Developmental and reproductive response of *Brachmia macroscopa* (Lepidoptera: Gelechiidae) to three host plants

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The sweet potato leaf folder, *Brachmia macroscopa* Meyrick (Lepidoptera: Gelechiidae), which is a significant pest of plants in the family Convolvulaceae, is rapidly expanding its range in South China and other subtropical regions. Studies were designed to examine the effects of three different host plants (*sweet potato*, *Ipomoea batatas* (L.) Lam.; *water spinach*, *I. aquatica* Forsskål; and *morning glory*, *Pharbitis purpurea* (L.)) on the development and life table parameters of *B. macroscopa* under laboratory conditions. We found that the intrinsic rates of increase of *B. macroscopa* were 0.17 ± 0.004, 0.21 ± 0.005 and 0.16 ± 0.004 on *I. batatas*, *I. aquatica* and *P. purpurea*, respectively. The highest net reproduction rate was 158.06 ± 18.22 per female reared on *I. aquatica*. The larvae had five instars when reared on *I. batatas* and *I. aquatica*, but required six instars on *P. purpurea*. The mean generation lengths of *B. macroscopa* ranged from 24.32 ± 0.18 days when reared on *I. aquatica* to 29.40 ± 0.24 days on *P. purpurea*. The survival of all stage and fecundity curves was intuitively manipulated using the age-stage-structured and two-sex population life table method, to enable comprehensive descriptions of the stage and population trends of *B. macroscopa* on the three Convolvulaceae plants. Our results indicated that *I. batatas* and *I. aquatica* were more suitable host plants than *P. purpurea*.

The relationships between insects and their host plants are considered to be co-evolutionary interactions. In the process of long-term evolution and adaptation to their environment, insects have gradually produced selectivity to their hosts. The host preference may not only influence the growth and development of insects, it may also play an important role in the growth of their population. Feeding on different host plants can also affect the susceptibility of some insect species to certain pesticides. Some studies have shown that the response of insects to the host is based on their demand for external nutrition, while other researchers are of the opinion that the insects are affected by secondary metabolites in the host plants. In general, when insects fed on plants that they are adapted to, their growth and survival rates will be optimal and their reproductive capacity will be at a high level, and vice versa. Host plants, in order to discourage insect feeding behavior, are also continually developing an array of defensive strategies, including phenological defenses, physical defenses, chemical defenses, etc. The overuse of chemical pesticides to control lepidopteran (and other) pests during the past few decades, has forced targeted insects to evolve in terms of inherent behavioral mechanisms, and altered ecological, genetic and physiological factors, with the end result being the development of resistance to many chemical controls. For example, in using the insecticide fenvalerate in the field to control the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), and spraying 10 or more times a year for only two years, has resulted in local populations of the moth that are as much as 12,000 times more resistant to pyrethroid insecticides than other populations.

The sweet potato leaf folder, *Brachmia macroscopa* Meyrick (Lepidoptera: Gelechiidae), is a widely distributed pest in Europe, Russia, Caucasus, Transcaucasian region, West Kazakhstan, central Asia, Korea, Japan, China, and northern India. It mainly damages *Dioscorea esculenta*, *Ipomoea aquatica*, *Calystegia sepium*, *Croomia japonica* and other crops in the Convolvulaceae family. The damage to crops by larvae is significant greater than it is the adult stage. The host plant leaves are damaged by the larvae skeletonizing the surface, leaving only the transparent...


Table 1. The mean (±SE) duration of immature stages (days) of Brachmia macroscopa reared on three hosts under laboratory conditions. Note: Data in the table are stated as mean ± SE. Means in the same row marked with different letters are significantly different at the 5% level using the Tukey-Kramer test. n, effective replicate number; \( \bar{x} \), mean value; SE, standard error; df, degree of freedom; F, value of Levene’s Test; P, statistical significance.

