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Studies of the Genetics and Expression of Prowng (Pw): A Primitive Homeotic Mutant of the German Cockroach, *Blatella germanica*

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**ABSTRACT**—The prowng, T (9: 10)/9; 10 Pw, is a homeotic mutant of the German cockroach, *Blatella germanica*. Adults are characterized by winglike extensions from the pronotum. This trait is associated with a reciprocal translocation of chromosomes 9 and 10. Translocation heterozygotes express the trait and homozygotes are lethal. The expression of Pw is variable in adults. Individuals with excellent expression show that the pronotal extension is undoubtedly a primitive wing, judging from its venation. We crossed adults with different degrees of expression and found that crosses between parents with excellent expression tended to produce F1 with excellent expression and those with poor expression produced F1 with poor the expression. This suggests that more than one factor is involved in the expression of the trait, and that the different expressions cannot be due to different "expressivity". We also found that the expression Pw was greatly reduced when prowngs were crossed with the Nara wild strain, although this did not happen when they were crossed with individuals with wild-type expression from the Pw strain. This suggests that at least one more factor participates in the expression of Pw. We observed meiosis clearly even in the adult stage. We examined many male adults and confirmed that the reciprocal translocation cause Pw expression without an exception. We also observed the frequencies and stages of embryonic death of F1, from both Pw and Pw × wild type parents. The results agreed well with the ratio between alternate and adjacent disjunction at metaphase I. Pw individuals tended to be delay in nymphal development compared with the wild type.

**INTRODUCTION**

The Pw was first described by Ross (1964), and has been maintained in the Genetic Stock Center for the German Cockroach in the Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA., USA. Genetic studies showed that Pw is inherited as an autosomal, semi-dominant lethal trait (Ross and Cochran, 1965). Subsequently, it was discovered that Pw is associated with a reciprocal translocation between chromosomes 9 and 10, T(9; 10)/9; 10 Pw (Cochran and Ross, 1969). Because pronotal winglets also characterize a deficiency of chromosome 9, it is thought that the trait is associated with the breakage of chromosome 9, (Ross and Cochran, 1971). Pw is characterized by winglike-expansion of the pronotum in the adult stage and a tracheal pattern like that of the mesothoracic wing buds in nymphs. The prowng resembles the paraterral lobes of ancestral insects. Fossil evidence indicates that extinct pterygotes had wing on every thoracic and abdominal segment (Kukalova-Peck, 1978; Carroll et al., 1995). This mutant of the German cockroach is very interesting, since it is a rare case of extant insects bearing a pair of prothoracic wings. It is known that the expressivity of Pw is variable; some individuals have large protrusions that look like wings but others bear only tiny protuberances. However, this expressivity has not been studied quantitatively. Studies of the expressivity may reveal the factors that are involved in the expression of the trait. The purpose of the present study was to examine the combinations of crosses of individual cockroaches with different expressions of Pw and to investigate the meiocytes of the translocation heterozygotes. These date will serve as a foundation for future studies using this variable mutant.

**MATERIALS AND METHODS**

*Maintenance of stock*

Translocation heterozygotes T(9; 10)/9; 10 Pw are characterized by pronotal winglets. The homozygote is lethal. Thus, both crosses (Pw/+ × Pw/+ and Pw/+ × +/+) can be used for maintenance of the stock. The former cross results in Pw/+ : +/+ = 2:1 in the ratio of offspring, but embryonic trapping caused by neighboring dead embryos due to lethal Pw/Pw and adjacent disjunction increases the frequency of embryonic death. The latter cross results in a high percentage of viable offspring, but the ratio of +/+ increases. Therefore, we used both crosses to maintain the stock. Newly molted adult males with +/+ expression were eliminated twice a week, because males can copulate about 4 days after adult eclosion. This means that
both crosses \((Pw^+ \text{ male } \times Pw^+ \text{ female})\) and \((Pw^+ \text{ male } \times +/+ \text{ female})\) take place in the stock container. The simple energy-saving method may be the best way to maintain the \(Pw\) strain.

