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POTENTIAL FOR POPULATION GROWTH OF THE SMALL HIVE BEETLE *AETHINA TUMIDA* (COLEOPTERA: NITIDULIDAE) ON DIETS OF POLLEN DOUGH AND ORANGES

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ABSTRACT

The small hive beetle *Aethina tumida* Murray, is an African native that has become an invasive pest of honeybees in North America. The beetle is capable of rapid population growth on pollen, honey, and bee brood. It is also capable of feeding and reproducing on various kinds of fruit, but its ability to sustain population growth on diets other than bee products has remained unknown. We examined this question by observing *A. tumida* on 2 diets: pollen dough (inoculated with a species of yeast carried by the beetle) and orange. Age-schedules of survival (l_x) and fecundity (m_x) were constructed for each diet and used to calculate the intrinsic rate of natural increase (r), which was used to calculate other demographic parameters. The results showed potential for population growth on both diets ($r > 0$), but the potential was less on orange ($r = 0.0631$) than on inoculated pollen dough ($r = 0.1047$). The calculated multiplication per generation on pollen dough was nearly double that on orange and the generation time was shorter by more than a third. Survival of *A. tumida* populations on oranges, or any other alternative diet, in a given environment would depend on the value of r relative to the strength of environmental conditions opposing population increase. The ability to use alternative diets (fruit, possibly fungi, or other food resources) would confer an adaptive advantage upon beetles dispersing over a landscape in which honeybee colonies occur as small, widely scattered patches.

Key Words: honeybee pest, demography, intrinsic rate of natural increase, nutrition

Supplemental material online at <http://www.fcla.edu/FlaEnt/fe932.htm#InfoLink1>.

RESUMEN

El escarabajo pequeño de las colmenas, *Aethina tumida* Murray, es nativo de África y ha llegado a ser una plaga invasora de las abejas de miel en Norteamérica. La población del escarabajo puede crecer de forma rápida sobre polen, miel y la cría de abejas. También, puede alimentarse y reproducirse sobre varias frutas, pero su capacidad de sustentar el crecimiento de su población sobre otras dietas además de los productos de abejas es desconocida. Examinamos esta pregunta observando *A. tumida* sobre 2 dietas: masa de polen (inoculada con una especie de levadura llevada por el escarabajo) y naranja. Los programas de sobrevivimiento (l_x) y fecundidad (m_x) según su edad fueron contruidos para cada dieta y usados para calcular la tasa intrínseca de crecimiento natural (r), y otros parámetros demográficos. Los resultados demostraron potencial para el crecimiento de la población sobre ambas dietas ($r > 0$), pero el potencial fue menor sobre las naranjas ($r = 0.0631$) que en la masa de polen inoculada ($r = 0.1047$). La multiplicación calculada por generación sobre masa de polen fue casi el doble de aquella sobre naranja y el tiempo de generación fue mas corto por mas de una tercera parte. La sobrevivencia de poblaciones de *A. tumida* sobre naranjas, o cualquier otra dieta alternativa en un ambiente dado, dependerá del valor de r en relación de la fuerza de las condiciones ambientales en contra del aumento de la población. La capacidad de utilizar dietas alternativas (fruto, posiblemente hongo, u otros recursos alimenticios) conferirá una ventaja adaptiva sobre los escarabajos para esparcirse en terrenos donde las colonias de abejas estan ampliamente distribuidas en pequeñas parches.

The small hive beetle, *Aethina tumida* Murray, is an African native that was unintentionally introduced into North America, where it has become an invasive pest of honeybee colonies. The eggs are laid in cracks and crevices inside hives or on the combs, and adults as well as larvae feed on pollen, honey, and bee brood. Upon completing development, larvae leave the hive and fall to the ground, where they burrow into the soil and pupate. Emerging adults disperse in search of suitable hosts and either re-enter nearby honeybee colonies or scatter over the landscape.