|                      | Ipomoea batatas | Ipomoea aquatica | Pharbitis purpurea |
|----------------------|-----------------|-----------------|--------------------|
| Egg stage            | 139 (150)       | 142 (149)       | 145 (150)          |
|                      | \( 5.00 \pm 0.00a \) | \( 4.00 \pm 0.00a \) | \( 4.00 \pm 0.00a \) |
| 1st instar stage     | 138 (139)       | 140 (142)       | 137 (145)          |
|                      | \( 1.85 \pm 0.04a \) | \( 1.15 \pm 0.03c \) | \( 1.33 \pm 0.05b \) |
| 2nd instar stage     | 138 (138)       | 138 (140)       | 134 (137)          |
|                      | \( 1.96 \pm 0.03a \) | \( 2.02 \pm 0.06a \) | \( 1.71 \pm 0.07b \) |
| 3rd instar stage     | 135 (138)       | 137 (138)       | 125 (134)          |
|                      | \( 2.08 \pm 0.02b \) | \( 2.20 \pm 0.06ab \) | \( 2.26 \pm 0.07a \) |
| 4th instar stage     | 132 (135)       | 132 (137)       | 121 (125)          |
|                      | \( 2.20 \pm 0.05a \) | \( 2.25 \pm 0.04a \) | \( 2.29 \pm 0.07a \) |
| 5th instar stage     | 129 (132)       | 125 (132)       | 121 (121)          |
|                      | \( 4.41 \pm 0.08a \) | \( 3.91 \pm 0.06b \) | \( 2.46 \pm 0.07c \) |
| 6th instar stage     | —               | —               | 119 (121)          |
|                      | —               | —               | \( 4.43 \pm 0.08a \) |
| Larval stage         | 129 (129)       | 125 (125)       | 119 (119)          |
|                      | \( 12.46 \pm 0.11b \) | \( 11.50 \pm 0.11c \) | \( 14.36 \pm 0.14a \) |
| Pupal stage          | 127 (129)       | 119 (125)       | 119 (119)          |
|                      | \( 5.04 \pm 0.03b \) | \( 5.10 \pm 0.03b \) | \( 5.68 \pm 0.10a \) |
| Total pre-adult period | 127 (127)   | 119 (119)       | 119 (119)          |
|                      | \( 22.50 \pm 0.12b \) | \( 20.48 \pm 0.10c \) | \( 24.06 \pm 0.18a \) |

Results

Larval stages. B. macroscopa was capable of completing its entire life cycle when fed on each of the three host plants tested, although the duration of each stage varied (Table 1). The developmental time of the egg stage was 4 days on I. aquatica and P. purpurea, which was shorter than eggs laid on I. batatas (5 days). The B. macroscopa larval developmental durations were significantly different (\( P < 0.0001 \)) when reared on the three plants. When fed on P. purpurea, the larvae required six instars to complete development with a developmental period of 14.36 ± 0.14 d, which was the longest total growth period among the three host species. The larval development on I. batatas and I. aquatica required only five instars, and lasted 12.42 ± 0.11 d and 11.50 ± 0.11 d, respectively. Significant differences occurred in the developmental duration (\( P < 0.0001 \)) of the 1st and 5th larval stage when reared on the three host plants, but were not found in the 4th instar stage (\( P = 0.536 \)). There was no significant difference between I. batatas and I. aquatica in the duration of the 2nd instar (\( P = 0.448 \)), or in the 3rd instar (\( P = 0.116 \)); nor were there significant differences in the 3rd instar stage between I. aquatica and P. purpurea (\( P = 0.454 \)), although the duration of the 2nd instar when fed on I. aquatica was longer than on P. purpurea. No significant difference occurred in the 3rd instar between I. batatas and I. aquatica (\( P = 0.116 \)). The 2nd instar larval development duration when fed on I. aquatica was longer than on P. purpurea. The reverse, however, was true during the 3rd and 4th instars. There were no significant differences between the lengths of the pupal periods after being fed on I. batatas and I. aquatica (\( P = 0.479 \)). The total durations of the larval developmental periods of B. macroscopa fed on the three host plantsdid show significant differences: the relationship of the lengths was: P. purpurea > I. batatas > I. aquatica, (24.06 ± 0.18 d, 22.50 ± 0.12 d and 20.48 ± 0.10 d, respectively).