**Crosses**

Newly molted adults were used for crosses in most cases. All females used were newly molted adults of the males, newly molted adults were preferably used as parents. However, a few males with degrees of \(Pw1\) and \(Pw2\) (see below) in \(Pw\) expression were used from the stock container, because these degrees were relatively rare and it is sometimes difficult to achieve good timing for mating only newly molted males were to be used. The \(Pw\) expression of the parents was categorized into 4 grades: poor (\(Pw1\)), intermediate (\(Pw2\)), good (\(Pw3\)) and excellent (\(Pw4\)). Individuals with completely wild type expression from the \(Pw\) strain were also used (\(Pw^+\)). Nara wild individuals (Nara) were also mated with every expression (\(Pw^+ \times Pw4\)) of the \(Pw\) strain. For the judgment of \(F_1\) expression, degrees were classified into 7 grades: \(Pw\) 0, 1, 1, 2, 3, 4 and 4*; in addition to the grades used in the parents, the two grades of marginally poor (1) and exceptional (4*) were added. In the calculation of the average, the degrees of \(Pw\) expression 1, 2, 3, 4, and 4* were given the values 0.5, 1, 2, 3, 4, and 4.5, respectively. To identify the stage of embryonic death, the developmental table of the German cockroach was used (Tanaka, 1976).

**Chromosome observation**

The testes of the fourth to the last instars and adults were observed. The testes were dissected and then immersed in water for 5 min. to make them swell. The left and right testes were placed separately in droplets of 15% acetic acid on a glass slide, and excess fat body was removed from the testes forceps. The testes were stained with acetic orcein less than 5 min. covered with a cover glass, and pushed gently with the head of a forceps; the excess orcein was thus soaked up. Each testis was then wrapped with tissue paper, put upside down and, pushed forcefully by the examiner’s thumb from behind the slide to flatten the testis. Fingernail polish was then spread along the edge of the cover glass. The specimen was observed with a phase contrast microscope.

**RESULTS**

The expressivity of \(Pw\) in adults was variable. Expression was often similar between the left and right sides, as shown in Fig. 1, but sometimes differed between the sides. Individuals without the translocation (+/++) in the \(Pw\) stock showed wild type expression, as in Fig. 1a. The translocation heterozygotes showed a large variety of \(Pw\) expression (Fig. 1b-e). A few \(Pw\) individuals in the \(Pw\) stock showed still poorer expression, designated as (1*), which was often encountered in the heterozygotes outcrossed to the Nara wild strain. Close examination confirmed the finding of Ross (1964) that postero-lateral protrusions of the pronotum are serially homologous with wings and similar to structures in early fossil insects, although sometimes this seemed doubtful in gross examinations, especially when the degree of expression was poor. Figure 2 shows that veins occur in pronotal winglets like those of the wing (also see Ross 1964, Fig. 5c-d).

Table 1 shows the percentages of \(Pw\) expression in \(F_1\), individuals between parents with various expression of \(Pw\). Crosses between phenotypical wild type siblings of \(Pw\) resulted in no \(F_1\), with \(Pw\) expression. Reciprocal crosses between Nara wild strain and \(Pw^+\) also resulted in no \(Pw\) expression in the \(F_1\). The percentages of \(Pw\) individuals from crosses between the Nara wild and \(Pw\) strain with \(Pw\) expression fluctuated in the range from 41.0% to 53.3% by the degrees of \(Pw\) expression. The average of these was 46.6%, nearly equal to the expected 50%. The percentages of \(Pw\) from crosses within the \(Pw\) strain between wild type siblings and \(Pw\) (\(Pw\) 1-4) ranged from 46.5% to 57.6%. The average was 52.3%, also nearly equal to the expected 50%. The percentages of \(Pw\) from crosses between parents with \(Pw\) expression fluctuated from 59.4% to 83.3% by the degrees of expression. The average of 16 combinations was 72.1% \(Pw\), close to the expected value, 69% (see Discussion).

