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Biology of *Bonagota cranaodes* (Meyrick) (Lepidoptera: Tortricidae) on Seven Natural Foods

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Biologia de *Bonagota cranaodes* (Meyrick) (Lepidoptera: Tortricidae) em Sete Dietas Naturais

RESUMO - Foi avaliado, em laboratório, o efeito de sete dietas naturais sobre o desenvolvimento e a reprodução de *Bonagota cranaodes* (Meyrick). Os experimentos foram conduzidos a 23 ±1ºC de temperatura, 70 ± 10% de UR e fotoperíodo de 16:8h (L:E). As larvas foram criadas em macieira, videira e madresilva (*Lonicera japonica*). Para os dois primeiros alimentos foram utilizados três tipos de dietas: folhas de primavera, folhas de verão e frutos. O número de ínstares larvais variou entre cinco e sete. As larvas criadas em folhas de macieira apresentaram, de modo geral, menor número de ínstares, quando comparadas com aquelas criadas em folhas de videira e madresilva. A duração do desenvolvimento larval diferiu entre dietas. As larvas criadas em folhas de macieira-primavera apresentaram a menor duração e as criadas em frutos a maior duração. A sobrevivência de larvas foi menor em frutos que em folhas, principalmente em maçã (17,8%). As pupas fêmeas criadas em madresilva foram mais pesadas que as criadas nas demais dietas. O ciclo de ovo a emergência de adultos variou entre 41 dias em folhas de macieira-primavera e 60 dias em maçã. As fêmeas criadas em madresilva e folhas de macieira-primavera foram as mais fecundas, sendo que aquelas provenientes de maçã não ovipositaram. Madresilva e folhas de primavera foram os alimentos mais adequados; em contraposição, as maçãs foram a dieta menos adequada, o que sugere que dificilmente as larvas possam completar o ciclo sobre esse alimento.

PALAVRAS-CHAVE: Insecta, lagarta-enroladeira, dieta, planta hospedeira, fase imatura, biologia reprodutiva

ABSTRACT - The effect of seven natural diets on the development and reproduction of *Bonagota cranaodes* (Meyrick) was evaluated under laboratory conditions. The experiments were carried out at the temperature of 23 ± 1ºC, with 70 ± 10% of RH and a photoperiod of 16:8h (L:D). The larvae were reared on apple, grapevine and honeysuckle (*Lonicera japonica*). On the first two foods three types of diet were used: spring leaves, summer leaves and fruits. The number of instars varied from five to seven. The larvae reared on apple leaves had, in general, fewer instars than those reared on grapevine and honeysuckle leaves. The duration of larval development differed between diets. The larvae reared on spring apple leaves showed the shortest duration, and those on fruit the longest. The larvae survival was lower on fruit than on leaves, and on apples it was particularly low (17.8%). The female pupae reared on honeysuckle were heavier than those reared on the other diets. The cycle from the egg to the emergence of adults varied between 41 days on spring apple leaves and 60 days on apples. The females reared on honeysuckle and spring apple leaves were the most fecund, whereas the females on apples did not oviposit. Honeysuckle and spring leaves were the most suitable foods. Apples, on the other hand, were the least suitable diet, which leads one to think that larvae could hardly complete their whole cycle on this fruit.

KEY WORDS: Insecta, leafroller, diet, host plant, immature stage, reproductive biology

Bonagota cranaodes (Meyrick) is a native tortricid which in Uruguay is found on honeysuckle (*Lonicera japonica*), ceibo (*Erythrina cristagalli*), privet (*Ligustrum* spp.) and other ornamental plants, as well as on some weeds (Bentancourt and Scatoni 1995). However, in the last two decades it has expanded its range of hosts, and nowadays it is commonly found on fruit trees, especially apple, but also pear, plum and grapevine (Bentancourt and Scatoni 1995). It is an important pest of the apple tree, on which it causes serious damage (Bentancourt and Scatoni 1999). It is also a frequent pest on grapevine, although on this crop specific control measures are usually not necessary. In the last years it has also come to prominence in Brazil because of the damage that it causes to apples, with losses in the main producing regions which amount to between 3% and 5% of production (Kovaleski *et al*. 1998, Botton *et al*. 2000).

