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Forum

Fast Population Growth in Physogastry Reproduction of *Luciaphorus perniciosus* (Acari: Pygmephoridae) at Different Temperatures

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Abstract

Luciaphorus perniciosus Rack is one of the most serious pests of several cultivated mushroom species including *Ganoderma lucidum* (Fr.), *Flammulina velutipes* Karst., *Auricularia polytricha* (Mont.) Saac., *Lentinus polychrous* Lev., and *Lentinus squarrosulus* (Mont.) Singer in Thailand. Adult female *Lu. perniciosus* produce offspring inside their physogastric hysterosomas, with all embryos developing through to the adult stage while remaining in the abdomen. Once the abdomen ruptures, the female parent dies and the offspring consisting of mostly fertilized female adults along with a few male adults continue to emerge from the cadaver of the mother for a period of several days. This peculiar type of reproduction after the death of the mother is a special case for life table analysis and has not been discussed previously in demographic analyses. In this study, the life table data of this mite fed on *Le. squarrosulus* were collected at 25, 30, and 35 °C and analyzed by using the age-stage, two-sex life table. The standard errors of population parameters were estimated by using the bootstrap technique (200,000 bootstraps). At 25, 30, and 35 °C, females started reproduction at ages 9, 5, and 3 d, respectively; the net reproductive rates (R_0) were 192.27, 253.81, and 234.11 offspring. Due to their rapid development and high fecundity, the r values were as high as 0.4189, 0.8653, and 1.0892 d^{-1} at 25, 30, and 35 °C, respectively. Computer projection indicated that the mushroom mites *Lu. perniciosus* is capable of a threefold daily increase at 35 °C.

Key words: *Luciaphorus perniciosus*, physogastry, life table, Pygmephoridae

Cultivation of edible mushrooms is a thriving agricultural business in the tropical regions of Asia, including Thailand, where a number of mushroom species including *Auricularia polytricha* (Mont.) Sacc., *Au. auricular* (Bull.) Wettst., *Lentinus squarrosulus* (Mont.) Singer, *Le. polychrous* Lev., *Ganoderma lucidum* (Fr.), and *Flammulina velutipes* Karst. are widely cultivated. Several species of mites have been reported as destructive pests of cultivated mushrooms worldwide (Gurney and Hussey 1967; Wicht 1970; Wicht and Snetsinger 1971; Clift 1979; Clift and Toffolon 1981a,b; Gao et al. 1986, 1990; Wu and Ma 1988; Wu and Zhang 1993a,b; Okabe 1993; Zou et al. 1993; Gao and Zou 2001). The mite, *Luciaphorus perniciosus* Rack (Acari: Pygmephoridae), which is one of the most serious pests of the above cultivated mushrooms species in Thailand, can infest all stages of mushrooms leading to retarded mycelial growth and suppressed sporophore formation (Kantaratanakul and Jitrat 1984, Charanasri et al. 1985). Severe mite infestation may cause ~50–80% yield loss. This mite species can be dispersed by phoresy on other insect species, airflow, or by transport on contaminated tools and spawn during fungal inoculation (Clift and Larsson 1987). Economic losses due to *Lu. perniciosus* infestation have been reported in many areas of the country, especially in the central, northern, and eastern parts where *Au. polytricha* and *Le. squarrosulus* are grown. This mite, which was first found infesting *Au. polytricha* in Bangkok and initially identified as

Luciaporus hauseri (Mahunka 1981), was later re-described as *Lu. perniciosus* (Rack 1983). The mite has subsequently been observed in several provinces of Thailand, including Bangkok, Ratchaburi, Phetchaburi, Maha Sarakham, Kalasin, Roi Et, Khon Kaen, and Ubon Ratchathani (Charanasri et al. 1985, Bussaman et al. 2004).

The life cycle of *Lu. perniciosus* (identified as *Luciaphorus hauseri* Mahunka) was reported by Kantaratanakul and Jitrat (1984). Because they resemble fish-eggs, they are also commonly referred to as fish-egg mites. Male mites have the ability to fertilize the females while still inside their mother's body (Bussaman et al. 2004). Kantaratanakul and Jitrat (1984) reported that *Lu. perniciosus* develops only on the mycelia and sporophores of Jew's ear mushroom, *Au. polytricha*, and that no damage had been detected in mycelia of other mushroom species, even though they were cultivated in the same mushroom house. Bussaman et al. (2004, 2006), however, found that this mite could damage *Le. squarrosulus*, *Le. polychrous*, *A. auricula*, and *F. velutipes* in northern and northeastern areas of Thailand.