Total duration and longevity of the adult stage. It is evident from Table 2, that when B. macroscopa larvae are fed on different host plants, the average lifespans of both male and female adults were significantly different with P. purpurea < I. aquatica < I. batatas (\( P < 0.0001 \)), although there were no significant differences (\( P = 0.101 \)) found in the adult female longevity after feeding on I. batatas (31.70 ± 1.27 d) and I. aquatica (28.91 ± 1.37 d). Adult females reared on P. purpurea had significantly (\( P < 0.05 \)) shorter average life spans (19.90 ± 0.85 d) compared to the other two groups. The lowest larval survival rate, 79.19% occurred when fed on I. aquatica, although the rate on P. purpurea, 79.33%, was very similar. The highest larval survival rate, 84.67%, occurred in the group fed on I. batatas.

Oviposition period and fecundity. Significant differences (\( P < 0.05 \)) were found in B. macroscopa adult females reared on the three host plants for the adult pre-oviposition period (APOD; the period of time between the emergence of an adult female and the onset of her first oviposition), the total pre-oviposition period (TPOP;
showed that 0.95, 0.97, 0.83 and 0.99, respectively.

Table 2. The mean (+SE) duration of adult lifespan, longevity (days) and mortality of immature stages of Brachmia macroscopa reared on three hosts under laboratory conditions. Note: Data in the table are stated as mean ± SE. Means in the same row marked with different letters are significantly different at the 5% level using the Tukey-Kramer test. n, effective replicate number; χ, mean value; SE, standard error; df, degree of freedom; F, value of Levene’s Test; P, statistical significance.

Table 3. The mean (+SE) duration of oviposition periods (days) and fecundity rates of Brachmia macroscopa reared on three hosts under laboratory conditions. Note: Data in the table are stated as mean ± SE. Means in the same row marked with different letters are significantly different at the 5% level using the Tukey-Kramer test. n, effective replicate number; χ, mean value; SE, standard error; df, degree of freedom; F, value of Levene’s Test; P, statistical significance.

the time interval from birth to the beginning of oviposition), the oviposition period and total fecundity (total number of eggs produced during an individual’s reproductive period) (Table 3). Although the APOP of B. macroscopa female adults from I. batatas (1.45 ± 0.12 d) and P. purpurea (1.39 ± 0.10 d) were similar and not significantly different (P = 0.734), the APOP on I. aquatica (0.44 ± 0.10 d) was significantly shorter (P < 0.05) than the other two groups. The results demonstrated that the fecundity of adult females from I. aquatica (427.20 ± 18.08) was significantly higher (P < 0.05) than it was in the I. batatas (298.18 ± 11.42) and P. purpurea (299.03 ± 8.86) groups.

Since only female adults produce offspring, there is only a single curve representing the female age-stage-specific fecundity (f_{xj}). The age-stage-specific fecundity (f_{xj}) on the three different host plants occurred at 25, 22, and 28 days with corresponding f_{xj} values of 27.71, 61.40 and 33.48, respectively (Fig. 1) (single female fecundity per day). The highest and lowest age-specific fecundity values (m_j) were found on I. aquatica and I. batatas separately. The f_{xj}, m_j and λ, values for B. macroscopa fed on the three plants were in the order: I. aquatica, P. purpurea, I. batatas.

Survival rate. The age-stage-specific survival rates (S_{xj}) of B. macroscopa fed on the three different host plants are shown in Fig. 2. It displays the survival rates at various developmental stages (egg, larva, pupa, adult) and the differences in developmental rates of different ages (eggs, 1st instar, 2nd instar, 3rd instar, 4th-6th instar larvae, pupae, and male and female adults). This graphic display demonstrates the overlapping phenomenon of different ages. When B. macroscopa larvae fed on I. batatas, I. aquatica and P. purpurea, the probabilities of newly produced eggs successfully developing into adult females were 0.51, 0.62 and 0.59, respectively. Comparable values for the adult males were 0.64, 0.59 and 0.41. The experimental results also showed that the survival rates of different aged B. macroscopa fed on I. batatas were higher than on I. aquatica and P. purpurea. The survival rates of the egg, larval and pupal stages of B. macroscopa on I. batatas, I. aquatica and P. purpurea were 0.93, 0.93, 0.99, 0.95, 0.89, 0.95, 0.97, 0.83 and 0.99, respectively.

