity curve for which individual oviposition activities of 23 females collected on 10 February 2006 were integrated. In the integrated oviposition curve the first peak is distinctive but the following peaks are indistinguishable and form a widely spread valley, indicating closer shape with the actual field patterns. Such valley must have been formed by variations of individual oviposition activities. Also, the last oviposition peak (partially the last two peaks) may not be seen in the field condition because of higher mortality of overwintered females during the later oviposition period caused by biotic or abiotic mortality factors, and of overlapping with the crawlers from subsequent generation (Kim et al., 2007). Consequently, it is reasonable to consider that the significant oviposition cycles of *U. yanonensis* in the field is up to the 3rd oviposition. For these reasons the discrepancy might occur during the later peak period. Also, many researchers may have reported two occurrence peaks in the field condition (Murakami, 1970; Adachi and Korenaga, 1991). To increase fitting ability of the model to the field circumstances,
it is required to include the individual variations of oviposition activity of females into the model and to exclude the 4th oviposition from the model. Consequently, the estimated curve in Fig. 5 was re-generated from the data sets in Fig. 4 by removing the 4th oviposition cycle in individual level and integrating all the replicates to incorporate individual oviposition variations. Also, female age in days was converted to degree-days with a lower threshold temperature 13°C. For the purpose of comparison, the nymph numbers were scaled to a ratio against the peak nymph number.

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