Because life tables provide the most comprehensive analysis and description of the development, survival, and reproduction of insect and mite populations, they are the basis of population ecology and pest management. Since traditional female age-specific life tables (Lewis 1942, Leslie 1945, Birch 1948, Carey 1993) ignore the male population and cannot describe the stage differentiation, their application is limited. Huang and Chi (2012a) discussed the problems associated with the application of the female age-specific life tables. The age-stage, two-sex life table (Chi and Liu 1985, Chi 1988) takes both sexes and the stage differentiation into consideration and has become widely accepted in ecological research. Despite the important of life table data, there is currently no information available on the life table of *Lu. perniciosus* infesting *Le. squarrosulus*, nor information on the effects of temperature on the development of the mite. To complicate matters, the peculiar physogastric reproduction found in *Lu. perniciosus* causes unique difficulties in life table analysis. Because the death of female adults occurs immediately prior to the release of the fertilized offspring, the survival curve (l_x) of the female adult decreases to zero and is then followed by a rise in the fecundity curve (m_x). Because of this abnormality, it is impossible to calculate the population parameters by using standard life table analysis. In the current study, we collected the life table data of *Lu. perniciosus* at 25, 30, and 35 °C and analyzed the raw data using the age-stage, two-sex life table. We developed a new theory and devised an analytical method for use in situations involving physogastric reproduction. The information obtained in this study can be used for developing methods or strategies for controlling *Lu. perniciosus* mites, as well as in the analysis of life tables involving other physogastric species.

Materials and Methods

Mite Culture

Luciaphorus perniciosus mites were collected from *Le. squarrosulus* basidiocarps and composts at Rapeephan Mushroom Farm, Khon Kaen Province, in northeast Thailand. Mycelia of *Le. squarrosulus* were cultured on Potato Dextrose Agar (PDA; Sigma Ltd.) in plastic Petri dishes (9 cm diameter) and incubated at 25 °C with a photoperiod of 12:12 (L:D) h. The mushroom mycelia were inoculated into glass bottles (5 cm diam. and 8.5 cm high) containing sawdust and sorghum grain mixture to establish fresh spawn (Bussaman, 2005). After 10 d, a single fertilized female *L. perniciosus* mite was placed in each bottle and maintained at 28 °C for multiplication. Mites were transferred to new bottles with fresh spawn at monthly intervals.

Life Table Study

Because egg production and the development of all preadult stages of *Lu. perniciosus* occurs within the physogastric hysterosoma of the adult female mites and the adults of the offspring generation are released only when the abdomen of female adult ruptures, the life history data was recorded as two stages, i.e., the survival of the prerupture adult stage and the daily fecundity of the postrupture adult stage (the female succumbs but the offspring adults continue to emerge from the female's ruptured abdomen for several days). For the life table study, an individual, newly emerged, fertilized female was placed in each small vial (1 cm diameter, 4 cm long) containing *Le. squarrosulus* mycelia grown on PDA. Vials were covered with a rubber stopper and cultured at one of three constant temperatures (25, 30, and 35 °C), with a photoperiod of 12:12 (L:D) h for one generation. Afterwards, 372, 250, and 303 vials were selected for the life table study at 25, 30, and 35 °C, respectively. Twenty vials were randomly selected daily and the female opisthosomas were excised and all eggs were mounted on microscopic slides for detailed examination. The number and developmental stages of offspring inside the female body were recorded under a 40× stereomicroscope. The embryonic and preadult stage is divided into five stages (stages 1–5) according to Kantaratanakul and Jitrat (1984). At the first stage, the egg is composed of a light yellow periplasm with a considerable amount of grayish yolk in the center (Fig. 1A). This stage was only found in female bodies when they were 1–3 d old. In stage 2, the egg yolk is clearly visible in the middle of the egg and no appendages have been formed (Fig. 1B). In stage 3, some appendages have started to form (Fig. 1C). In stage 4, all appendages are clearly seen, but the sex is still not distinguishable (Fig. 1D). In the final stage, the mite body is segmented, appendages are fully developed with setae and sex is easily distinguished by the difference in the shape and size of legs I and IV (Fig. 1E). The male mites can easily be distinguished from the females by its active movement and the undeveloped mouthparts (Bussaman 2005).

After a female abdomen ruptured, the dead female was observed for 8 d and the number of emerged female adults, male adults, and unhatched eggs were recorded daily. The total numbers of female parents were 261, 124, and 180 individuals at 25, 30, and 35 °C, respectively.