Life expectancy and reproduction rate contribution value. The age-stage life expectancy (e_{xj}) is the expected lifespan of different individuals at age x and stage j when fed on different host plants (Fig. 3). Brachmia macroscopa had the longest life expectancy on I. batatas, followed by I. aquatica and then P. purpurea. The results showed that B. macroscopa growth on I. batatas was relatively slow. The reproductive value (v_{xj}) is the contribution of different individuals at age x and stage j to future population growth (Fig. 4). The reproductive value reached its highest peak on the 24th day (V_{24,7} = 130.01), 21st day (V_{21,7} = 212.97.01) and 25th day (V_{25,7} = 149.30) when fed on I. batatas, I. aquatica and P. purpurea, respectively.

Population parameters. The parameters relevant to population development: net reproductive rate (R_0), total reproduction rate (GRR), intrinsic rate of increase (r), finite rate of increase (λ), average mean generation
time ($T$), and standard error, that were calculated for $B. \text{macroscopa}$ populations reared on the three different host plants, are shown in Table 4. There were no significant differences ($P > 0.05$) in the $R_0$ and GRR of $B. \text{macroscopa}$ fed on the three hosts. The $R_0$ from high to low value occurred on $I. \text{aquatica}$, $I. \text{batatas}$ and $P. \text{purpurea}$ ($158.06 \pm 18.22$, $147.59 \pm 13.46$ and $122.01 \pm 12.55$), respectively. The highest GRR ($203.73 \pm 21.65$) was found in the $I. \text{aquatica}$ group, followed by $P. \text{purpurea}$ ($177.80 \pm 17.87$), with the lowest value ($175.98 \pm 14.80$) occurring in the $I. \text{batatas}$ group. There were no significant differences ($P > 0.05$) in the $r$, finite rate $\lambda$ and $T$ of $B. \text{macroscopa}$ reared on $I. \text{batatas}$ and $P. \text{purpurea}$. The $B. \text{macroscopa}$ group reared on $I. \text{aquatica}$, however, had significantly

Figure 1. Age-specific survival rate ($l_x$), age-specific fecundity ($m_x$), age-specific morpentry ($l_xm_x$) and age-stage-specific fecundity ($f_{x8}$) of $Brachmia \text{macroscopa}$ reared on three host plants under laboratory conditions.
P > 0.05) higher r and λ values than the other two groups, although the T on *I. aquatica* (24.32 ± 0.18 d) was shorter than it was on *I. batatas* (28.76 ± 0.23 d) and *P. purpurea* (29.40 ± 0.24 d) (*P* < 0.05).

**Discussion**

The development period and fecundity of lepidopterous insects, as well as insect populations in general, are influenced by many factors, including the availability of suitable host plants. The selection of appropriate local host plants plays a vital role in determining whether a natural population will grow or decline. An ideal means of deciphering the factors that enter into this selection is via the use of life tables. Life tables are also useful in
providing applied and practical information regarding a given pest’s survival, fecundity and developmental times. Moreover, difference in the individual’s growth and developmental when feeding on different plants can also be determined. Damage caused by B. macroscopa to the three widespread hosts selected for this study, I. batatas, I. aquatica and P. purpurea, has been widely recorded in many countries besides China. Because insecticides have traditionally been used to suppress outbreaks of this pest, it is hoped that further understanding the life history of B. macroscopa will allow growers to decrease their dependence on pesticides in attempts to control this widespread pest in the future.

In the present study we used the age-stage life table to compare the effects of the above three host plants on the life history parameters of B. macroscopa. The age-stage-specific survival rate (Sxj) indicates the survival rate at different stages as well as demonstrating the generation overlapping phenomenon. The study of the life table of the geometrid Problepsis superans (Butler) on different hosts indicated that at the age of 13 d, the 1st instar larvae coexisted with the 2nd and 3rd instars when P. superans fed on Ligustrum lucidum Aiton, while the insect populations on L. vicaryi (Beckett) Rehder and L. quihoui (Carr.) coexisted in the 2nd and 3rd instars at 13 d. Alami et al. (2014) and Naseri et al. (2014) reported the age-stage, two-sex life table of Chrysodeixis chalcites (Esper) (Lepidoptera: Noctuidae) and Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae) on different bean cultivars, and described the same phenomenon. This shows that the overlapping generations that occur in insect life histories should not be overlooked. While this phenomenon is an integral component of the age-stage life table survival curve, this critical information is lacking in traditional life tables. In the present study, it is evident from Fig. 3 that B. macroscopa obviously has this overlapping phenomenon in the development of its immature stages and can exist in multiple stages on any given day.