The larvae develop on the vegetative parts and fruit of the hosts. The damage to fruit is extremely severe, especially in the summer. On apple they cause irregular superficial damage, which reduces the commercial value of the fruit. On grapevine they impair the quality of the bunches when they feed directly on the grape berries. After the veraison, the attacks become more serious since the damage provide an entry site for bunch rot organisms. It is common for this species to attack jointly with another tortricid fruit tree pest, *Argyrotaenia sphaleropa* (Meyrick), which means an increase in damage to the crops (Bentancourt and Scatoni 1999).

In recent years, colonies of these two tortricidae have been maintained in the laboratory on artificial diets and natural foods, in particular apple, grapevine, and honeysuckle, which is a habitual host for larvae in winter. Preliminary observations show that there are big variations in the development and reproduction of *B. cranaodes* that are related to the natural food used. The differences noted can be seen even on the same hosts depending on whether the rearing is done on leaves or on fruit, and in the case of leaves it depends on the season, spring or summer.

The insects establish different kinds of interaction with host plants, and these have important consequences for essential aspects of their life. Many studies have been done on this aspect of the influence of food on the biology of lepidoptera. Different biological parameters are affected in important ways by the quantity and quality of the food (Feeny 1970, Pencoe and Martin 1982, Pashley *et al*. 1995). Although there have been recent contributions to the biology and control of this species (Parra, *et al*. 1995, Nuñez *et al*. 1998, Botton 1999, Botton *et al*. 2000), these do not in any way reflect the effects that different natural diets can have on its development and reproduction. Given the importance that *B. cranaodes* has assumed in recent years on apple and grapevine crops in Uruguay, the aim of this study was to examine the effects of seven natural diets (apple and grapevine leaves and fruit, and honeysuckle leaves) on its development and reproduction.

Materials and Methods

Mature larvae and pupae of *B. cranaodes* were collected from apple and grapevine crops in the fruit-producing area of Melilla, in the Province of Montevideo. The studies were done on the first generations of material from the field. In the laboratory, the colonies on leaves from these crops were maintained at 23 ± 1ºC, 70 ± 10 R.H. and a photoperiod of 16h photophase. Closed glass boxes with a saturated solution of sodium chloride were used to maintain relative humidity (Winston and Bates 1960). Apple leaves and fruit (Red Delicious), grapevine leaves and fruit (Muscat of Hamburg) and honeysuckle leaves were used as sources of food for the tests. The tests on apple and grapevine leaves were carried out in spring (November-December) and summer (January-February), while those on honeysuckle leaves were done in the fall-winter (May-July). The tests on apples and grapes were started in February, the time when the worst attacks in the field are known to start.

The methodology and the materials described below have been used for years in the entomology laboratory of the Faculty of Agronomy (University of the Republic, Uruguay) for rearing tortricid fruit tree pests (Bentancourt and Scatoni 1986, Scatoni and Bentancourt 1988). The tests on leaves were done in transparent plastic boxes 70 mm in diameter and 30 mm deep, which had filter paper on the bottom. Recently emerged larvae were placed individually in the boxes on new apple, grapevine or honeysuckle leaves. The observations were made at 24h intervals until the end of the larval stage or the death of the larvae. The number of instars and their duration was determined by the presence of cephalic capsules that had been shed during the moults. Once the larvae had moulted, the maximum width of the abandoned cephalic capsule was measured, except in the last instar when measurements were taken of the larvae themselves. The pre-pupal stage was not considered, as it was taken into account together with the last larval instar. The leaves were changed every one or two days so that the food was always fresh. Two tests of 50 larvae each were carried out for each diet.

