Instar Differences in *Marmara gulosa* (Lepidoptera: Gracillariidae)

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ABSTRACT The number of feeding instars of *Marmara gulosa* Guillén & Davis (Lepidoptera: Gracillariidae), a pest on citrus in the southwestern United States, was investigated from laboratory and field samples. Larvae passed through four to seven feeding instars before the final transitional and spinning instars. An influence of temperature on the number of feeding instars was observed, with low temperatures increasing the proportion of larvae with a higher number of instars. Characterization of instars by the width of the larval head capsule was attempted, and major differences in head capsule width were observed between the same instars of larvae passing through four, five, and six feeding instars. Growth ratios of head capsule width between successive instars were higher for larvae with fewer instars than for those with a higher number, and last feeding instars for each group reached a similar final size.

KEY WORDS peelminer, instars, citrus, head capsule width, temperature

Marmara gulosa GUILLEN & Davis (Lepidoptera: Gracillariidae) is a pest on citrus in the southwestern United States (Vinal 1917; Lockwood 1933; Woglum 1948; USDA 1960; Atkins 1961, 1971; Reeves 1995; Gibson et al. 1997; Guillén et al. 2001). Damage is caused by the larvae, which form long and serpentine superficial mines on the fruit, rendering them unacceptable for the fresh fruit market; green stems of citrus plants are occasionally mined (Atkins 1971; Gibson et al. 1997). Willow is believed to be the principal host for *M. gulosa*, and citrus, oleander, cotton, avocado (Guillén et al. 2001), and sweet pepper (M.G., unpublished) are alternate host plants.

Larvae of *M. gulosa* are hypermetamorphic with three distinct forms: a series of sap-feeding or mining instars, a transitional instar, and a spinning instar (Guillén et al. 2001). The feeding larva is a highly specialized form with a semitransparent-yellowish, depressed body adapted to mining beneath the epidermis of host plants; the spinning larva is a more generalized caterpillar form with a red-banded orange cylindrical body in its final phase; between both forms there is a largely inactive, nonfeeding transitional form that does not molt but remains within the cuticle of the last mining instar (Guillén et al. 2001). When the succeeding final, spinning instar emerges, it proceeds to shed the cuticles of both the last spinning and transitional instars.

Variability in the number of feeding instars has been reported for other species of *Marmara*. In *Marmara elotella* Busck, Vinal (1917) reported the number of feeding instars to be four; in *M. fraxinicola* Fitzgerald, the number of feeding instars varied between six and nine (Fitzgerald and Simeone 1971); and *M. arbutiella* Busck was reported to pass through six to eight feeding instars (Wagner et al. 2000).

In this study, the number of feeding instars of *M. gulosa* on grapefruit was investigated. Results from preliminary studies conducted in the laboratory were compared with those from field populations, and the influence of seasonal conditions on the number of molts was investigated. Characterization of instars by the width of the larval head capsule also was attempted because determination of the number of instars and the means to identify instars by using head capsule size is necessary to track development in laboratory studies, assess development under field conditions, and determine phenological patterns of attack by parasitoids.

Materials and Methods

Preliminary Laboratory Trials. Development of *M. gulosa* larvae on Rio Red grapefruit developing from eggs from a laboratory colony (Guillén et al. 2001) was monitored at different temperatures. Infested fruit (mature green fruit starting color break) were held in small, clear plastic containers (49.5 by 20.3 by 22.2 cm) with white paper toweling on the bottom provided for pupation. Containers were kept in incubators maintained at a constant temperature of 14, 20, 26, or 32 ± 0.5°C and a photoperiod of 14:10 (L:D) h. Relative humidity was maintained at 75 ± 10% over a saturated salt solution. After pupation, each cocoon was cut out from the paper towel and placed in a small vial (15 by 45 mm) closed with a small piece of cotton for adult emergence. The number of feeding instars was determined by marking the position of the larvae every day and recording molting periods based on the inactivity

Table 1. Duration (days $\pm$ MSE [range]) (days) of larval feeding instars of *M. gulosa* on grapefruit at different temperatures in the laboratory