**Figure 3.** Age-stage-specific life expectancy (e1) of Brachmia macroscopa reared on three three host plants under laboratory conditions.
The egg stage lasted 4 days on *I. batatas* and *I. aquatica*, and 5 days on *P. purpurea*. This was within the range (3–6.35 days) reported by Ma *et al.* when studying the effects of varying temperature on *B. macroscopa*\(^1\)
\(^{13}\). The length of the egg stage was also close to that observed in several other species of Gelechiidae. A study by Karimi-Pormehr *et al.*\(^2\)\(^{20}\) reported that the length of the egg stage of, *Sitotroga cerealella* (Olivier) (Lepidoptera: Gelechiidae) on ten different barley cultivars was from 4.83 to 4.97 days. Rostami *et al.*\(^2\)\(^{21}\) reported the egg stage of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) lasted from 4.43 to 4.64 days on three tomato cultivars, but other researchers, found the egg stage ranged from 5 to 7 days in the species\(^2\)\(^{22}, 23\). *B. macroscopa* also has a shorter pupal stage compared to *T. absoluta*. In our study, the *B. macroscopa* pupal stage ranged from 5 to 6 days.

**Figure 4.** Age-stage-specific life reproductive value (\(v_{xj}\)) of *Brachmia macroscopa* reared on three three host plants under laboratory conditions.
Insects on most suitable host for survival rates in the larval stage, and the adult fecundity were the highest, suggesting that plants can affect the food digestibility and fecundity of a pest; secondarily, a high fecundity and short TPOP determines whether it suitable for an insect population or not. Of prime importance, the quality and quantity of nutrition contained in a host plant changes are often vital to the insect’s population dynamics in the wild. The nutrition is a mixture of nutrients in order to complete the processes of growth, development, and reproduction. On the contrary, different host plants can also affect insects’ growth and reproduction, which can potentially lead to a change of their life history. These changes are often vital to the insect’s population dynamics in the wild. The nutrition contained in a host plant determines whether it suitable for an insect population or not. Of prime importance, the quality and quantity of the plants can affect the food digestibility and fecundity of a pest; secondarily, a high fecundity and short TPOP will directly lead to a high intrinsic rate. When B. macroscopa larvae fed on I. aquatica, the total fecundity was higher than in the other two hosts with 427.60 eggs, the TPOP was the shortest with 20.58 days and the intrinsic rate (r) was also the highest, as were the R₀, GRR and λ values. These results would suggest that I. aquatica is the most suitable host for B. macroscopa. The r and λ values of B. macroscopa were the second highest on I. batatas. Insects on I. batatas had the shortest pupal period as well as the longest adult duration. These results indicated that B. macroscopa was able to develop adequately on I. batatas, did not do well on P. purpurea. Finally, B. macroscopa apparently has considerably stronger host adaptability on Ipomoea than it does on Pharbitis plants.

### Materials and Methods

#### Tested plants

Based on preliminary field investigations conducted in Changsha, Hunan Province, China, we screened I. batatas, I. aquatica, and P. purpurea to use as hosts for our research. All plants used in the research were grown in pesticide free environments.

#### Insect

The colony of B. macroscopa used in this study was collected from an experimental farm in Hunan Agricultural University, Changsha, Hunan Province, China; N28°110, E113°40. The larvae were cultured separately on fresh leaves of the three host species (I. batatas, I. aquatica, and P. purpurea) in the laboratory. Newly emerged females and males were individually paired in an insect rearing cage containing young plants of each

| Ipomoea batatas | Ipomoea aquatica | Pharbitis purpurea |
|-----------------|-----------------|------------------|
| R₀ ± SE         | 147.59 ± 13.46a | 158.00 ± 18.22a  |
| GRR ± SE        | 175.98 ± 14.80a | 203.73 ± 21.65a  |
| r ± SE          | 0.17 ± 0.004b   | 0.21 ± 0.005a    |
| λ ± SE          | 1.09 ± 0.004b   | 1.23 ± 0.006a    |
| T ± SE          | 28.76 ± 0.23a   | 24.32 ± 0.18b    |