The tests on fruit were done in transparent boxes 80 mm in diameter and 90 mm deep, covered on top with a polythene membrane (Rolopac®). An apple or part of a bunch of grapes was placed in each box. The apples used were of a similar size (approx. 60 mm in diameter), color and shape. The bunches of grapes selected were collected between 20 and 35 days before the harvest, and were cut into pieces 60 to 70 mm long. Two recently emerged larvae were put in each box, preferably in the calyx and stem cavities of the apples, and between the berries of the bunches of grapes. After the first 72h, daily observations were made so as to detect the presence of excrement as the main indicator of larval activity. The daily observation of larvae is difficult on fruit since they do not remain exposed, so, in order to avoid interfering with larval development, the duration of each instar was not determined. Therefore, the time that this stage of development took was measured from the emergence of larvae until the time they pupated. The larvae were only removed from the fruit when it lost turgidity or started to rot, which happened with greater frequency on grapes. A total of 60 larvae per test were reared.

Recent pupae formed they were transferred individually to plastic boxes 60 mm in diameter, and placed on moistened filter paper. Within 24h to 48h they were sexed and weighed.

For oviposition, cylindrical glass boxes 90 mm in diameter and 100 mm deep, were used, and they were lined inside with paraffined paper. A couple of adults were put in each box. A solution of honey at 10% was used as food, and this was renewed once a day. The oviposition boxes were maintained until the death of both adults. They were observed every day, preferably in the morning, so as to remove from the paraffined paper the eggs laid the previous night. The egg masses taken out were placed individually in transparent plastic boxes on moistened filter paper. As embryonic development progressed and the black cephalic capsules became visible, the number of eggs was counted, and later on the number of eggs that hatched was recorded. These data were used to calculate the life table of fertility for *B. cranaodes* on seven natural foods, based on Silveira Neto *et al*. (1976) and Begon *et al*. (1996). The couples which did not oviposit or which limited oviposition to a low number of non-viable eggs were eliminated from the test.

For the statistical analysis, the Generalized Linear Model (McCullagh & Nelder 1991) was used, supposing a Poisson distribution with a logarithm link function for the counting variables (number of eggs, durations, fecundity and fertility) and binomial distribution with a logit link function for the proportions (viability). Maximum likelihood estimates and tests of the model were done with F test or the Chi-square statistics. For the continuous variables (weight of the pupae and width of the cephalic capsule) the General Linear Model (ANOVA) and the Tukey test for mean comparisons were used. The analyses were done with the GENMOD procedure of the SAS (1997) statistical analysis system.

Results

Variability in the Number of Instars and the Width of the Cephalic Capsule. The majority of the larvae reared on leaves developed through five or six instars (Table 1). Larvae with seven instars were only frequent among those reared on summer grapevine leaves, and, with a lesser percentage, those on honeysuckle. Females tend to moult more times than males, so the greater proportion of larvae with six or seven instars were female. In general, the larvae reared on apple had fewer instars than those reared on grapevine and honeysuckle. On spring apple leaves all the larvae had five instars, while on summer apple leaves most of the male larvae had five instars and the females six. On spring grapevine leaves a high percentage of larvae, particularly females, developed through six instars, whereas on summer leaves a clear predominance of larvae of both sexes with six and seven instars was observed. On honeysuckle, larvae of both sexes with six instars predominated.

Irrespective of the kind of food, larvae with the same number of moults showed a similar width of the cephalic capsule (Table 2). The differences in the size of the cephalic capsule between larvae with five and with six instars was significant from the second instar in males, and from the third in females, and for larvae with six or seven instars it was significant from the fourth in females and from the sixth in males. Within the same sex, larvae with a higher number of instars had a larger cephalic capsule. In all cases, females had a larger cephalic capsule than males.

Duration of the Development and Weight of the Pupae. There were significant differences in larval development between the three apple diets (Table 3). The larvae fed on spring leaves showed the shortest duration while those fed on fruit showed the longest, with values of around double those observed on spring leaves. Similar results were found on grapevine; the three diets differed significantly from each other. The shortest duration of larval development occurred on spring grapevine leaves, and the longest on fruit. The female larvae fed on honeysuckle had a duration that was

Table 1. Percentage of larvae of *B. cranaodes* with different numbers of instars, reared on different diets (Temperature: 23 ± 1ºC, R.H.: 70 ± 10% , photoperiod: 16h).