Instars	Developmental time						
	20°C			26°C		32°C	
	Four	Five	Six	Four	Five	Four	Five
1st	9.7 ± 2.2 (7–14)	9.0 ± 1.1 (7–12)	9.0	3.5 ± 0.1 (3–4)	4.2 ± 0.4 (3–5)	2.6 ± 0.2 (2–3)	3.0 ± 0.0 (3–3)
2nd	5.3 ± 1.3 (4–8)	5.8 ± 0.5 5–7	8.0	2.9 ± 0.1 (2–3)	2.2 ± 0.2 (2–3)	2.4 ± 0.3 (2–4)	2.3 ± 0.3 (2–3)
3rd	5.0 ± 0.0 (5–5)	5.0 ± 0.4 (4–6)	6.0	2.6 ± 0.2 (2–4)	2.8 ± 0.2 (2–3)	2.4 ± 0.3 (2–4)	2.0 ± 0.0 (2–2)
4th	6.7 ± 0.7 (6–8)	5.0 ± 0.4 (4–6)	5.0	3.1 ± 0.2 (2–4)	3.4 ± 0.2 (3–4)	3.0 ± 0.3 (2–4)	4.0 ± 0.6 (3–5)
5th		7.5 ± 0.3 (7–8)	5.0		2.0 ± 0.3 (1–3)		3.3 ± 0.5 (2–4)
6th			7.0				
Total	26.7 ± 1.5a (24–29)	32.8 ± 1.5b (29–35)	40.0	13.1 ± 0.3a (11–14)	15.4 ± 0.7b (13–17)	11.3 ± 0.4a (10–13)	14.7 ± 1.0b (12–17)
n	3 (1f+2m)	4 (1f+3m)	1 (1m)	16 (5f+11m)	5 (4f+1m)	9 (4f+5m)	4 (3f)

Numbers followed by the same letter within a row within a group are not significantly different (Tukey's test, $P = 0.05$) (groups are defined by temperature). f, female; m, male.

of larvae from the first feeding instar after egg eclosion, to the last feeding instar before the transitional and spinning larval stages. The duration of each larval feeding stage and sex of emerged adults were recorded.

Field Data. Summer (August–September 1998 and 2001; large green fruit), winter (January 2001; mature yellow fruit), and spring (April–May 1998, 2001, and 2003; senescent fruit) samples were collected from commercial grapefruit groves in the Coachella Valley to determine the number of feeding instars in field populations of *M. gulosa* under different seasonal or fruit quality conditions. Samples consisted of grapefruits with complete mines of *M. gulosa* in which the trail could be followed from the egg to the cut through which the spinning instar left the mine. In the laboratory, head capsules of mining larvae were removed from the mines, slide-mounted in Hoyer's solution, and their width measured using an ocular micrometer. The number of feeding instars was recorded by counting head capsules found in each completed mine (Fitzgerald and Simeone 1971, Kishi 1971, Wagner et al. 2000). Statistical analyses were conducted using Minitab Inc. 1985.

Results

Laboratory Trials. In total, 42 larvae were followed that passed through four (66.7%), five (31.0%), and six (2.4%) feeding instars. The number of feeding instars varied for both males and females (Table 1), but the number of feeding instars was not related to sex ($\chi^2 = 3.765$, df = 2, $P = 0.152$). An influence of temperature on the number of feeding instars from these laboratory studies could not be shown ($\chi^2 = 6.209$, df = 4, $P = 0.184$); only one larva of 42 passed through six feeding instars at a low temperature of 20°C. In general, for each temperature, feeding larvae that passed through fewer instars developed faster than those passing

through more instars (Table 1). Differences in developmental time at 20, 26, and 32°C were observed, with larvae taking significantly longer to develop through five rather than four feeding instars ($F = 9.49$; df = 1, 5; $P = 0.027$ [20°C]; $F = 17.54$; df = 1, 20; $P < 0.001$ [26°C]; $F = 12.60$; df = 1, 9; $P = 0.006$ [32°C]) (Table 1). The single larva that passed through six instars took longer to develop than for larvae passing through four and five feeding instars at the same temperature (Table 1).

