The Small Hive Beetle: Oviposition, Longevity, and Intrinsic Rate of Natural Increase on Two Diets

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INTRODUCTION

The small hive beetle, *Aethina tumida* Murray, is capable of rapid population growth on the concentrated resources (honey, pollen and brood) available in honeybee colonies. It is also capable of feeding and reproducing on various kinds of fruit (Ellis et al. 2002, Keller 2002, Arbogast et al. 2009), which is of interest, because alternative diets could maintain populations outside bee colonies and aid long range dispersal. However, the beetle's ability to sustain population growth on diets other than bee products remains unknown. To examine this ability, we compared its potential for population increase on a fruit (oranges) with that on a diet that included pollen (pollen dough). Population growth potential was expressed numerically as the intrinsic rate of natural increase, which can be defined as the constant *r* in the exponential growth equation $N = N_0 e^{rt}$. It is the infinitesimal rate of increase of a population having a stable age distribution and living in an environment free of the suppressive effects of crowding, predators, disease, etc. The requirement for a stable age distribution is not a serious limitation, because age distributions gradually move toward stability, and once stable they tend not to change (Lotka 1925). The value of *r* is determined by life history traits (rate of development, age-specific fecundity, age-specific mortality) and is characteristic of a particular species or strain, but its expression is influenced by the prevailing physical conditions (temperature, humidity, etc.) and by the nutritional situation. For this reason, *r* is useful in comparing the effects of various physical conditions and diet on an insect's potential for population increase.

MATERIALS AND METHODS

Calculation of *r* is based only on the female population and requires construction of female life-tables (l_x) and tables of age-specific-fecundity (m_x). The former gives the probability at hatching of being alive at age *x*, and the latter gives the mean number of female eggs laid in a unit of time by a female at age *x*. We used one day as the time unit and assumed that all eggs were laid at the midpoint of each one-day interval.

Beetles used in the experiments were from stock cultures that had been maintained at room temperature in our laboratory for about 4 years. They were reared on commercially available pollen dough (Global Patties, Airdrie, Alberta, Canada) that had been inoculated with *Kodamaea ohmeri*, a species of yeast carried by adult *A. tumida* that induces fermentation of pollen stored in honeybee colonies. All experiments were done at constant temperature and humidity (27.5 ± 0.5º C, 60 ± 5% RH).

The average developmental time from egg to adult was taken as the initial age (*x*) in the adult life table, and the proportion of immature stages reaching adulthood was taken as the probability (l_x) of surviving to that age. These parameters were determined by rearing beetles from egg to adult on each diet and making daily observations until adult emergence was complete.

The adult portions of the l_x and m_x tables were obtained in two experiments, one for inoculated pollen dough and one for orange. For each experiment, pupae were collected from stock cultures, sorted by sex, and held for adult emergence. As adults emerged, one male and one female were placed in each of 50 clear plastic petri dishes (100 x 15mm) with diet. The number of eggs laid and adult deaths were recorded daily until all of the females had died. Because the sex ratio of *A. tumida* reared on either diet is 1:1 (Arbogast et al. 2009), only half of each daily total egg count was entered in the m_x tables.

The l_x and m_x tables were entered in an Excel spreadsheet, which was then used to calculate the values of *r* by substituting trial values in the following equation until the left hand side rounded to unity at five decimal places:

$$\Sigma\, e^{-rx} l_x m_x = 1$$

RESULTS AND DISCUSSION

Table 1. Development was more rapid on orange than on pollen dough, but the immature survival rate was much lower.

[1] Significantly different, Mann-Whitney test, $P < 0.01$.
[2] Significantly different, *t*-test, $P < 0.01$.