Diet	Instars					
	V		VI		VII	
	Males	Females	Males	Females	Males	Females
Apple						
Spring leaf	100.0	100.0	-	-	-	-
Summer leaf	94.5	16.7	5.5	83.3	-	-
Grapevine						
Spring leaf	61.5	14.3	38.5	85.7		
Summer leaf	6.2	-	81.3	18.2	12.5	81.8
Honeysuckle	27.8	16.6	72.2	79.2	-	4.2

Table 2. Mean (±SE) width (mm) of the cephalic capsule of larvae of *B. cranaodes* with five, six and seven instars (Temperature: 23 ± 1ºC, R.H.: 70 ± 10%, photoperiod: 16h).

Number of instar/sex	Instars						
	I	II	III	IV	V	VI	VII
5 males	0.22 ± 0.00a	0.33 ± 0.00a	0.50 ± 0.00a	0.75 ± 0.01b	1.14 ± 0.01b		
5 females	0.22 ± 0.00a	0.33 ± 0.00a	0.50 ± 0.01a	0.82 ± 0.01a	1.27 ± 0.01a		
6 males	0.22 ± 0.00a	0.31 ± 0.00b	0.45 ± 0.01b	0.61 ± 0.01d	0.84 ± 0.01d	1.19 ± 0.01b	
6 females	0.22 ± 0.00a	0.32 ± 0.00ab	0.46 ± 0.00b	0.67 ± 0.01c	0.96 ± 0.01c	1.34 ± 0.01a	
7 males	0.22 ± 0.00a	0.31 ± 0.01b	0.43 ± 0.02b	0.57 ± 0.05d	0.71 ± 0.05d	0.95 ± 0.06c	1.31 ± 0.06a
7 females	0.22 ± 0.00a	0.32 ± 0.00ab	0.45 ± 0.01b	0.61 ± 0.02d	0.78 ± 0.02d	1.04 ± 0.02c	1.38 ± 0.03a

Numbers within columns followed by the same letter are not statistically different at the 5% level of probability, according to the Tukey-Kramer test.

Table 3. Mean (±SE) duration (days) of eggs, larvae, pupae and total of *B. cranaodes* reared on different diets (Temperature: 23 ± 1ºC, R.H.: 70 ± 10% , photoperiod: 16h).

Diet	Eggs	Larvae		Pupae		Total	
		Female	Male	Female	Male	Female	Male
Apple							
Spring leaf	7.9 ± 0.10a	22.8 ± 1.02aA	21.5 ± 1.20aA	10.6 ± 0.71aB	11.7 ± 0.88 bA	41.7 ± 1.41 aA	41.3 ± 1.66 aA
Summer leaf	8.5 ± 0.11e	31.8 ± 1.63cB	25.7 ± 1.19bA	10.7 ± 1.09abA	11.3 ± 0.79abA	49.8 ± 2.35 cA	45.2 ± 1.54 bB
Fruit	-	42.2 ± 3.25eA	41.2 ± 3.21dA	9.7 ± 1.56aB	11.7 ± 1.97abA	60.2 ± 3.88 eA	65.9 ± 4.69 eB
Grapevine							
Spring leaf	8.1 ± 0.08b	27.7 ± 1.41bB	23.6 ± 1.40bA	9.83 ± 0.91aB	10.7 ± 0.99aA	45.5 ± 1.95 bA	42.3 ± 2.06 aB
Summer leaf	8.3 ± 0.13d	36.8 ± 1.83dB	30.9 ± 1.39cA	10.4 ± 1.02aA	10.9 ± 0.85abA	55.5 ± 2.36 dA	50.1 ± 1.83 cB
Fruit	8.2 ± 0.13bc	40.9 ± 2.13eA	37.9 ± 1.65dA	11.4 ± 1.19bA	11.0 ± 0.92ab	60.2 ± 3.88 eA	56.0 ± 2.08 dB
Honeysuckle	8.2 ± 0.06cd	33.0 ± 1.17cB	29.8 ± 1.32cA	10.4 ± 0.69aB	11.2 ± 0.84abA	51.9 ± 1.54 cA	49.2 ± 1.75 cB

Numbers within columns followed by the same lower-case letter or within rows followed by the same upper-case letter are not statistically different at the 5% level of probability, according to the Chi-square test.

statistically similar to that observed among females on summer apple leaves, but different from the rest of the diets. The male larvae had similar development to that observed among males reared on summer grapevine leaves, but different from the rest of the male larvae. In all cases the duration of larval development among females was longer on average than among males, although on spring apple leaves, on apples and on grapes the differences were not significant.