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Dispersing beetles are subject to many hazards, not the least of which is failure to locate a bee colony, so alternative diets would confer a significant adaptive advantage. Hoffman et al. (2008) recognized the adaptive advantage of lower host specificity when they demonstrated

host shift of *A. tumida* to bumblebees. The ability of *A. tumida* to feed, develop, and reproduce on various species of fruit is well known (Ellis et al. 2002; Keller 2002; Arbogast et al. 2009b), and the beetle's nitidulid affinities suggest additional diets. Nitidulids exhibit a wide range of trophic habits, but they are primarily saprophagous or mycophagous and are characteristically associated with yeasts and fungi that cause fermentation in tree wounds, under bark, or among decaying leaves, fruits, or flowers (Parsons 1943; Lawrence 1991; Cline 2005). Although *A. tumida* has become highly adapted to life in bee colonies, its ability to develop and reproduce on fruit suggests that it has retained ancestral nitidulid food habits that confer an adaptive advantage. These habits may include mycophagy as well as saprophagous feeding on materials other than fruit, although this remains to be demonstrated. Dispersing adults are attracted to shady areas (Arbogast et al. 2007, 2009a) and may feed on fungi, fallen fruit, or other decaying materials in woodlands. Adult beetles have been captured by baited flight traps placed in woodlands near an apiary (Arbogast et al. 2009a) as well as in woodlands 2.7 km or more from the nearest known bee colonies (Arbogast et al. 2009b).

The adults, in both Africa and the U. S., carry a strain of the yeast *Kodamaea ohmeri* (NRRL Y-30722) that induces fermentation of bee-collected pollen (Teal et al. 2006; Torto et al. 2007c). Stored pollen becomes naturally inoculated with the yeast when adult beetles invade a hive, and the resulting fermentation produces volatiles that mimic the honeybee alarm pheromone, which is a potent attractant for the beetles. The volatiles thus act as an aggregation kairomone indicating a local concentration of pollen (Torto et al. 2007a, b, c). Also, there is evidence that the yeast may have nutritional value (Arbogast et al. 2009b).

Aethina tumida is capable of rapid population growth on the concentrated resources found in honeybee colonies, but its ability to sustain population growth on diets other than bee products is unknown. Arbogast et al. (2009b) compared the ability of the beetle to develop and reproduce on pollen dough (either yeast-inoculated or not) with its ability to develop on several kinds of fruit: oranges, inoculated oranges, green grapes, and cantaloupe. The number of adult progeny produced on inoculated pollen dough and on inoculated oranges were the same, and significantly higher than on either pollen dough or oranges without inoculation. Inoculated pollen dough and non-inoculated oranges can therefore be expected to provide a marked contrast in ability to support population growth of the beetle, and for this reason, we selected them for our experiments. The former represents a favorable

diet, similar to that found in infested bee hives; and the latter is one of the least satisfactory of the fruit diets studied. Although natural infestation of fallen oranges has not been demonstrated even though a few unpublished attempts have been made to do so, the negative results do not prove that such infestation never occurs. Other species of nitidulids are known to infest fallen oranges (Vogt 1951; Lima & Davies 1981), and dispersing small hive beetles would be likely to encounter such oranges, especially when hives are placed in groves for pollination and production of orange blossom honey.

We determined the duration of immature development, survival of the immature stages, age-specific fecundity, and age-specific survival of *A. tumida* on each of the 2 diets under controlled laboratory conditions. The data was then used to construct life tables and tables of age-specific fecundity for calculation of the intrinsic rate of natural increase and other demographic parameters (Birch 1948).

The intrinsic rate of natural increase can be defined as the constant r in the exponential growth equation $N = N_0 e^{rt}$, where N_0 is the initial number of individuals and N is the number after some time t . 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 (such as temperature, humidity, and other parameters) and by the nutritional situation. For this reason, r and other demographic parameters derived from it are useful in comparing the effects of various physical conditions and diet on an insect's potential for population increase.