Statistic	Developmental period (days)		Survival rate (proportion)	
	Pollen dough	Orange	Pollen dough	Orange
N	208	86	3	3
Minimum	26.0	24.0	0.67	0.25
Maximum	31.0	31.0	0.87	0.40
Median	29.0[1]	27.0[1]	0.79	0.36
Mean	28.5	27.5	0.78[2]	0.34[2]
SD	1.07	1.49	0.098	0.076

Figure 1

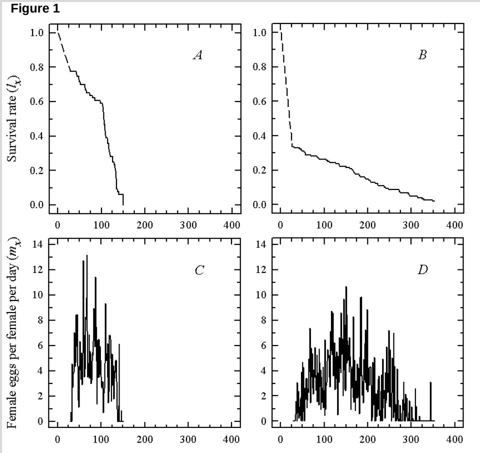


Fig. 1. Life table (l_x) and age-specific fecundity (m_x) plots for *A. tumida* on inoculated pollen dough (A, C) and orange (B, D). The dashed lines in the l_x plots represent immature stages. The average lifespan (immature + adult) was much shorter on pollen dough than on orange (A, B). Adult longevity was significantly lower on pollen dough (Mann-Whitney test, $P < 0.001$), but lifetime fecundity on pollen dough and orange did not differ (Mann-Whitney test, $P = 0.809$). Lifespan ranged from 15 to 123 days on pollen dough with a median of 85. On orange, it ranged from 16 to 345 days with a median of 157. Females that laid no eggs were assumed not to have mated. When these females were ignored, fecundity ranged from 2 to 2,614 on pollen dough with a median of 612.5, and from 4 to 4,775 on orange with a median of 445.0.

Figure 2

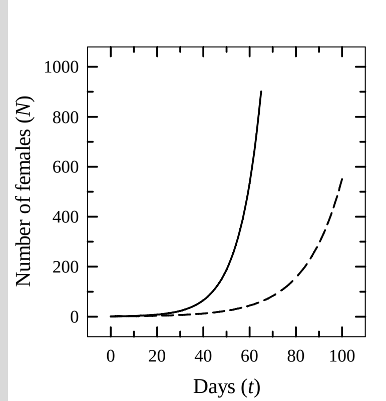
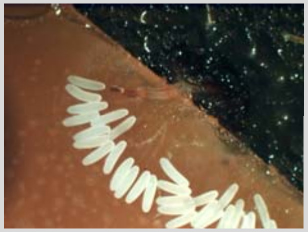


Fig. 2. Potential population growth of *A. tumida* at 27.5 ºC on inoculated pollen dough (solid line, $r = 0.1047$) and on orange (dashed line, $r = 0.0631$). $N_0 = 1$ is the initial number of females.

The results showed a lower potential for population growth on oranges than on inoculated pollen dough, which is consistent with earlier findings that adult weight and progeny production are lower on oranges (Arbogast et al. 2009). Although the positive *r* indicates that population increase on oranges is possible, the rate of increase would be lower than on inoculated pollen dough, and the capacity to overcome environmental resistance factors would be diminished in proportion. Whether or not *A. tumida* would be able to survive on oranges, or on any other alternative diet, in a particular setting would depend upon the value of *r* relative to the strength of environmental conditions opposing population increase.

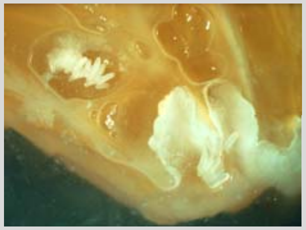
The lower *r* value on oranges can be attributed to a higher immature mortality rate and a long oviposition period. Values of *r* increase with: (1) decreasing developmental period, (2) increasing survivorship to reproductive maturity, and (3) increasing concentration of oviposition early in adult life. Although the developmental period of *A. tumida* was 2 days less on oranges than on inoculated pollen dough, this was more than offset by much lower immature survival and by a long oviposition period, in which the maximum rate (10.7 eggs/♀) occurred 150.5 days after adult emergence. In comparison, the maximum rate on inoculated pollen dough (12.7 eggs/♀) was reached in 60.5 days.

Small hive beetle adults on orange.



Ovipositing on pollen dough.

Eggs on pollen dough.



Eggs on orange.

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