Data Analyses and Statistics

All raw data were analyzed according to the age-stage, two-sex life table theory (Chi and Liu, 1985) using the method described by Chi (1988) and Huang and Chi (2011). Data collected from excised mites were used for the description of embryonic development, while the data obtained from mites that gave birth naturally (rupture of abdomen) were used in the life table analysis. The computer program TWOSEX-MSChart (Chi 2016b) was used for life table analysis. TWOSEX-MSChart is available for free download at http://140.120.197.173/Ecology/prod02.html (National Chung Hsing University, Taichung, Taiwan). The population parameters (r, the intrinsic rate of increase; λ, the finite rate of increase, $\lambda = e^r$; R_0, the net reproductive rate; and T, the mean generation time) were calculated according to Huang and Chi (2011).

When an offspring female adult emerges from the ruptured abdomen of its mother mite, it is necessary for it to find a mycelium to feed on before the embryo inside her body can develop. Because all of the preadult stages of the offspring develop inside the mother's body and the emergence of offspring begins on the same day immediately following the death of the mother, there is no clear reproductive stage. This particular type of reproduction that occurs after the

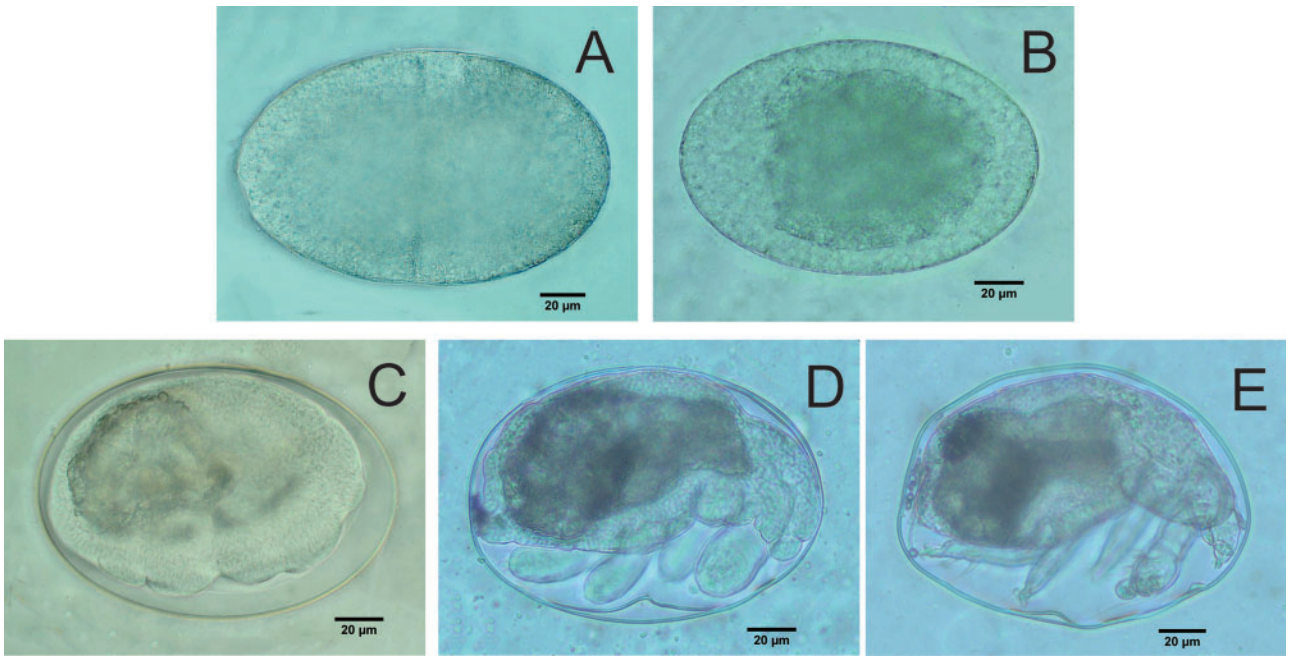

Fig. 1. Embryonic development of *Luciaphorus perniciosus* at room temperature (**A**) Stage 1, (**B**) Stage 2, (**C**) Stage 3, (**D**) Stage 4, and (**E**) Stage 5.

mother's death leads to problems in calculating population parameters. For convenience of data analysis and to allow comparisons, we separated the intact female adult stage into two stages: the feeding-pregnant (FP) stage, and the final day of the intact stage, which we refer to as the rupture-ready (RR) stage. Obviously, the longevity of the female, which is the sum of the FP and RR stages, can be used to construct the female survival rate ($l_{x,F}$) of the cohort, while the number of individuals in the RR stage can be used to calculate the age-specific fecundity. Moreover, because the reproduction of each female individual was extended beyond its death and lasted for several days afterwards, the reproductive duration of the abdomen-ruptured females (AF) extended beyond the longevity (FP + RR) of the mother. We used the duration of the female longevity (FP + RR) and the reproductive period of dead females (AF) to calculate the reproductive proportion curve ($l_{x,R}$). Instead of $l_{x,F}$, the curve of $l_{x,R}$ is used to calculate the population parameters. Because the mothers were already dead when their offspring emerged from their abdomens, we omit the "survival" in the term "reproductive proportion."

