Developmental Patterns in Stagmomantis limbata (Mantodea: Mantidae): Variation in Instar Number, Growth, and Body Size

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Developmental patterns in *Stagmomantis limbata* (Mantodea: Mantidae): variation in instar number, growth, and body size

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Abstract

Development affects many components of life history and fitness, including body size. The present study examined the influence of developmental pattern, specifically the number of nymphal instars, on body size (pronotum length) in the praying mantid *Stagmomantis limbata* Hahn. Mantids were reared in the laboratory from hatching, on standardized diet, to examine variation in instar number. These lab data were then used to assess developmental patterns for field-collected female nymphs. Laboratory-reared males and females varied in number of instars. Most females required 6 nymphal instars to reach adulthood (64%), whereas 36% underwent 7 instars. Seven-instar females reached the 4th, 5th, and 6th instars faster than six-instar females, but had shorter pronota than the six-instar females at each of these stages. Seven-instar females were longer than six-instar females at adulthood. Interestingly, the total developmental period from hatching to adulthood was similar for lab-reared seven-instar and six-instar females. In the lab, most males (91%) underwent 6 instars, with the remaining 9% following a five-instar pattern. By the 4th instar, differences between the sexes began to appear. From the 4th instar onwards, females typically took less time than males to reach each instar. From the 5th instar onwards, females were longer than the males, and were longer as adults. Variation in developmental pattern (number of instars) was evident among siblings from the same ootheca; such intra-clutch variability in number of instars may be a bet-hedging strategy by ovipositing females in a variable environment. The laboratory data allowed for the detection of six-instar and seven-instar patterns among the field-collected females. The field-collected data suggest that females undergoing 6 nymphal instars reach adulthood later in the season, and at smaller body size, than seven-instar females.

Key words

body size, growth, development, Dyar's Law, Mantodea, mantis, *Stagmomantis limbata*

Introduction

Body size is an important feature of organisms, influencing many components of life history and fitness (Peters 1983; Roff 1992; Stearns 1992; Hone & Benton 2005). In many organisms, increased body size confers benefits, such as increased diet breadth, longevity, mating success and reproductive output, both between and within species (Wilson 1975; Peters 1983; Honěk 1993; Cohen *et al.* 1993; Andersson 1994; Bonduriansky 2001; Kingsolver & Pfenning 2004; Kingsolver & Huey 2008; Chown & Gaston 2010). These patterns are seen in insects, including orthopteroids, where large body size often correlates with longevity and reproductive success within species (Honěk 1993; Sokolovska *et al.* 2000; Akman & Whitman 2008; Whitman 2008). Yet, large body size can involve costs as well, such as increased metabolic, ecological, and movement costs (Peters 1983; Gotthard *et al.* 1994; Blanckenhorn 2000; Hone & Benton 2005; Teuschl *et al.* 2007).

Body size is particularly important for solitary predators, whose food intake hinges on individual predation success, which, in turn, is often driven by the relative sizes of predator and prey (Wilson 1975; Claessen *et al.* 2002; McCoy *et al.* 2011). Praying mantids (Order Mantodea) are elongate solitary predators, whose body dimensions were predicted to influence prey size by Holling's morphometric models (Holling 1964; Holling *et al.* 1976). Indeed, natural mantid populations exhibit considerable intraspecific size variation, and this variation has ecological and reproductive consequences. In the field, length variation has been documented among mantid nymphs of the same instar (Hurd & Eisenberg 1989), as well as among adult females within and between years (Matsura *et al.* 1975; Eisenberg *et al.* 1981; Maxwell & Eitan 1998; Maxwell & Frinchaboy, in press). In *Tenodera aridifolia* Saussure, larger nymphal instars are more likely to attack larger prey, in addition to being more likely to attack smaller conspecific instars (Hurd 1988; Iwasaki 1991; Whitman & Vincent 2008). For *T. angustipennis* Saussure, Matsura *et al.* (1975) suggest a positive relationship between body length and ootheca (egg case) mass. For *Pseudomantis albofimbriata* Stål, Barry (2013) indicates that longer adult females are more attractive to males than shorter females. In *Stagmomantis limbata* Hahn, female pronotum length positively correlates with prey size in the field, as well as fecundity and ootheca mass (Maxwell & Frinchaboy, in press).