Field Data. Developing larvae of *M. gulosa* passed through either four (51.2%), five (38.7%), six (9.7%), or seven feeding instars (0.3%). The proportion of the number of feeding instars changed significantly during the year ($\chi^2 = 150.771$, df = 4, $P < 0.001$); during summer, larvae passed through four or five feeding instars with most larvae passing through four (88.2%) ($n = 94$); during winter, larvae passed through four to seven instars with the majority passing through five (62.1%), an intermediate proportion through six (29.5%), a few through four (7.4%), and one through seven (1.0%) ($n = 95$); and during spring, larvae passed through four (58.0%) and five feeding instars (42.0%) ($n = 100$). There were no significant differences among the proportion of instars for larvae collected during the different sampling periods for different years for spring ($\chi^2 = 0.113$, df = 2, $P = 0.945$; $n_{1998} = 13$, $n_{2001} = 46$, $n_{2003} = 41$) and summer ($\chi^2 = 0.015$, df = 1, $P = 0.904$; $n_{1998} = 33$, $n_{2001} = 61$); winter samples could not be compared because they are based on only a single sample.

No significant differences in head capsule width of larvae within an instar from the same season over different years were observed for summer ($F = 0.49$; df = 1, 385; $P = 0.484$; $n_{1998} = 132$, $n_{2001} = 255$) and spring ($F = 0.30$; df = 2, 439; $P = 0.737$; $n_{1998} = 57$, $n_{2001} = 204$, $n_{2003} = 181$); thus, data were pooled for further analysis.

Table 2. Width of head capsules (days ± MSE [range]) (mm) of feeding instars of *M. gulosa* dissected from complete mines in field collected fruit

Instar	Head capsule width of feeding instars			
	Four instars	Five instars	Six instars	Seven instars
First	0.187 ± 0.001a (0.150–0.225)	0.178 ± 0.001b (0.150–0.225)	0.174 ± 0.001b (0.150–0.200)	0.175
Second	0.270 ± 0.002a (0.200–0.375)	0.244 ± 0.002b (0.200–0.300)	0.235 ± 0.003b (0.200–0.275)	0.225
Third	0.415 ± 0.004a (0.300–0.525)	0.345 ± 0.003b (0.250–0.425)	0.310 ± 0.005c (0.275–0.400)	0.300
Fourth	0.589 ± 0.004a (0.475–0.700)	0.471 ± 0.004b 0.350–0.625)	0.408 ± 0.007c (0.325–0.500)	0.375
Fifth		0.555 ± 0.008a (0.500–0.700)	0.517 ± 0.008b (0.425–0.600)	0.475
Sixth			0.608 ± 0.007 (0.525–0.725)	0.575
Seventh				0.625
n	148	112	28	1

Numbers followed by the same letter within a row are not significantly different (Tukey's test, $P = 0.05$).

The differences in head capsule width between seasons were minor when comparing larvae passing through four and five feeding instars (six and seven instars were observed only from winter samples). Significance was only found between larvae passing through four instars in spring and summer for third ($F = 4.64$; df = 2, 145; $P = 0.011$) and fourth instars ($F = 6.66$; df = 2,145; $P = 0.002$), with those in summer larger than in the spring (Table 2). No significant difference was found between winter collections with either of the summer or spring collections.

To be able to further analyze the results from the different groups of larvae passing through four, five, or six feeding instars, head capsule widths for spring, summer, and winter were pooled. Mean values for head capsule width increased with instar for the three groups of larvae as defined by the number of feeding instars (Fig. 1). Differences in head capsule width between these groups of larvae were observed for most instars. The head capsule width of all feeding instars of larvae passing through four feeding instars was significantly larger than those for the same larval instars passing through five and six instars; the head capsule width for all feeding instars of larvae passing through five feeding instars was also significantly larger than those for the same larval feeding instars passing through six feeding instars except for first and second instars ($F = 12.43$; df = 2, 285; $P < 0.001$ [first instar]; $F = 47.95$; df = 2, 285; $P < 0.001$ [second instar]; $F = 135.10$; df = 2, 285; $P < 0.001$ [third instar]; $F = 332.77$; df = 2, 285; $P < 0.001$ [fourth instar]; $F = 99.00$; df = 1, 138; $P < 0.001$ [fifth instar]). These major differences did not allow pooling of measurements to obtain a single range of head capsule width for each instar. No significant differences were found between head capsule widths of last instars of larvae passing through four, five and six instars ($F = 3.96$; df = 2, 285; $P = 0.020$; Tukey's test), indicating that all larvae reached a similar average final size.