MATERIALS AND METHODS

The beetles used in experiments were from cultures that had been maintained at room temperature in our CMAVE laboratory for ~4 yr. They were reared on commercially available pollen dough (4% pollen with sugar, soy, yeast, and water) (Global Patties, Airdrie, Alberta, Canada) that had been inoculated with *K. ohmeri* to produce fermentation. The rearing procedures were the same as described by Arbogast et al. (2009b). All experiments were conducted at constant temperature and humidity ($27.5 \pm 0.5^\circ\text{C}$, $60 \pm 5\%$ RH) in an environmental chamber (Percival model I36VLC8, Perry, IA).

Demographic Calculations

The intrinsic rate of natural increase (r) was calculated as outlined by Birch (1948). This calculation 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 1 d as the unit of time and assumed that all eggs were laid at the midpoint of each 1-d interval.

The l_x and m_x tables were entered in a spreadsheet (Microsoft Office Excel, Microsoft Corp., Redmond, WA), which was then used to calculate the values of r by substituting trial values in the Euler-Lotka equation until the left hand side rounded to unity at 5 decimal places:

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

The values of r were then used to calculate the following demographic parameters for each diet: the net reproduction rate ($R_0 = \sum l_x m_x = e^{rT}$), which is the multiplication per generation, or the mean number of females produced by each female in a lifetime; the generation time ($T = \ln R_0 / r$), which is the mean time between generations, or the mean time from birth of parents to birth of offspring; and the finite rate of increase ($\lambda = e^r$), which is the multiplication rate of a population with a stable age distribution expressed as ♀ ♀/♀ /unit time.

Developmental Period and Survival of Immature Stages

The mean time required for development 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 in clear plastic boxes (19 × 13.5 × 10 cm) provided with a 3-cm layer of autoclaved soil (900 g soil to 100 g water) for pupation. The 2 diets (50 g of each), contained in petri dish lids lined with filter paper, were placed on the soil in separate boxes. Eggs were collected by confining about 50 pairs of adults in each of two 800-ml mason jars with pollen dough (about 25 g) and 3 egg strips—strips of transparency film (5 × 4.5 cm) folded in thirds (in the form of a Z) and stapled to provide 2 crevices for insertion of eggs. The strips were removed after 24 h, the eggs were counted, and 3 strips with eggs were placed on each diet. Observations were made daily until adult emergence

ended. The period in days from oviposition to adult emergence was recorded for each emerging adult, and the total number that emerged was divided by the number of eggs to determine the proportion surviving.

This experiment was repeated 3 times. The mean developmental period for each diet was calculated by pooling the 3 replicates, adding the developmental times for all of the adults that emerged, and dividing by the total number of adults. The mean proportion surviving was calculated by adding the proportions from the 3 replicates and dividing by 3.

Adult Female Survival and Age-specific Fecundity

Data for constructing the adult portions of the l_x and m_x tables were obtained in 2 experiments, 1 for inoculated pollen dough and 1 for orange. For each experiment, pupae were collected from stock cultures, sorted by sex, and held for adult emergence. As adults emerged, 1 male and 1 female were placed in each of 50 clear plastic petri dishes (100 × 15 mm) with diet.

Orange slices were presented as wedges (30 × 30 × 5 mm), with 1 wedge and 1 egg strip per dish. Most eggs were inserted into the egg strips, but some were placed elsewhere, especially under the orange. Inoculated pollen dough was presented as a thin layer smeared on one surface of a standard microscope slide. A small spot of pollen dough applied to each end of the other side attached the slide to the bottom of the dish, leaving it slightly elevated. Most eggs were laid in the crevice between the slide and the dish, but others were scattered throughout the dish. This procedure for determining oviposition was necessary, because adults often burrowed into larger amounts of pollen dough and laid eggs where they could not be seen. Larvae also became hidden by burrowing.