The duration of the development of female pupae varied from 9.7 days on apples to 11.4 days on grapes (Table 3). This latter figure differs significantly from the other diets, with the exception of summer apple leaves. On the other hand, the duration of development of the male pupae varied between 10.7 days on spring grapevine leaves and 11.7 days on the fruit and leaves of the spring apple tree, with significant differences between the two extreme values. Similarly, there were differences between the sexes in the duration of pupae. The development of the female pupae was faster than that of the males, with significant differences on all diets except for summer apple leaves, summer grapevine leaves and grapes.

The duration of embryonic development varied between 7.9 days on spring apple leaves to 8.5 days on summer apple leaves. Even though, from a biological point of view, the differences between the two extreme values are minor, there are statistical differences between the diets due to the low standard error calculated as a consequence of having counted the total number of eggs.

The female pupae reared on honeysuckle were significantly heavier than those reared on other diets (Table 4). Similarly, the male pupae reared on honeysuckle also weighed more, although in this case there were no significant differences from the pupae on spring apple leaves. Sex had a decisive influence on the weight of the pupae; the female pupae were heavier than the male ones, with significant differences that were independent of the diet.

Survival. The larvae survival was higher on leaves than on fruits, although the larvae reared on grapes did not differ statistically from those reared on summer grapevine leaves (Table 5). Survival was significantly low on apples (17.8%). The highest survival was on summer apple leaves (91.2%), although this does not differ statistically from the others reared on leaves. The survival of pupae was 84.4% in all cases, and no differences between the diets were recorded. In the egg stage, survival was above 80.3%, and again there were no statistical differences between different diets.

The Effect of Diet on Reproduction. The females reared on honeysuckle and on spring apple leaves had the highest fecundity, although the latter did not show statistical differences from the females on summer grapevine leaves (Table 6). The lowest fecundity occurred on grapes, although this value did not differ from that obtained on summer apple leaves. Females from apples did not oviposit, partly because the mortality that occurred substantially limited the possibility of forming couples, and partly because the emergence of

Table 4. Mean (±SE) weight (mg) of pupae of *B. cranaodes* reared on different diets (Temperature: 23 ± 1ºC, R.H.: 70 ± 10%, photoperiod: 16h).

Diet	Female	Male
Apple		
Spring leaf	27.4 ± 0.61 bB	15.1 ± 0.74 abA
Summer leaf	16.1 ± 0.83 cdB	11.3 ± 0.67 cA
Fruit	27.1 ± 1.43 bB	12.1 ± 1.40 bcA
Grapevine		
Spring leaf	19.7 ± 0.76 cB	12.2 ± 0.78 bcA
Summer leaf	15.6 ± 0.86 dB	10.0 ± 0.71 cA
Fruit	16.6 ± 0.95 cdB	10.6 ± 0.76 cA
Honeysuckle	31.8 ± 0.58 aB	17.0 ± 0.69 aA

Numbers within columns followed by the same lower-case letter or within rows followed by the same upper-case letter are not statistically different at the 5% level of probability, according to the Tukey-Kramer test.

Table 5. Mean (±SE) survival of eggs, larvae and pupae of *B. cranaodes* reared on different diets (Temperature: 23 ± 1ºC, R.H.: 70 ± 10%, photoperiod: 16 h).