According to Huang and Chi (2011), if the number of offspring of different sexes produced by females varies with the female age, the net reproductive rate of the parent cohort can be calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_{x,R} m_{x,total} = \sum_{x=0}^{\infty} l_{x,R}(m_{x,F} + m_{x,M} + m_{x,N}) \quad (1)$$

where $l_{x,R}$ is the reproductive proportion of female parents at age x, while $m_{x,F}$, $m_{x,M}$, and $m_{x,N}$ are the female, male, and N-type offspring produced by female parents at age x (N-type offspring are those offspring that cannot develop to the adult stage). It is clear that

$$\begin{aligned} R_0 &= \sum_{x=0}^{\infty} l_{x,R} m_{x,F} + \sum_{x=0}^{\infty} l_{x,R} m_{x,M} + \sum_{x=0}^{\infty} l_{x,R} m_{x,N} \\ &= R_{0,F} + R_{0,M} + R_{0,N} \end{aligned} \quad (2)$$

Where $R_{0,F}$, $R_{0,M}$, and $R_{0,N}$ are the net reproductive rates of female, male, and N-type offspring of the parent cohort. Because the sex ratio of the parent cohort is actually only a sample and the offspring sex ratio varies with the female age, the population will approach the stable age-stage-sex distribution when the population approaches a stable increase rate (i.e., the intrinsic rate of increase r and finite rate λ), and vice versa. According to Huang and Chi (2011), the intrinsic rate can be estimated from the following equation:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_{x,R} m_{x,F} = 1 \quad (3)$$

We then used the result to calculate the stable sex ratio (F:M:N) accordingly. The cumulative net reproductive rate (R_x) and curtailed intrinsic rate (r_δ) were calculated according to Chi and Su (2006).

The variances and standard errors of population parameters were estimated by using the bootstrap technique (Efron and Tibshirani 1993, Huang and Chi 2012b) with 200,000 resampling. The paired bootstrap test was used to evaluate the differences between treatments. The bootstrap method is embedded in the computer program TWOSEX-MSChart.

Population Projection

The survival, development rate, and fecundity data collected in the life table study were used to project the growth of *Lu. perniciosus* populations by using the computer program TIMING-MSChart (Chi 2016a). The population growths at three temperature treatments were simulated using an initial population of 10 newly emerged females.

Results

Mite Development and Reproduction

The numbers for each of the five embryonic and preadult developmental stages of *Lu. perniciosus* are presented in Fig. 2. At 25 °C, individuals in developmental stages 1, 2, 3, 4, and 5 were found inside the mother's abdomen on the 3rd, 4th, 5th, 6th, and 7th day, respectively. On day 9, most eggs were in stage 5. Adults of both sexes of the offspring generation began to emerge when their female parents were 9 d old and continued until day 18. At 30 °C, *Lu. perniciosus*

developed considerably faster than those reared at 25 °C. Individuals in stages 1, 2, and 3 were observed on the 3rd day, while stages 4 and 5 were noted on the 4th and 5th day, respectively. The offspring female and male adults began to emerge when their female parents were 5 d old and then decreased in subsequent days. More than 65% of offspring adults emerged on the mother's fifth day. At 35 °C, individuals in both stages 1 and 2 were noted as soon as the 2nd day, while stages 3, 4, and 5 occurred on the 3rd day. High peaks of stage 5 individuals were observed on day 4 and 5. At 35 °C, out of an initial 180 parent females, 28 females (15.56%) died at age 4 d, releasing the offspring adults.