The dishes were checked daily for eggs and adult deaths until all of the females were dead. When eggs were found, the adults were transferred to clean dishes with fresh diet and (in the case of orange) egg strips, and the old dishes were monitored for at least 5 d to count hatching larvae and un-hatched eggs. To minimize error due to hidden eggs and larvae, the final egg count was taken as the largest of total eggs, total larvae, or total larvae plus un-hatched eggs. The total was divided by the number of surviving females to obtain the mean number of eggs per female for each day. Because the sex ratio of *A. tumida* reared on either inoculated pollen dough or orange is 1:1 (Arbogast et al. 2009b), only half of each mean daily egg count was entered in the m_x tables.

Statistics

Descriptive statistics were calculated and statistical comparisons made for developmental pe-

riod, immature survivorship, oviposition pattern, fecundity, and adult lifespan with SigmaStat 3.5 (Systat Software, Inc., Point Richmond, CA). Before making statistical comparisons, all data were tested for normality and equal variance. Data that passed both tests was analyzed by a *t*-test; other data was analyzed by the nonparametric Mann-Whitney test.

RESULTS AND DISCUSSION

Life-table and age-specific fecundity curves for *A. tumida* breeding on either inoculated pollen dough or orange revealed a marked effect of diet on its life cycle (Fig. 1). Development from egg to

adult was faster on orange than on pollen dough, and the adult female lifespan was longer, but the survival rate of immature stages was two-fold less (Table 1). The average oviposition period was 66 d longer on orange than on pollen dough (Fig. 1C-D) (Mann-Whitney test, $P < 0.01$), but there was no difference in lifetime fecundity (Mann-Whitney test, $P = 0.81$). Females that laid no eggs (8% of those on pollen dough and 10% of those on orange) were assumed not to have mated. When these females were ignored, lifetime fecundity ranged from 2-2,614 on pollen dough with a median of 612.5, and from 4-4,775 on orange with a median of 445.0. We cannot explain this extreme range, but it could be related in part to wide vari-