In order to study the \(Pw\) expressivity between \(P_1\), and \(F_1\), crosses of various degrees of expression were carried out. Individuals showing the typical degrees 1-4 (Fig. 1) were selected as parents. The Nara wild strain was also used as a control of the outcross. In the observation of \(F_1\), besides the typical degrees 1-4, very poor expression (\(Pw1\)) and exceptional (\(Pw4^+\)) were encountered. Therefore, in the calculation of the average expression, \(Pw1\) and \(Pw4^+\) were given the values 0.5 and 4.5, and \(Pw1\) to \(Pw4\) were assigned the values 1 to 4, respectively. Table 2 summarizes the results of these crosses. In the experiment with parents both with \(Pw\) expression, \(Pw4 \times Pw4\) resulted in the highest average value (3.53), but less than the parental value of 4. Likewise, \(Pw4 \times Pw3\) resulted in the value 3.26, the reciprocal average of 101 offspring (61 from \(Pw3\) male \(\times Pw4\) female and 40 from \(Pw3\) female \(\times Pw4\) male). The value from the \(Pw3 \times Pw3\) cross (2.85) was nearly equal to that of the reciprocal averages of \(Pw4 \times Pw2\) (3.01). The next highest values appeared in the reciprocal averages of \(Pw3 \times Pw2\) (2.85) and \(Pw4 \times Pw1\) (2.55). These values were almost equal to the average of the parents. The value of \(Pw2 \times Pw2\) was 2.28, and the reciprocal average of \(Pw3 \times Pw1\) was 2.38; both values were slightly higher than the values of the parental average. The next lowest value was found in the \(Pw2 \times Pw1\); the reciprocal average was 1.78, also somewhat higher than that of the parents. The lowest average (1.50) was from the \(Pw1 \times Pw1\) cross; this value was higher than that of the parents. In the crosses between \(Pw\) and wild type siblings (\(Pw^+\)), the reciprocal averages of \(Pw^+ \times Pw1\), \(Pw^+ \times Pw2\), \(Pw^+ \times Pw3\), and \(Pw^+ \times Pw4\) were 1.88, 2.42, 2.29, and 3.01, respectively. These values did not suggest any inhibitory factors of \(Pw\) expression from \(Pw^+\) parents, especially in the crosses of \(Pw^+ \times Pw1\), and \(Pw^+ \times Pw2\). In contrast, when \(Pw1\), \(Pw2\), \(Pw3\), and \(Pw4\) were outcrossed to the Nara wild strain, the reciprocal averages much lower, i.e., 0.92, 1.18, 1.24, and 1.08, respectively, suggesting that the Nara wild strain has inhibitory factor(s) on \(Pw\) expression. The \(F_1\) of Nara wild \(\times Pw^+\), and \(Pw^+ \times Pw^+\) all showed wild type expression, as expected.

Table 3 shows the percentages of hatching and deaths at various embryonic stages. Both crosses of Nara wild \(\times Pw^+\) and \(Pw^+ \times Pw^+\) resulted in high percentages of hatching. The former showed the normal percentage of the Nara wild standard. In the latter, a few embryos (3.42%) died before stage 12; the reason for this unknown. There were no
Fig. 1. Wild type (a) and various expressions of Pw. Degrees of 1–4+(b)–(f), respectively. 1, poor; 2, intermediate; 3, good; 4, excellent; 4+, exceptional.

Table 1. The percentages of Pw individuals in F1 from crosses with various degrees of Pw expression, including outcrosses to Nara wild strain.

<table>
<thead>
<tr>
<th></th>
<th>Nara</th>
<th>Pw+</th>
<th>Pw1</th>
<th>Pw2</th>
<th>Pw3</th>
<th>Pw4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nara</td>
<td></td>
<td>0.0 (277)</td>
<td>41.9 (160)</td>
<td>48.4 (128)</td>
<td>49.7 (173)</td>
<td>53.3 (122)</td>
</tr>
<tr>
<td>Pw1</td>
<td>44.4 (215)</td>
<td>57.1 (119)</td>
<td>83.3 (54)</td>
<td>65.3 (72)</td>
<td>69.7 (109)</td>
<td>75.0 (68)</td>
</tr>
<tr>
<td>Pw2</td>
<td>41.0 (173)</td>
<td>48.8 (160)</td>
<td>59.4 (69)</td>
<td>72.7 (66)</td>
<td>75.6 (90)</td>
<td>77.6 (67)</td>
</tr>
<tr>
<td>Pw3</td>
<td>44.3 (183)</td>
<td>56.7 (171)</td>
<td>71.2 (52)</td>
<td>80.9 (68)</td>
<td>71.6 (102)</td>
<td>77.2 (79)</td>
</tr>
<tr>
<td>Pw4</td>
<td>51.1 (219)</td>
<td>54.1 (146)</td>
<td>67.0 (94)</td>
<td>69.9 (73)</td>
<td>72.7 (55)</td>
<td>68.7 (67)</td>
</tr>
</tbody>
</table>