The female longevity, i.e., the duration of time between a female emerging from her mother's ruptured abdomen to the rupturing of her own abdomen, was 12.75, 6.28, and 5.06 d at 25, 30, and 35 °C, respectively (Table 1). There were significant differences in female longevity between the three temperatures. Females survived significantly longer than the males at all temperatures (Table 1). The curves of the FP, RR, and AF are shown in Fig. 3. At 25 °C, the rupture-ready (RR) stage began at age 9 d and the reproduction

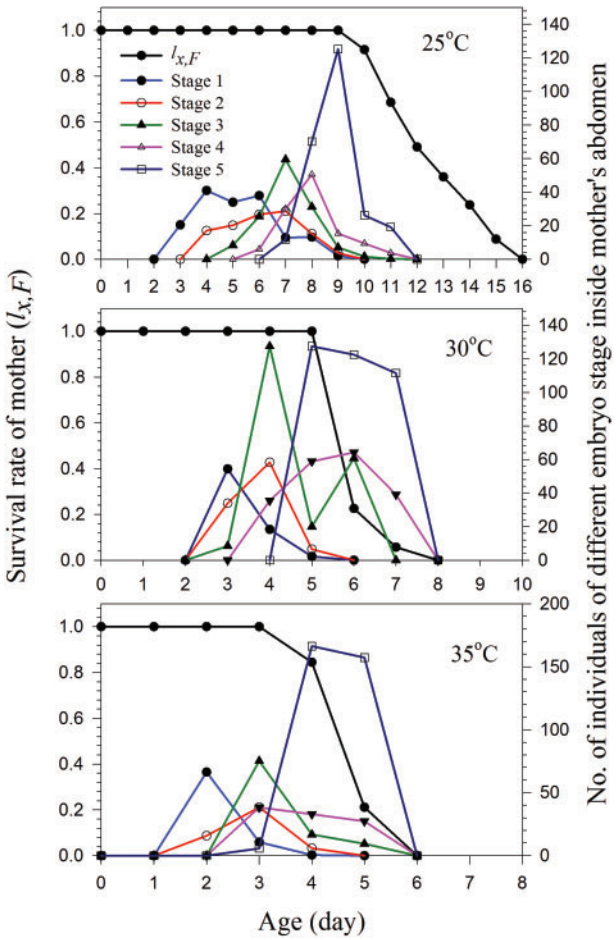

Fig. 2. The age-specific survival rate of female parents ($l_{x,F}$) and the number of individuals at different developmental stages of embryos inside mother's abdomen at different temperatures.

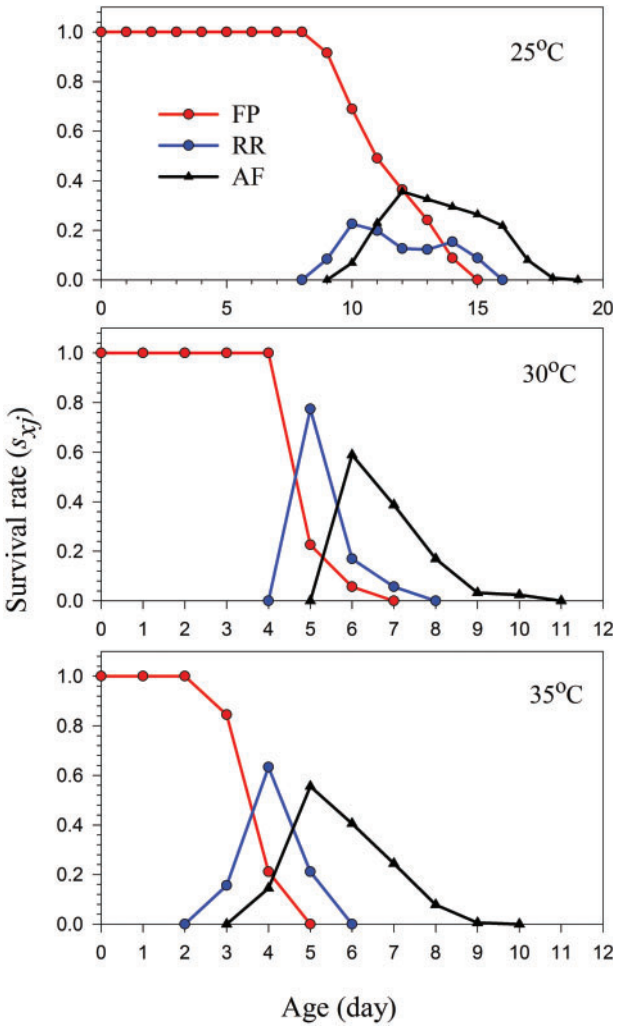

Fig. 3. The age-stage proportion (s_{xj}) of the FP-stage (feeding-pregnancy stage), rupture-ready stage (RR), and abdomen-ruptured female (AF) of female parents at different temperatures.