Table 4. The mean (±SE) of life table parameters (days) of Brachmia macroscopa reared on three hosts under laboratory conditions. Note: Data in the table are stated as mean ± SE. Means in the same row marked with different letters are significantly different at the 5% level using the Tukey-Kramer test.
host to encourage mating and to act as an oviposition substrate. A mesh net and a cotton ball soaked with a 20% honey solution were placed in the rearing cages for ventilation and nutrition, respectively. The insects used in the experiments had been laboratory bred for at least two generations on each host species. All tested insects were maintained in an artificial climate chamber at 27 ± 1 °C, 75 ± 20% RH and 10L:14D, and reared on one of the three host plants mentioned above.

**Experiments.** One hundred and fifty healthy, well developed, recently laid eggs that were oviposited during the spawning peak, were collected and placed in an artificial climate chamber set at 27 ± 1 °C, 75 ± 20% RH, and a photoperiod of 10:14 (L: D) h. Hatching was observed and recorded daily. The newly hatched larvae were transferred using a brush into petri dishes (15 cm in diameter, 1.5 cm in height) and provided with fresh leaves from *I. batatas*, *I. aquatica* or *P. purpurea* plants. The petioles of these leaves were inserted into water-soaked cotton to maintain freshness. The larval mortality was recorded and the leaves replaced daily. Newly pupated individuals were transferred into separate glass tubes (2 cm in diameter, 10 cm in height) with a water-soaked cotton ball to retain moisture and covered with gauze. The pupae were observed daily until emergence as adults. Detailed records were kept on the durations and survival of each larval instar, pupal stage and adult longevity. Upon eclosion, females and males emerging within a 24 h period from each of the host plants were paired and maintained in a plastic oviposition chamber (13 cm in diameter, 17 cm in height). A small host plant, planted in a disposable cup, was added to each container as an oviposition substrate. A cotton ball soaked with a 20% honey solution was placed in the cup to serve as a food source for adults and was replaced daily. The numbers of newly produced eggs were totaled every 24 h until all the adults had died.

**Life table parameters.** The age-stage, two-sex life table method was used to analyze the raw data. The age-stage-specific survival rates (*s*) were determined for each of the three treatments. These are the survival rates at age *x* (days) and stage *j* (where the first through eighth stages represent the egg stage (1), the 1st through 4th larval instars (2–5), the 5th (or combined 5th + 6th - when present) instars (6), the pupal stage (7) and the adult stage (8), respectively). The age-stage specific fecundity (*f*) is defined as the quantity of eggs produced by each individual per day at age *x* (days) and stage *j*; the age-specific survival rate (*l*) is the probability that a newly produced egg will survive to age *x*; the age-specific fecundity (*m*) is the mean number of female eggs laid per female adult at age *x*. The population parameters were calculated according to the procedure developed by previous researchers. The intrinsic rate of increase (*r*) was calculated using the iterative bisection method where \[ \sum_{x=0}^{\infty} e^{-rx} \cdot x \cdot m_x = 1 \]. The net reproductive rate (*R*<sub>0</sub>) was estimated as \( \sum_{x=0}^{\infty} m_x \). The life parameters GRR (total reproductive rate), \( \lambda \) (finite rate of increase) and \( T \) (mean generation time, which is the duration that a population needs to increase to \( R_0 \)-fold its size before reaching the stable age-stage) were calculated as \( GRR = \sum m_x \cdot \lambda = e^\lambda \) and \( T = (\ln R_0)/R_0 \). Finally, the means, standard errors and variances of the population parameters were bootstrapped using the computer program TWOSEX-MSChart. The graphs were created using Sigma plot 12.5.

**Data analysis.** The raw life-history data of *B. macroscopa* reared on each host species were entered separately into Microsoft Excel 2015, and the data analyzed by one-way ANOVA using SPSS 22.0. The correlation coefficient differences were compared using the Tukey method (*P* < 0.05).

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Author Contributions
G.-H.H., L.M. and X.W. designed the experiments. L.M. and N.L. wrote the main manuscript text and prepared figures. L.M., Y.L. and Mi.-Z.S. performed the experiment and organized the raw data. G.-H.H. and X.W. reviewed the manuscript.

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