Numbers of F1 that reached adulthood are shown in parentheses. Nara, Nara wild strain; Pw+, wild-type expression of Pw stock; Pw1, Pw2, Pw3 and Pw4, degrees 1–4 expression of Pw stock, respectively (see Fig. 1).

Fig. 2. Evidence that a pronotal protrusion is actually a small wing, judging from its venation.
significant differences between Nara wild × Pw (1–4) and Pw+ × Pw (1–4) in the percentages of hatching and embryonic death, in spite of great differences in Pw expression (Table 2). Both crosses showed about 68% hatching, very close to the theoretical value, 67% (see Table 4). The embryonic death rate before stage 17 was about 30%, also close to the theoretical value (33%). In the crosses between parents with Pw expression (1–4), 11% of the embryos died by embryonic trapping (Keil and Ross, 1977) due to the death in neighboring compartments of the ootheca. High percentages of embryonic death, 48.21% before or at 12 and 10.33% from st.13 to st.17, caused siblings to fail to hatch due to embryonic trapping within the ootheca. The percentage of hatching including those of embryonic trapping reached about 41%, close to the theoretical value, 36% (see Discussion ). The total death rate by stage 17 was about 59%, also close to the theoretical value (64%).

The diploid number of chromosomes of Blattella germanica females is 2n = 24, XO type (Suomalainen, 1946). We found that meiosis is easily observable, even in the adult stage. We examined many testes of adult males with or without Pw expression, and found that all translocation heterozygotes show Pw expression and all wild type zygotes have wild type pronota. Figures 3 and 4 show some comparisons between translocated and wild type meiocytes. There was a clear difference at the diplotene stage. Eleven paired chromosomes and an X chromosome were always found in the wild type (Fig. 3a), whereas configurations typical of reciprocal translocations were always found in the Pw males (Fig. 3b). At diakinesis in the wild type, 12 groups of chromosomes were found including X, some as rings, others as rods, according to the number of chiasmata which were already terminalized (Fig. 3c). In contrast, in the Pw at diakinesis, 11 groups of chromosomes were found; one was a large ring consisting of 4 member chromosomes (Fig. 3d). The wild type at metaphase I is shown in Fig. 4a. The Pw meiocytes showed either the adjacent type of disjunction (Fig. 4b) or the alternate type (Fig. 4c), as described by Cochran (1977).

Table 4 shows all possible combinations of chromosomes from the matings between translocation heterozygotes. The theoretical average percentage of such undeveloped embryos is 64% (both parents are Pw+) or 33% (one of parents is +/+ ) if the alternate:adjacent ratio is 2:1, the same ratio as in the testis and ovary. Dead embryos were easily distinguished from normal ones. Figure 5 shows some examples of oothecae including such embryos together with normal ootheca. Figure 5a is a normal wild type ootheca. An advanced- stage embryo can be seen in each compartment. When one of the parents was Pw, about 1/3 of the embryos died during embryonic development (Fig. 5b). About 2/3 of the embryos died when both parents were Pw (Fig. 5c).

We compared the period of nymphaal development between individuals with various degrees of Pw expression and wild type expression (Table 5). The total period from hatching to adult ecdysis was recovered in all individuals. Siblings from the same ootheca were divided into groups: reaching adulthood in the first half period among the siblings, and reaching adulthood in the last half period. The date of the individuals from all oothecae in each type of cross are
Fig. 3. Meiosis I of Blattella germanica (n=12). (a) and (b), diplotene–early diakinesis; (c) and (d), diakinesis; (a) and (c), wild type; (b) and (d), prowing. A diamond shape (b) and a large ring (d) show reciprocal translocation.