Table 1. Duration of development (mean ± SE) of *Luciaphorus perniciosus* Rack

Statistics	25 °C		30 °C		35 °C	
	n	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE
Female longevity (d)	261	12.75 ± 0.11aA	124	6.28 ± 0.05bA	180	5.06 ± 0.04cA
Male longevity (d)	92	8.47 ± 0.44aB	62	4.05 ± 0.17bB	65	2.43 ± 0.08cB
Reproductive period (female offspring) (d)	261	2.79 ± 0.08aA	124	2.18 ± 0.08bA	180	2.39 ± 0.09bA
Reproductive period (male offspring) (d)	261	1.75 ± 0.05aB	124	1.45 ± 0.05bB	180	1.62 ± 0.06aB
TPOP (female offspring)	261	11.79 ± 0.11aA	124	5.28 ± 0.05bA	180	4.06 ± 0.05cA
TPOP (male offspring)	261	11.77 ± 0.11aA	124	5.28 ± 0.05bA	180	4.06 ± 0.05cA

Standard errors were estimated using bootstrap technique with 200,000 resampling. Differences among treatments were compared with paired bootstrap test. The means followed by a different lower-case letter indicates differences between temperatures, while an upper-case letter indicates differences between sexes.

period lasted for 9 d, while at 35 °C, the RR stage began at age 3 d with the reproduction period lasting 6 d.

The survival curves (l_x) are shown in Fig. 4. Because of the faster development rate of *Lu. perniciosus* at temperatures 30 and 35 °C, females began to produce offspring earlier than the lower temperature (25 °C). The first age-specific fecundity ($m_{x,F}$) occurred at age 9, 5, and 3 d at 25, 30, and 35 °C, respectively; while the highest daily offspring female adult production was 51.8, 152.1, and 122.8 observed on age 14, 5, and 4 d at 25, 30, and 35 °C, respectively (Fig. 4). Although the total prereproductive periods for producing female and male offspring were the same, the periods for producing female offspring (daughters) were 2.79, 2.18 and 2.29 d at 25, 30, and 35 °C (Table 1), respectively; all of which were significantly longer that the durations for producing male offspring (sons).

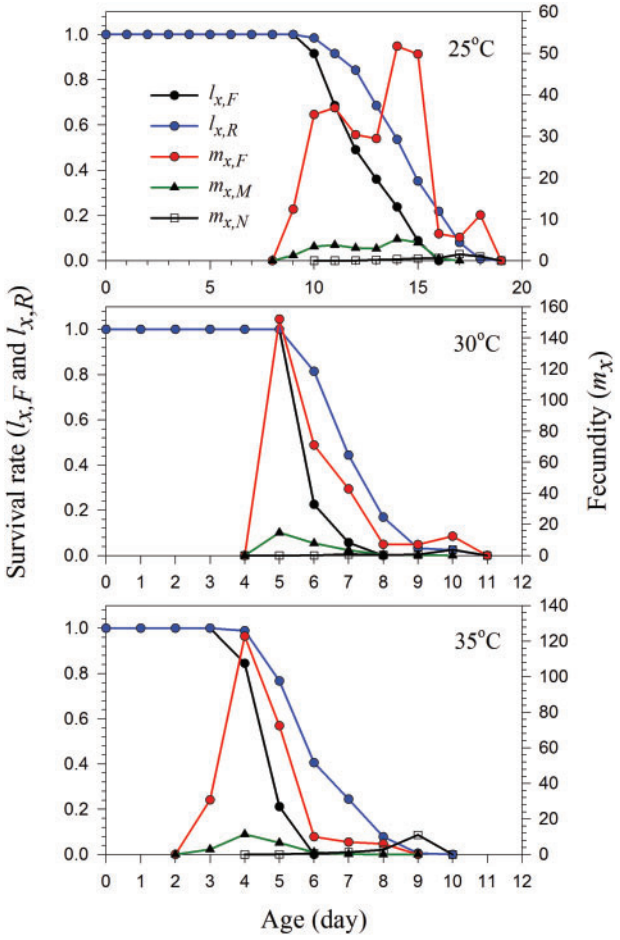

Fig. 4. The age-specific survival rate of female parents ($l_{x,F}$), reproductive proportion of female parents ($l_{x,R}$), age-specific fecundity for female offspring ($m_{x,F}$), age-specific fecundity for male offspring ($m_{x,M}$), and age-specific fecundity for N-type offspring ($m_{x,N}$) at different temperatures.

Life Table Parameters

In all three temperature treatments, *Lu. perniciosus* mainly produced female offspring (Table 2). The values of $R_{0,F}$ were 174.34, 230.56, and 213.74, at 25, 30, and 35 °C, respectively; while the $R_{0,M}$ values were 17.11, 22.71, and 19.50, respectively.