When plotting the frequency distribution of the head capsule widths for the three groups of larvae (four, five, and six feeding instars), peaks showing the number of instars can be clearly observed only for larvae going through four feeding instars (Fig. 1). For the three groups, the ranges of width overlap, with no discrete gaps between peaks. Some of the measurements (Fig. 1, dots) correspond to single larvae with unusual head capsule width (too large or small compared with the rest of the measurements for the same instar) that can be considered as outliers. If we place those data out of the ranges established for each instar, range overlap decreases. Based on these results, it would be possible to predict, only in an approximate way, larval instars by the head capsule width, and only if the total number of feeding instars is known.

There was significant variation in growth rates between the groups of larvae ($F = 123.21$; df = 2, 1,029; $P < 0.001$). Larval growth ratios between successive instars decreased with increasing number of feeding instars (Table 3). The 95% confidence intervals were calculated to compare growth ratios within a group by looking at common values in successive molts. For larvae going through four feeding instars, the growth ratio of head capsule width for the second instar was higher than for the others (Table 3). For larvae passing through five instars, the growth ratio for the first instar was smaller than that of the second, and the last instar grew less than the others (Table 3). The growth ratio of head capsule width of larvae going through six feeding instars was similar for all instars except for the last, which grew less (Table 3).

Discussion

A variable number of feeding instars was documented for *M. gulosa* on grapefruit. From four to six instars were observed for laboratory and field-reared larvae, with a winter-developing single larva passing through seven in the field. The total number of larval instars for *M. gulosa* would be from six to nine, if we add the transitional and spinning larvae to the investigated feeding instars. Atkins (1961) reported six instars for this species with five feeding instars and the spinning stage larva, from laboratory studies carried out at 26.7°C. He did not mention either the host on which he recorded development nor the sample number. Supernumerary instars are known for many Lepidoptera (Peterson and Haeussler 1928, Gaines and Campbell 1935, Beck 1950, Drooz 1965, Leonard 1970, Schmidt and Lauer 1977, Roberts et al. 1978). Many factors regulate the number of instars in various species of insects. Conditions producing extra larval instars may be hereditary (Wigglesworth 1972) or determined by external factors such as temperature or
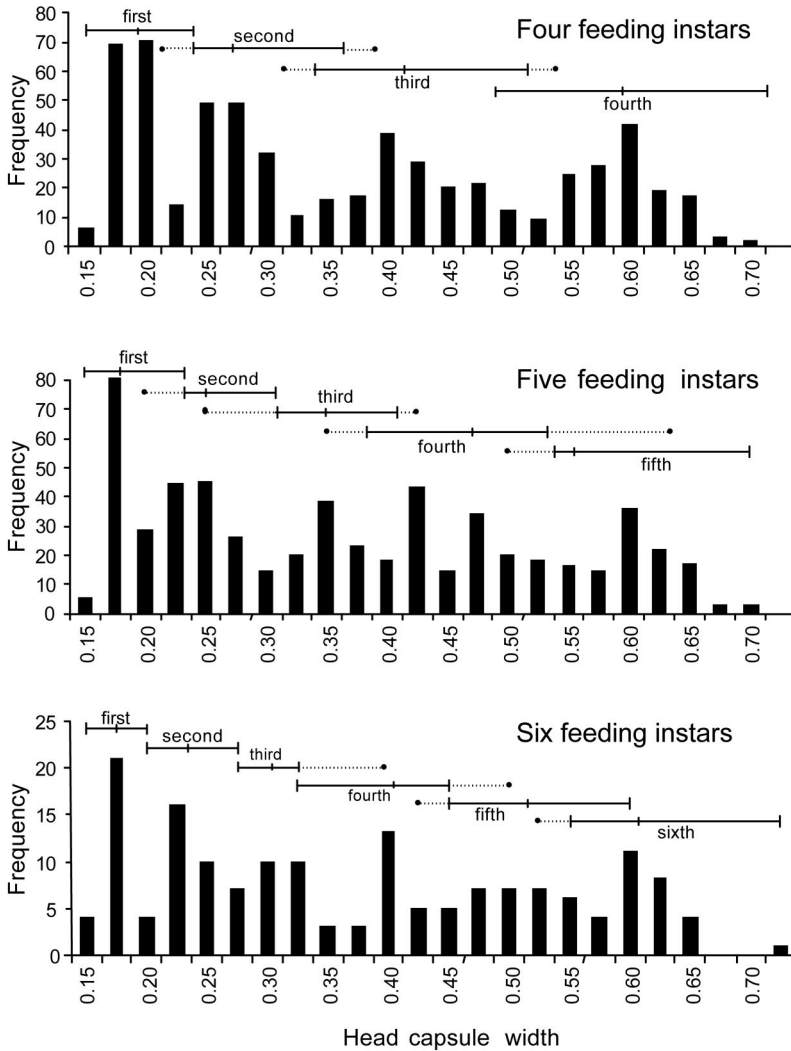
Fig. 1. Frequency distribution of head capsule width (millimeters) and number of feeding instars of field-collected *M. gulosa* developing on grapefruit (lines correspond to ranges and dots represent single measurement considered as outliers; smaller lines correspond to the average for each instar).