Diet	Eggs	Larvae	Pupae
Apple			
Spring leaf	80.3 ± 0.66a	84.4 ± 5.88a	97.4 ± 2.63a
Summer leaf	99.4 ± 0.29a	91.2 ± 5.09a	90.3 ± 5.59a
Fruit	-	17.8 ± 13.52d	100.0 ± 0.00a
Grapevine			
Spring leaf	95.1 ± 0.42a	81.0 ± 7.15ab	84.4 ± 6.99a
Summer leaf	99.6 ± 0.11a	76.3 ± 7.89abc	89.7 ± 5.97a
Fruit	96.7 ± 0.82a	57.5 ± 10.31c	95.6 ± 4.35a
Honeysuckle	83.6 ± 0.68a	83.6 ± 4.95a	95.3 ± 3.29a

Numbers within columns followed by the same letter are not statistically different at the 5% level of probability, according to the Chi-square test.

adults was staggered in time, limiting still more the number of couples it was possible to form. Moreover, the females of the only two couples that formed did not oviposit. On the other diets, the females generally started oviposition between the second and fourth night following their emergence. The shortest pre-oviposition period was 1.7 days on honeysuckle, and the longest was 3.6 days on grapes, even though the former value did not differ from those observed on spring grapevine leaves, and the latter value did not differ from those observed on the other diets. The oviposition period varied between 5.5 days on spring grapevine leaves and 12.7 days on summer grapevine leaves. The former value did not differ from summer apple leaves or from grapes, while the latter value was statistically similar to honeysuckle. On all the diets the females lived longer than the males. The longevity of adults on apples was not considered since they did not exhibit reproductive activity. The greatest longevity of females was on summer grapevine leaves, although this did not differ from grapes or honeysuckle. On the other hand, the shortest longevity of females was on spring grapevine leaves, although this value did not differ from those obtained on the other diets except for summer grapevine leaves and honeysuckle.

The greatest number of eggs laid in a day was on spring apple leaves. On all the diets with the exception of summer grapevine leaves, the greatest number of eggs laid was on the first day of oviposition, and it generally declined in the succeeding days. On the first day of oviposition, the females deposited between 10.8% (summer grapevine leaves) and 28.8% (grapes) of the total of eggs, while by the fifth day the percentages of eggs that had been laid varied between 63.1% (summer grapevine leaves) and 79.6% (grapes) of the total.

The mean generation time (T) of *B. cranaodes*, calculated using the life table of fertility, varied in function of the food source utilized for the development of the insect (Table 7). The variation was from 44.62 days on apple spring leaf to 62.37 days on grapes. The net reproductive rate (R_o) also showed differences in function of diet: honeysuckle was the food associated with the highest reproductive rate, wich was six times higher than that obtained on grape. The intrinsic rate of natural increase (r_m) varied from 0.04 to 0.09, and was highest on apple spring leaf. The finite rates of increase (λ) were very similar for all food sources, although the highest values were obtained for larvae fed on spring leaves, and these also yielded the lowest mean time generation (T).

Table 6. Mean (±SE) longevity, preoviposition and oviposition periods (days), fecundity and fertility of *B. cranaodes* reared on different diets (Temperature: 23 ± 1ºC, R.H.: 70 ± 10%, photoperiod: 16h).

Diet	Preoviposition	Oviposition	Longevity		Fecundity (total eggs)	Fertility (viable eggs)
			Female	Male		
Apple						
Spring leaf	2.7 ± 0.48bc	7.9 ± 0.81b	14.4 ± 1.10ab B	10.3 ± 0.97a A	363.8 ± 6.03de	292.3 ± 5.41bc
Summer leaf	3.3 ± 0.90bc	7.0 ± 1.32ab	14.7 ± 1.92ab A	12.2 ± 1.56ab A	193.5 ± 6.96^{a}b	192.3 ± 6.93ab
Fruit	-	-	-	-	-	-
Grapevine						
Spring leaf	2.2 ± 0.45ab	5.5 ± 0.71a	13.3 ± 1.05a A	11.0 ± 0.92a A	239.9 ± 4.67bc	228.2 ± 4.55b
Summer leaf	3.0 ± 1.00bc	12.7 ± 2.05c	20.7 ± 2.28c B	12.7 ± 2.05ab A	258.0 ± 4.64bcd	257.0 ± 4.63bc
Fruit	3.6 ± 0.85c	5.8 ± 1.08ab	16.2 ± 1.80abcB	11.0 ± 1.48a A	119.7 ± 5.47a	115.7 ± 5.38 a
Honeysuckle	1.7 ± 0.49a	10.6 ± 1.23c	17.0 ± 1.56bc A	14.7 ± 1.45b A	417.4 ± 7.72e	349.0 ± 7.06c