The cumulative net reproductive rate (R_x) and curtailed intrinsic rate (r_δ) are plotted in Fig. 5. These show that the R_x value of 30.7 at age 3 d already rendered a high intrinsic rate of 0.856 d^{-1} at 35 °C, while at 30 and 25 °C, high r values (0.837 and 0.360 d^{-1}) could be realized with R_x values of 152.1 and 47.1 offspring being produced at age 5 and age 10 d, respectively.

Population Projection

The population projections with stage structure are shown in Fig. 6. The population increase rate at 25 °C was significantly slower than that at 30 and 35 °C. The curves at 35 °C showed that *Lu. perniciosus* will approach the stable age-stage distribution after 18 d. A linear regression using data from after age 18 d shows that the curve of the FP stage has a slope of 0.4728. The value of $10^{0.4728}$ is 2.9703, which is very close to the finite rate (2.9718 d^{-1}) of *Lu. perniciosus* at 35 °C.

Discussion

According to life table theory, the value of the intrinsic rate is calculated by using the age (x), the age-specific survival rate (l_x), and the age-specific fecundity (m_x) (Euler 1760, Lewis 1942, Leslie 1945, Chi 1988). Lewontin (1965) pointed out the first reproductive age (the beginning of the m_x curve) and the age of reproductive peak (peak of the $l_x m_x$ curve) play a determinative role in the population growth rate. These concepts are useful criteria for critical evaluation of published data (Chi 2015, Akca et al. 2015). Bruce and Wrensch (1990) observed highly female-biased sex ratios in the straw itch mite, *Pyemotes tritici* (Lagreze-Fossat and Montane) (Acari: Pyemotidae); they used a simplified method to estimate the intrinsic rate of increase of *P. tritici* and obtained an extraordinary high intrinsic rate of 0.63 d^{-1}, claiming that *P. tritici* clearly has one of the highest reproductive rates measured for any animal species. In the

Table 2. Population parameters (mean ± SE) of *Luciaphorus perniciosus* Rack

Population parameters	25 °C	30 °C	35 °C
Cohort size (n) (F:M:N)	261:92:3	124:62:9	180:65:6
Female proportion	73.31 ± 2.34%a	63.59 ± 3.44%b	71.71 ± 2.85%ab
Intrinsic rate of increase (r) (d^{-1})	0.4189 ± 0.0040c	0.8653 ± 0.0064b	1.0892 ± 0.0134a
Finite rate of increase (λ) (d^{-1})	1.5203 ± 0.0061c	2.3759 ± 0.0153b	2.9718 ± 0.0397a
$R_{0,T}$ (total offspring)	192.27 ± 3.67c	253.81 ± 6.98a	234.11 ± 6.13b
$R_{0,F}$ (female offspring)	174.34 ± 3.34c	230.56 ± 6.53a	213.74 ± 5.69b
$R_{0,M}$ (male offspring)	17.11 ± 0.42c	22.71 ± 0.73a	19.50 ± 0.59b
$R_{0,N}$ (N-type offspring)	0.82 ± 0.13c	0.55 ± 0.25a	0.86 ± 0.19b
Mean generation time (T) (d)	12.32 ± 0.11a	6.29 ± 0.04b	4.93 ± 0.06c
Stable sex distribution (F:M:N)	0.9666:0.0330:0.0004	0.9457:0.0541:0.0002	0.9425:0.0574:0.0002

Standard errors were estimated using bootstrap technique with 200,000 resampling. Differences among treatments were compared with paired bootstrap test. (N-type is individual that died in the preadult stage.)

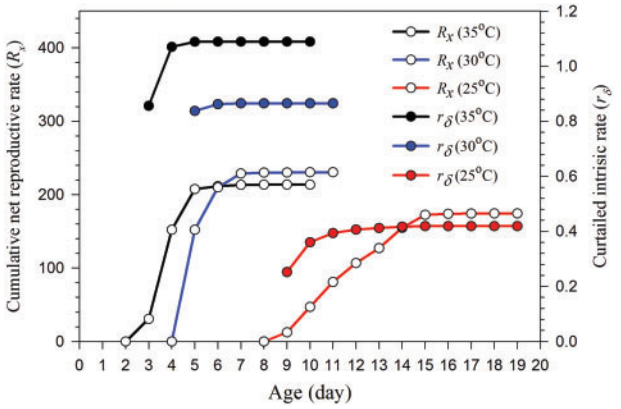

Fig. 5. The cumulative net reproductive rate (R_x) and curtailed intrinsic rate (r_d) at different temperatures.