nutrition (Peterson and Haeussler 1928, Gaines and Campbell 1935, Beck 1950, Drooz 1965, Leonard 1970, Roberts et al. 1978).

Fitzgerald and Simeone (1971) reported six to nine feeding instars in *M. fraxinicola* and attributed variability, in part, to parasitism and, in part, to its habit of

Table 3. Growth ratios of head capsule width (mean ± SEM [95% confidence interval]) of *M. gulosa* larvae passing through four, five, six and seven feeding instars in field-collected fruit

	Average growth ratio for larvae			
	Four instars	Five instars	Six instars	Seven instars
2nd/1st	1.44 ± 0.01 (1.42,1.47)	1.35 ± 0.01 (1.33,1.37)	1.34 ± 0.02 (1.30,1.38)	1.28
3rd/2nd	1.54 ± 0.01 (1.51,1.57)	1.41 ± 0.01 (1.38,1.43)	1.31 ± 0.02 (1.27,1.35)	1.33
4th/3rd	1.43 ± 0.01 (1.41, 145)	1.37 ± 0.01 (1.35,1.39)	1.31 ± 0.02 (1.28, 135)	1.25
5th/4th		1.28 ± 0.01 (1.26,1.30)	1.27 ± 0.02 (1.24,1.30)	1.27
6th/5th			1.18 ± 0.02 (1.14,1.22)	1.21
7th/6th				1.09
Average	1.47	1.35	1.28	1.23
n	148	112	28	1

molting immediately after resuming mining in the spring, regardless of the duration of the active phase of the terminal fall stadium. Another gracillariine, *Caloptilia azaleella* Brants, has a variable number of feeding instars, with four and sometimes five instars. It was hypothesized that the variability in *C. azaleella* could be due to an extra ecdysis by females, which are larger than males, although it was not confirmed (Mizell and Schiffhauer 1991). In *M. gulosa*, males passed through four, five, and six feeding instars and females through four and five instars. Excluding the single male outlier found with six instars (females also can probably pass through six feeding instars; our sample size was just too small, and the sex was unknown for the field-collected larva with seven instars), the number of feeding instars is not related to sex.