Numbers within columns followed by the same lower-case letter or within rows followed by the same upper-case letter are not statistically different at the 5% level of probability, according to the Chi-square test.

Table 7. Parameters of life table of fertility for *B. cranaodes* reared on different diets under laboratory conditions (Temperature: 23 ± 1ºC, R.H.: 70 ± 10%, photoperiod: 16h).

Diet	T	R_o	r_m	λ
Apple				
Spring leaf	44,62	53,11	0,09	1,17
Summer leaf	51,97	22,76	0,06	1,10
Fruit	-	-	-	-
Grapevine				
Spring leaf	48,10	38,38	0,08	1,15
Summer leaf	59,94	34,01	0,06	1,08
Fruit	62,37	11,00	0,04	1,07
Honeysuckle	55,37	64,82	0,08	1,13

T= mean generation time (days), R_o = net reproductive rate, r_m = intrinsic rate of natural increase, λ = finite rate of increase.

Discussion

In a system containing alternative hosts, the economic status of polyphagous pests is influenced by nutritional quality as well as by the relative abundance of all host plants (Ali *et al*. 1990). Longer development time, low pupal weight, high mortality and an increase in the number of instars are criteria that indicate the bad quality of the host (Pencoe & Martin 1982). Our results show that food (the seven natural diets tested) plays an important role in the growth and development of *B. cranaodes*. The duration of larval development varied in function of diet. On fruit (apples and grapes) the larvae required more time to complete their development than on leaves. On apple trees, the cycle from the egg to the emergence of the adults was approximately 41 days on spring leaves, 48 days on summer leaves, and 60 days on apples. In this last case the duration of embryonic development was estimated at eight days, due to the fact that on this diet there was no reproductive activity. On grapevine, total duration was 44 days on spring leaves, 53 days on summer leaves and 59 days on grapes. Botton *et al.* (2000) reported a total duration of 47.4 days for specimens reared on an artificial diet at 22ºC. These results are similar to those obtained on summer apple leaves and honeysuckle (50 days on the latter diet). The influence of diet on the rate of development is common among Lepidoptera, and has been reported for *Lymantria dispar* (L.) (Barbosa *et al*. 1983) and for *Spodoptera frugiperda* (J.E. Smith) (Barfield & Ashley 1987, Pencoe & Martin 1982).

The duration of the development of female larvae was longer than that of the male ones on all seven diets. The differences varied from one day on spring apple leaves to 6.1 days on summer apple leaves. This trend was inverted in the pupae; the male pupae had a longer duration than the female pupae except on grapes, for which the duration was similar. The differences observed varied between 0.5 days on summer grapevine leaves and 1.1 days on spring apple leaves. These results agree with those reported by Parra *et al.* (1995), who obtained a longer duration for the male pupae than for the females. Except on spring apple leaves, the differences in pupal duration did not compensate for those in larval duration. The male cycle was between 0.4 and 5.4 days shorter than the female cycle, except on apples. Eiras *et al*. (1994), working with two artificial diets, also found that the males had a shorter development time than the females.