Fig. 4. Metaphase I of Blattella germanica. (a) wild type; (b) prowing, adjacent disjunction (rectangle-shaped); (c) prowing, alternate disjunction (Z-shaped in the center of the photo).
Table 4. Zygotic combination from every disjunction type of gamete in the crosses between translocation heterozygotes, T(9; 10)/9; 10 Pw

<table>
<thead>
<tr>
<th>Sperm</th>
<th>Alternate</th>
<th>Adjacent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ab</td>
<td>t; t₂</td>
</tr>
<tr>
<td>ab</td>
<td>4 aabb</td>
<td>4 at₁</td>
</tr>
<tr>
<td>4</td>
<td>16+/+</td>
<td>16 Pw/+</td>
</tr>
<tr>
<td>t; t₂</td>
<td>4 abt₁</td>
<td>4 bt₁</td>
</tr>
<tr>
<td>4</td>
<td>16 Pw/+</td>
<td>16 Pw/Pw</td>
</tr>
<tr>
<td>at₁</td>
<td>4 aab₁</td>
<td>4 abt₁</td>
</tr>
<tr>
<td>1</td>
<td>4 at₁</td>
<td>4 at₁</td>
</tr>
<tr>
<td>bt₁</td>
<td>4 abt₁</td>
<td>4 bt₁</td>
</tr>
<tr>
<td>1</td>
<td>4 abt₁</td>
<td>4 abt₁</td>
</tr>
<tr>
<td>at₂</td>
<td>4 aab₁</td>
<td>4 at₁</td>
</tr>
<tr>
<td>1</td>
<td>4 at₁</td>
<td>4 at₁</td>
</tr>
<tr>
<td>bt₁</td>
<td>4 abt₁</td>
<td>4 bt₁</td>
</tr>
<tr>
<td>1</td>
<td>4 abt₁</td>
<td>4 abt₁</td>
</tr>
</tbody>
</table>

a and b indicate chromosome 9 and 10, respectively, in case of T(9; 10)/9; 10 Pw.
Ⅳ and Ⅰ; two different types of translocated chromosomes.
+/, wild type; Pw/+; phenotypic Pw; Pw/Pw; homozygotic lethal.
Other combinations are lethal due to an incomplete set of chromosomes.
Numbers indicate ratios in supposition that alternate: adjacent=2: 1

Fig. 5. Comparison of oothcae. (a) wild type (living); embryos of advanced stage can be seen through the surface of the ootheca in all compartments. (b) Pw × wild type (living); dead embryos (white appearance) are often found (theoretically 33% dead). (c) Pw × Pw (specimen in 80% ethanol); live embryos are dark, dead embryos are light-colored (theoretically 64% dead).

summarized in Table 5. In every type of cross, the wild type individuals tended to grow faster than those with Pw expression. In the cross of Nara wild to Pw, many F₁ with extremely poor expression (Ⅰ) appeared, and some were delayed in nymphal growth.

**DISCUSSION**

It was found that the expression of Pw is more or less inheritable (Table 2). Therefore, differences in the expression of Pw cannot be thought of as differences of the expressivity of genetically identical individuals. The data in Table 2 suggests that Pw expression may be related to three or more factors. Since Pw is associated with the breakage of chromosome 9...
(Ross and Kell, 1978), the site of chromosome breakage may include one or more inhibitory factor(s) of pronotal wings, because normal gene(s) in the site act as inhibitor(s) to completely suppress the primitive trait. The expression of the F₁ showed a gradient according to that of their parents in the crosses between two parents with Pw expression. This finding suggests that more than one factor is involved in Pw expression. Some factor(s) might not be in the translocation site. Another factor may exist because the average expression tended to be much less in the outcrosses to Nara wild strain than in the crosses to the +/+ of the Pw strain.

It has been believed that the meiosis of cockroaches is rarely encountered in adult testes and should thus be observed during the nymphal stage. We found here that many meiocytes can be frequently observed in the adult testes. The occurrence of early-stage meiocytes in adult males is possibly a reserve for later matings, since the males copulate several times during their life span. We confirmed the findings on Pw nymphs (Cochran and Ross, 1969) that individuals with Pw expression have translocated chromosomes and those with wild type expression have wild type chromosomes. The penetrance is thus 100%.