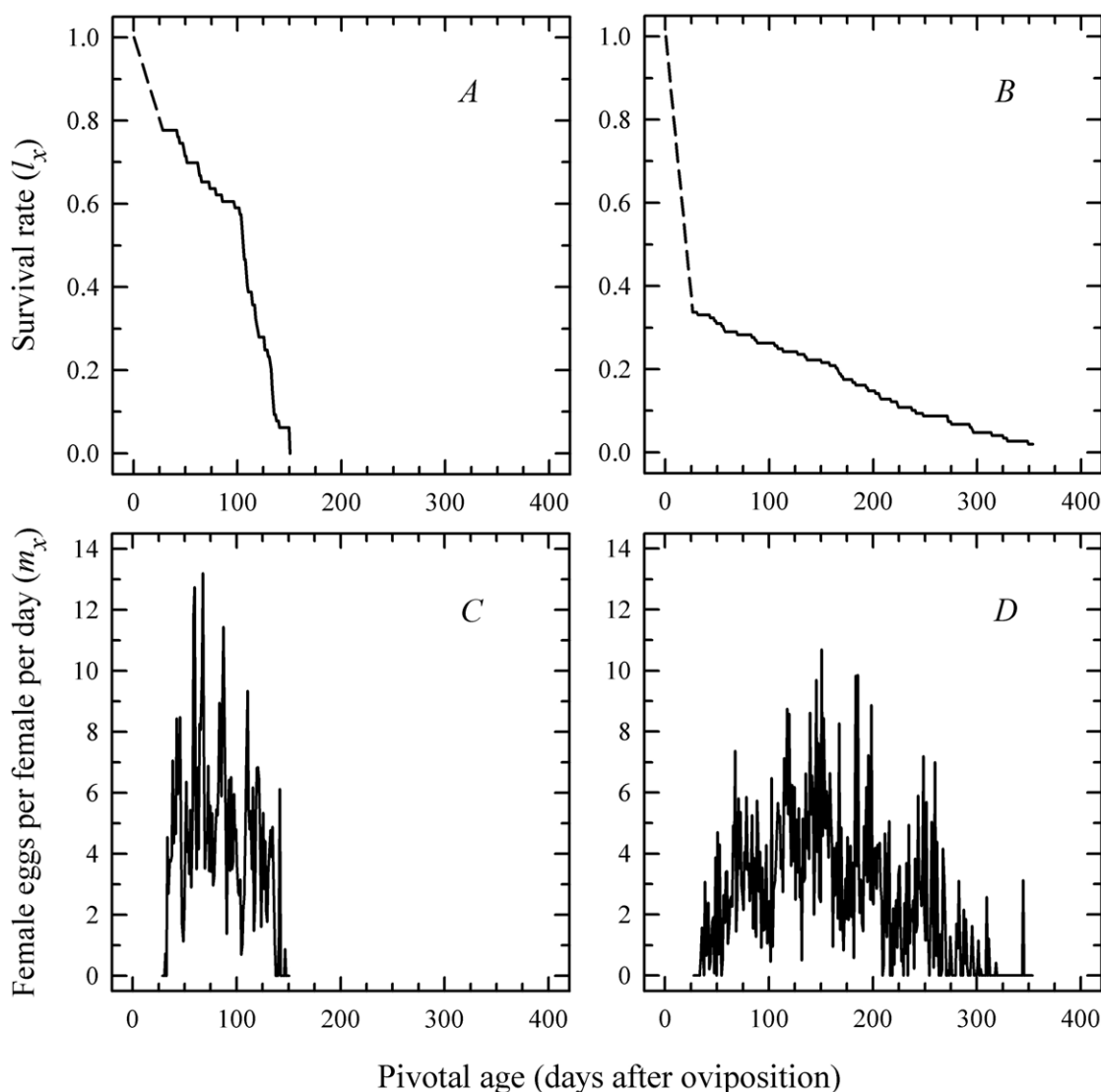


Fig. 1. Survival (l_x) and age-specific fecundity curves (m_x) for *A. tumida* at 27.5°C on inoculated pollen dough (A, C) and orange (B, D). Dashed lines in A and B represent immature stages.

TABLE 1. LIFE CYCLE OF *A. TUMIDA* ON INOCULATED POLLEN DOUGH (IPD) AND ON ORANGE.

Statistic	Developmental period (d)		Immature survival (proportion)		Adult female lifespan (d)	
	IPD	Orange	IPD	Orange	IPD	Orange
<i>n</i>	208	86	3	3	50	49
Median	29.0*	27.0*	0.79	0.36	85.0*	157.0*
Mean	28.5	27.5	0.78**	0.34**	81.3	163.4
SD	1.07	1.49	0.098	0.076	30.0	94.2

The number of observations is given by *n* (See Materials and Methods for explanation.). The difference between IDP and orange was significant ($P < 0.01$) for all 3 characteristics: developmental period, immature survival, and female lifespan. Developmental period and female lifespan data failed normality tests, so medians were compared with nonparametric Mann-Whitney test (*). Immature survival data passed normality and equal variance tests, so means were compared by a *t*-test (**).

ation in adult female lifespan (from 15-123 d on pollen dough and 16-345 d on orange). Total fecundity would be reduced by early death, and there was a tendency for adult lifespan and total fecundity to increase together on pollen dough (Pearson correlation coefficient = 0.51, $P < 0.001$). This was not true for orange, however, in which the coefficient was 0.08 ($P = 0.59$), and some females with a relatively long lifespan laid few eggs on either diet.

The temporal pattern of oviposition typically consisted of alternating episodes of egg laying and inactivity, as illustrated by the example in Fig. 2, and there was no significant difference between pollen dough and orange with respect to the period between episodes (Mann-Whitney test, $P = 0.151$), which ranged from 1-15 d for pollen dough and from 1-16 d for orange with a median of 1.0 in both.

The demographic parameters (Table 2) were all derived either directly or indirectly from the l_x and m_x tables, but they describe different aspects of population growth rate, each of which reflects the difference between inoculated pollen dough and orange. The finite rate of increase λ simply translates the infinitesimal rate (r) into a more easily comprehended finite rate, the number of females produced by each female per unit time. Although the values of λ differed by only 0.045 ♀/♀/d, the net reproduction rate (R_0)—the multiplication per generation—on pollen dough was nearly double that on orange, while the generation time (T) was shorter by more than a third. Clearly, *A. tumida* breeding on inoculated pollen dough showed a distinctly higher potential for population increase.