Regardless of sex, the number of larval instars, from hatching to pupation, varied in function of diet. Five larval instars are usually reported for this species (Parra *et al*. 1995, Botton 1999). In our study, only on spring apple leaves do 100% of the surviving larvae of both sexes had five instars. On the other diets, the number of instars varied from five to seven. Both on apple tree and on grapevine, the summer larvae exhibited a tendency to have a higher number of moults than the spring larvae. Similar results were obtained for *A. sphaleropa* (Meyrick) (Bentancourt *et al*. 2003). The two species were reared together, under the same conditions and on the same food (taken from the same plants). Factors such as nutrition, temperature, humidity and even photoperiod, have been suspected of causing supernumerary instars (Schmidt and Lauer 1977). In that study, all these variables were controlled except nutrition. The lower nutritive value of the summer leaves seems to be the main factor in explaining the variability observed. A similar effect occurs in *Hyphantria cunea* (Drury), in which the lower nutritive quality of the summer leaves and the humidity were determinant factors in explaining the greater number of moults (Morris 1967, Morris & Fulton 1970). The variability in the number of moults affected the duration of larval development, since the greater the number on instars the longer time the larvae took to complete their development. The larvae that had six instars required an average of two to five days more to complete their development than the larvae that did so in five instars, and there was a comparable difference between larvae with seven instars and those with six.

Although the survival of eggs and pupae was similar between diets, the survival of larvae showed big differences, with high percentages of mortality on apples and grapes. On apples, no sooner had the larval neonates settled than they invariably sought refuge in the stem or calyx cavities, but a high percentage did not manage to survive and died in the first instars. It was even possible to see incipient damage on the fruit due to the initial feeding of the larvae, although these larvae did not prosper afterwards. On grapes, deaths among the larvae occurred mainly during the first instars, but they showed better adaptation than on apple, probably because the larvae neonates not only feed on the grape berries but also on the peduncles and the rachis. The high mortality and the prolonged larval life which occur on fruit (apples and grapes) make these diets less favorable than leaves for development. Low percentages of survival among larval neonates on apples were also reported for *Epiphyas postvittana* (Walker) (Whiting *et al*. 1997) and for *A. sphaleropa* (Bentancourt *et al*. 2003). According to Chapman (1973), a large group of the tortricidae which attack apple trees feed on leaves and fruit. In fact, during their development, it is common for the larvae of *B. cranaodes* to feed both on the fruit and on the leaves which happen to be in contact with it. According to Botton (1999), once the larvae emerge they start their development on the lower surface of the leaves. On apple, initial feeding on leaves or alternating between leaves and fruit is probably the most satisfactory, since it reduces mortality and lessens the duration of development. On grapevine, although it is highly probable that initial feeding is on leaves, indications of alternate feeding between leaves and fruit are not common. In any case, the survival capacity of larvae on grapes is clearly greater than that observed on apples. Cultural practices, like thinning fruits on apple and pear trees or the thinning of grape berries, will tend to reduce the incidence of this species, eliminating places suitable for refuge and feeding.

The reproductive potential of a species does not only vary as a function of host plants, it can also vary within one host in function of phenological states or of the organs on which it feeds. When the larvae of *Cydia pomonella* (L.) develop on the walnut tree, they produce adults that are less fecund than those which develop on the apple tree (Cisneros & Barnes 1974), while females reared on stem or leaf tissue of the apple tree were sterile (Heriot & Waddell 1942, Howell 1991). In our studies, both fecundity and fertility differed between diets. The greatest fecundity occurred on honeysuckle (417 eggs) and spring apple leaves (364 eggs). Parra *et al*. (1995) reported mean fecundities on an artificial diet that varied between 187.1 and 229.6 eggs, depending on the substrate used for oviposition. These values are similar to the lower fecundities shown in our studies, but differ considerably from the maximum fecundities.

B. cranaodes feeds continuously throughout the year, with movement between different host plants. Honeysuckle is a habitual host for winter larvae, and the studies show that it is a potential alternative host for the development of this species, so special attention should be paid to orchards that are located near places where it is to be found. In spring, above all on apple tree, the larvae find new leaves a suitable host. In this context, at the start of the season the females on honeysuckle and apple are able to reach high reproductive potential, and this can have important consequences for the population density of the species and for the severity of the damage caused by subsequent generations. The grater nutritional suitability of apple spring leaves as a source of food is not only made evident by the greater finite rate of increase (l) and shorter mean generation time (T), but also by the fact that on this food the larvae showed the lowest number of instars.

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