The ratios between alternate and adjacent disjunction differ among mutants of translocation heterozygotes. It is known that the frequency of alternate disjunction in the growing mutant is 63–64% in male nymphs (Cochran and Ross, 1974; Cochran, 1977). Table 4 shows all zygotic combinations with the ratio in supposition that the alternate:adjacent ratio is about 2:1, close to the previous finding in the testes (Cochran and Ross, 1974). The observation of meiocytes in ovaries is almost impossible due to the large amount of yolk. Therefore, the same ratio was assumed in the ovary to make this table. The ratio of +/+ : Pw/+ : Pw/Pw (lethal); deficiencies (lethal) is 16:36:16:76 under the supposition of alt.:adj. = 2:1 in both male and female meiocytes. The percentages are theoretically 11%, 25%, 11%, and 53%, respectively. The average Pw expression of F₁ from the Pw/+ × Pw/+ crosses shown in Table 1 was 72.1%, which agrees well with the theoretical estimates of 69% and 67.1% from an earlier study (Ross and Cochran, 1965). Pw/Pw may correspond to late embryonic death, and chromosomal deficiency may cause early embryonic death. This supposition also explains the results shown in Table 3 that the incidence of late embryonic death was 10.33% and that of early embryonic death was 48.21%. The first column of Table 4 shows the results that would be expected from matings between Pw/+ and +/+ . The ratio of offspring of +/+ , Pw/+ , and deficiencies (lethal) are 33% each. Thus, the expected ratio of viable offspring between +/+ and Pw/+ is 1:1. This explains the results of Tables 1 and 5 that the frequency of Pw was 46.6% in Nara wild × Pw/+ and 52.3% in Pw/+ × Pw/+ . Both were close to 50% and agree with the data of Ross and Cochran (1965). The percentages of embryonic death as of stage 17, about 30% in both Nara wild × Pw/+ and +/+ × Pw/+ (Table 3), are also explained by the date in the first column of Table 4.

From the viewpoint that Pw expresses a primitive developmental pathway, it is of interest that the loci of other primitive traits such as notched sternite (stf) (Ross, 1966), miniature-wing (min) (Ross and Kell, 1978), stumpy (sty) (Ross, 1975; Tanaka and Ross, 1989), and maxillary-palp-elongate (mpe) (Ross and Tanaka, 1988; Tanaka and Ross, 1990) are on the same chromosome. Concerning the origin of insect wings, the pronotal wings of the German cockroach seems to favor the paratantal hypothesis (Hinton, 1963; Rasnitsyn, 1981), although other evidence seems to support the pleurral hypothesis (Wigglesworth, 1963; Kukalova-Peck, 1983).

ACKNOWLEDGMENTS

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Table 5. Comparison of nymphal period of F₁ between wild-type and Pw expression

<table>
<thead>
<tr>
<th>Cross</th>
<th>No. hatched before adulthood</th>
<th>No. died before adulthood</th>
<th>No. reached adulthood</th>
<th>+ Pw (1⁻) 1 2 3 4 4' (Average)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nara × Pw 1-4</td>
<td>1406</td>
<td>32</td>
<td>1374</td>
<td>F 422 288 83 116 78 11 – – (1.20)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>L 312 352 153 126 62 11 – – (1.02)</td>
<td></td>
</tr>
<tr>
<td>Pw+ × Pw 1-4</td>
<td>1273</td>
<td>61</td>
<td>1212</td>
<td>F 366 364 8 40 88 88 38 2 (2.44)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>L 212 370 14 54 135 118 42 7 (2.39)</td>
<td></td>
</tr>
<tr>
<td>Pw 1-4 × Pw 1-4</td>
<td>1243</td>
<td>58</td>
<td>1185</td>
<td>F 222 425 11 50 123 139 92 10 (2.66)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>L 109 429 8 64 122 166 63 6 (2.54)</td>
<td></td>
</tr>
</tbody>
</table>

*F and L, individuals reached adulthood during the first half period, or the last half period, respectively, of the total period of adult molts. 1:1, 1, 2, 3, 4 and 4' were given value 0.5, 1, 2, 3, 4 and 4.5, respectively, in calculation.
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