This is consistent with earlier findings that progeny production on yeast-inoculated pollen dough is higher than on orange (Arbogast et al. 2009b). The same study also showed that adult and pupal weights are lower on orange (inoculated or not) than on inoculated pollen dough. Although the positive r value indicated that population increase on oranges is possible, the rate of in-

crease would be lower than on inoculated pollen dough, and the capacity to overcome environmental resistance would be diminished accordingly. Whether or not *A. tumida* populations would be able to survive on oranges, or on any other alternative diet, in a particular environment would depend upon the value of r relative to the strength of environmental conditions opposing population increase.

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

The general effect of diet on the growth potential of insect and mite populations is well known, as can be illustrated by a few examples. The western flower thrips, *Frankliniella occidentalis* (Per-gande), is a generalist herbivore but also a natural enemy of the spider mite *Tetranychus urticae* Koch. On cotton leaves, the r value of the thrips depends on cotton variety (mite resistant or not) and the availability of cotton pollen and mite eggs; r is maximum when pollen is available ($r = 0.220$ on susceptible and 0.223 on resistant leaves) and lowest (0.021) on resistant leaves with no pollen or mite eggs (Trichlo & Leigh 1988). Hulshof & Vänninen (2002) found that when *T. urticae* feeds on cucumber leaves, r varies with the availability and species of pollen on the leaves, ranging from 0.163 without pollen to 0.240 on pine pollen. *Epiphyas postvittana* (Walker) is a leaf rolling tortricid moth known to feed on 123

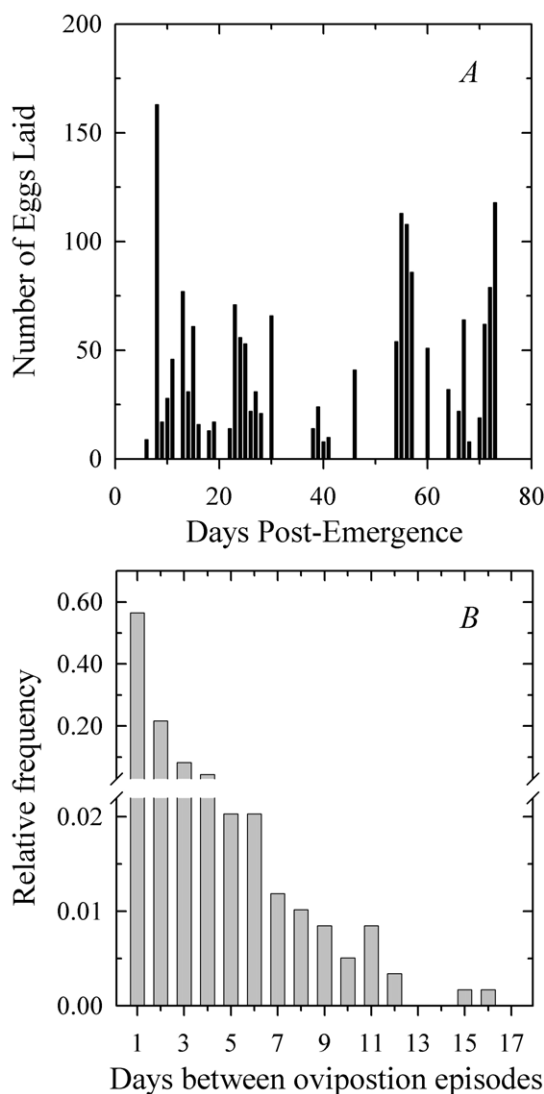


Fig. 2. Temporal pattern of oviposition in *A. tumida*. (A) Typical oviposition pattern, with episodes of oviposition and inactivity alternating, illustrated by a female ovipositing on inoculated pollen dough. (B) Relative frequency of periods (d) between episodes of oviposition in females that laid 1,500 or more eggs (data for inoculated pollen dough and orange combined, $n = 591$). One period of 57 d (on orange) was omitted in calculating relative frequency.