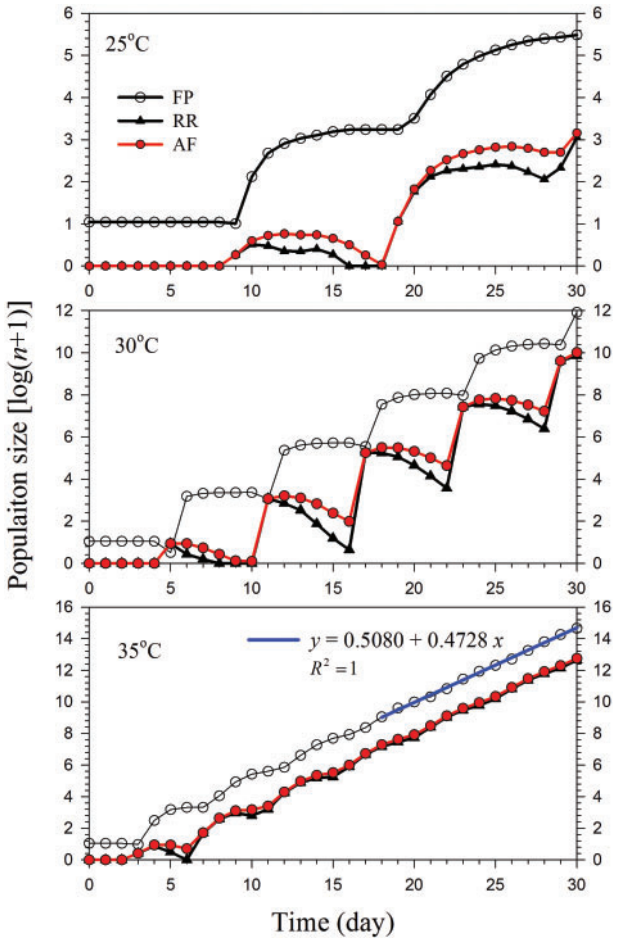

Fig. 6. Population projection showing the increase of each stage of *Luciaphorus perniciosus* Rack at different temperatures (FP, feeding-pregnancy stage; RR, rupture-ready stage; and AF, abdomen-ruptured females.) The blue dash line is the linear regression of population sizes during the time interval 20~30 d.

present study, the percentages of female offspring were higher than 90% in each of the three temperatures tested. Moreover, we used a very precise method and obtained much higher intrinsic and finite rates at 35 °C ($r = 1.0892$ d^{-1} and $\lambda = 2.9718$ d^{-1}), 30 °C ($r = 0.8653$ d^{-1} and $\lambda = 2.3759$ d^{-1}), and 25 °C ($r = 0.4189$ d^{-1} and $\lambda = 1.5203$ d^{-1}). Such extraordinarily high growth rates must be due to the rapid development and high fecundity of *Lu. perniciosus*. This demonstrates that the population is capable of increases almost 3-, 2.4-, and 1.5-fold per day at 35, 30, and 25 °C, respectively, after their population reaches a stable age-stage distribution. Such high intrinsic rates of increase can only be realized in organisms with a very short developmental period and high fecundity such as *Lu. perniciosus*. Gao and Zou (2001) reported the duration of female–female (i.e., the time period from the newly born female to the production of the next generation female), the mean fecundity, and the net reproductive rate R_0 for *Brennandania lambi* (Krczal) (Acari: Pygmephoroidea) at 28 °C as 10.3 d, 56.9 offspring, and 36.9, respectively; consequently, they obtained an intrinsic rate of 0.273 d^{-1}. For other organisms with longer developmental times, it is unlikely that such a high intrinsic rate would be observed. For example, Zou et al. (2015) reported a preadult duration of 20.58 d for the stinkbug, *Arma chinensis* (Fallou) (Heteroptera: Pentatomidae), with a high intrinsic rate (0.4441 d^{-1}). However, Chi (2015) pointed out the calculation errors in Zou et al. (2015), and Akca et al. (2015) further substantiated that the high intrinsic rate value found for *A. chinensis* as reported by Zou et al. (2015) was inaccurate.

Mushroom mites can readily be dispersed by being phoretic on other insect species, by air currents, or by transport on contaminated tools; moreover, they can rapidly increase in numbers at an extremely high intrinsic rate. Beginning with 10 newly emerged female adults, a population can reach a stable age-stage distribution and grow exponentially after 18 d. Once a mushroom culture bag is infested with mites, it is imperative that it be removed and destroyed to avoid further infestation. This demonstrates that frequent sampling, examination, and employing sanitary strategies in mushroom culture is of utmost importance to the success of the mushroom crop.

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