Two other factors, temperature and quality of fruit, are important. In the laboratory, temperature had an effect on larval development, with developmental time decreasing with increasing temperature. Additionally, larvae taking longer to develop pass through an additional instar compared with those developing faster under the same constant temperature. Six feeding instars were observed for only one larva (male) developing at 20°C (Table 2). Average temperatures in the Coachella Valley range from 10 to 16°C in fall and winter, from 18 to 24°C during spring, and from 29 to 33°C during summer. Developmental times were longest during the winter and shortest during the summer. It has been reported that, in general, rapid growth produces fewer instars than slower growth (Peterson and Haeussler 1928) and cool temperatures induce additional instars (Peterson and Haeussler 1928, Leonard 1970, Allen and Keller 1991); however, the opposite effect, with higher temperatures increasing the number of instars, also has been reported (Roberts et al. 1978, Kamata and Irigashi 1995). Larvae of *M. gulosa* developing under low field temperatures tended to go through more instars than those developing under higher temperatures. Growth ratios of head capsule width between successive instars were largest for larvae passing through four feeding instars and smallest for those going through six and seven instars. Additionally, no significant differences in size of last feeding instar head capsules were found for the different groups of larvae (with different number of instars). Thus, indicating that larvae with smaller growth ratios needed additional molts to reach the body size necessary to complete development. Furthermore, last instars grew at a slower rate than the others, especially for larvae going through five and six feeding instars, indicating that growth at the same rate as other instars was not necessary to achieve the final size.

Dyar's rule supposes a regular geometric progression between mean widths of head capsules in successive instars (Dyar 1890); in a perfectly geometrical progression, the growth ratios between succeeding instars would be constant (Gaines and Campbell 1935, Klingenberg and Zimmermann 1992). This rule does not apply in a strict sense to the growth of the head width for *M. gulosa;* all succeeding growth ratios are not constant (Got 1987, Hoxie and Wellso 1974) and 95% confidence intervals do not intersect for all molts (Klingenberg and Zimmermann 1992) (Table 3). The rule strictly applies only for the first five instars of larvae going through six feeding instars. It would apply approximately for larvae going through four instars and for the first four instars of larvae passing through five instars, because variation between growth ratios was small (range, of largest differences between mean growth ratios for each group, 0.06–0.11). The largest differences were found for the last molt of larvae passing through five and six instars, which had a lower growth ratio (0.13–0.16) (Table 3). Dyar's rule has been used to confirm the number of instars and detecting any missing instar; head capsule width of the different instars are estimated from the first or last instar by multiplying or dividing by the average growth ratio (Dyar 1890, Taylor 1931, Drooz 1965, Fox et al. 1972, Hoxie and Wellso 1974). The difficulty in applying this concept to the number of feeding instars of *M. gulosa* comes from the variability in the number of feeding instars and the overlapping ranges of head capsule widths for each instar for all the groups (Fig. 1). However, taking into account the temperature conditions under which larvae develop and the probability of having a determined number on feeding instars under those conditions, the growth ratios estimated in this study could be helpful in corroborating the number of instars or in detecting missing instars of *M. gulosa.*

Grapefruit quality changes during the year. Fruit set in the Coachella Valley grapefruit occurs in April, fruits start to ripen in September, and harvest time is variable from November to May. *M. gulosa* is naturally found feeding on both green and mature grapefruit. After harvest, miners develop on senescent fruit (shiners) left on the trees. When the new fruit set gets large enough for the miner development (from end of May to beginning of June), a preference for the new fruit versus senescent fruit (shiners) has been observed (Guillén et al. 2003). Assuming that the new fruit is preferred because it provides higher quality nutrition for the peelminer than the senescent fruit, development on these new fruit likely would be completed faster and through fewer instars (Peterson and Haeussler 1928, Gaines and Campbell 1935). We have no comparative field data for development on senescent fruits during the summer to test this hypothesis because very few senescent fruits are available or even being mined during summer. From our data, we have observed that, in early spring, a higher proportion of larvae, developing on senescent fruit left on the trees, went through more instars (five feeding instars, 42.0%; $n = 100$) than in summer, developing on green fruit (five feeding instars, 11.8%; $n = 94$); and in winter, there were more instars being produced on the yellow mature fruit (five feeding instars, 62.1%; six feeding instars, 29.5%; $n = 95$) than on the spring senescent fruit (five feeding instars, 42.0%; six feeding instars, 0%; $n = 100$). Based on our results, we can only conclude that seasonal changes in temperature seem to be influencing more clearly the number of feeding instars

of *M. gulosa* on grapefruit. The variation in the number of feeding instars makes it difficult to predict the instar of a larva of *M. gulosa* by measuring its head capsule alone without having any information on the total number of instars.

Acknowledgments

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