dicotyledonous plants in Australia and more than 250 in New Zealand. Wijesiri et al. (1995) determined its r value on 4 common host plants (curled dock, *Rumex crispus* L.; plantain, *Plantago lanceolata* L.; white clover, *Trifolium repens* L.; and apple, *Malus pumila* Mill.) at various temperatures. At 25.2°C, (the optimum except for *Malus*), r ranged from 0.146 on the best host (*Rumex*) to 0.080 on the poorest (*Trifolium*). The spotted boll-

worm, *Earias vittella* (F.), is a major pest of cotton but also feeds on a number of alternative hosts, including okra and mesta (kenaf), *Hibiscus cannabinus* L. Satpute et al. (2005) reported r values of 0.1334 on okra, 0.1111 on cotton, and 0.0888 on mesta. Nanthagopal & Utamasamy (1989) found that the r value of *E. vittella* also varies with species of cotton: 0.1960 on *Gossypium barbadense* L., 0.1928 on *G. hirsutum* L., 0.1175 on *G. herbaceum* L., and 0.0877 on *G. arboreum* L.

The effect of diet on r illustrated by these examples is much like that observed in our study of *A. tumida*. All of the r values indicate a potential for population increase, but at rates differing with the quality of the diet. It should be noted that because r occurs in the exponent of the population growth equation, a small difference in value has a large effect on population growth over short periods of time. The adaptive advantage of alternative diets, even diets of relatively low quality, lies in their potential for sustaining population growth when more suitable diets are unavailable.

This advantage becomes especially evident when we recognize that the environment of *A. tumida* extends beyond bee colonies and their proximity. Its total environment can, in fact, be viewed as a landscape in which honeybee colonies occur as small, widely scattered patches, and in which there are patches of alternative food resources. Given this view of its environment, it is reasonable to hypothesize that *A. tumida* is a generalist species that is able to maintain adequate levels of reproduction in marginal habitats but is able to attain high levels of reproduction in resource rich habitats such as bee colonies (Arbogast et al. 2009b). The generalist hypothesis is supported by the beetle's ability to feed, develop, and reproduce on fruit; by its nitidulid affinities; and by its occurrence in woodlands, apparently far removed from honeybee colonies. The hypothesis is further supported by its potential for population increase on orange, one of the least satisfactory of the fruit diets studied by Arbogast et al. (2009b).

The question remains: Does *A. tumida* actually utilize alternative diets to breed in natural habitats devoid of bee colonies? Laboratory studies and field observations strongly suggest that it has this capacity, but definitive proof of breeding populations is lacking. The presence of *A. tumida* larvae in fruit, fungi, or other alternative foods collected in natural settings lacking bees would provide positive proof. So also would capture of adults in emergence traps placed on the soil. Unfortunately, the sparse population levels indicated by our trapping efforts suggest that these methods would be unlikely to succeed. Our approach to proving the hypothesis will be to continue collecting adults in woodlands using various types of traps and lures, followed by testing of gut contents for evidence of feeding on materials other than bee products, especially on fungi.

TABLE 2. DEMOGRAPHIC PARAMETERS FOR *A. TUMIDA* BREEDING ON INOCULATED POLLEN DOUGH (IPD) OR ORANGES.

Parameter	IPD	Oranges
*Infinitesimal rate of increase daily (r)	0.1047	0.0631
Finite rate of increase (λ) ($\varnothing \varnothing / \varnothing / d$)	1.110	1.065
Net reproduction rate (R_0) ($\varnothing \varnothing / \varnothing / \text{generation}$)	296.6	161.7
Generation time (T) (d)	54.38	80.58

*The fraction by which a population would increase during a period of time arbitrarily close to but greater than zero. It is the natural logarithm of the finite rate of increase.

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