Within a species, variation in adult size can be generated through a combination of intrinsic and extrinsic factors that affect juvenile development (Stearns 1992; Arendt 1997; Nylin & Gotthard 1998; Day & Rowe 2002; Whitman 2008; Whitman & Ananthakrishnan 2009; González-Suárez *et al.* 2011). In arthropods, particularly important factors include immature growth and developmental rates, the number of nymphal instars, the duration of each instar, and genetic differences between the sexes and individuals (Higgins 1992, 2000; Higgins & Rankin 1996; Fagan & Odell 1996; Davidowitz *et al.* 2004; Whitman 2008; Blanckenhorn 2000; Chown & Gaston 2010; González-Suárez *et al.* 2011). In mantids, differences in food per capita among early instars affects body size and mass (Hurd & Eisenberg 1984; Matsura *et al.* 1984; Hurd & Rathet 1986; Paradise & Stamp 1991; Fagan & Hurd 1994; Dussé & Hurd 1997; Moran & Hurd 1997). Interestingly, developmental asynchrony and differences in the number of nymphal instars can occur among mantids reared under relatively constant, standardized conditions in the laboratory (Didlake 1926; Roberts 1937a, 1937b; Matsura *et al.* 1984; Iwasaki 1992), as in other insects (Esperk *et al.* 2007). In the studies on mantids, examinations of size differences between adults of different numbers of instars have been hampered by too few individuals reaching adulthood (Matsura *et al.* 1984; Iwasaki 1992).

While intraspecific variation in the number of nymphal instars has been demonstrated in the laboratory for at least five mantid species, including *Stagmomantis limbata*, two questions remain unanswered: 1) how do differences in instar number translate into size differences in the adult stage, and 2) does instar number vary in nature? The present study addresses these two questions in the mantid *S. limbata*. With regard to the first question, mantids were raised in captivity on standardized diets, to allow for the expression of different developmental patterns and resultant differences in adult size (pronotum length). These data on size and developmental patterns were then used to address the second question about instar number in the field.

The present study also examined the relationships among adult size, the timing of adult emergence, and the number of instars in the field. In *S. limbata*, new adult females can be readily identified by the diffuse yellow coloration of their underwings (Maxwell *et al.* 2010; Maxwell & Frinchaboy, in press). In nature, a negative correlation consistently appears between adult female pronotum length and the date of adult emergence (Maxwell & Frinchaboy, in press); that is, longer females emerge as adults earlier in the season, as appears to occur in other mantids *(e.g.,* Prokop & Vaclav 2008). The present study sought to determine whether developmental patterns (*i.e.*, number of instars) corresponded to date of adult emergence and adult length; that is, whether longer, early-maturing females typically underwent 6 or 7 nymphal instars.

Methods

Laboratory-reared, 1992.— To obtain mantids for rearing, nine oothecae were collected from field sites in Davis, California (38°33′ N, 121°44′ W) in October 1991. The oothecae were kept in ventilated containers in a shaded outdoor shelter until 01 April 1992, when they were brought into an environmental chamber maintained at 25°C. As part of an ecological study, the chamber's initial photoperiod was (12.5L:11.5D), and was changed 30 minutes every two weeks, to simulate the progress of the season, with one-month stases centered around midsummer and midwinter (15L:9D and 10L:14D, respectively). All developmental stages, from hatching through adulthood, were maintained in the environmental chamber.

The oothecae were checked daily for hatching. Hatching occurred between 29 April 1992 and 27 May 1992. The nine oothecae produced 915 hatchlings in total. Hatching is assigned as the start of the first nymphal instar. Hatchlings from the same ootheca that hatched on the same day were grouped into ventilated containers to track hatching date. The first three instars were group-reared (density = 1 nymph per 100 ml), and were misted daily with water. Each group of nymphs was checked daily for deaths and new molts. For the 1st and 2nd instars, each group was provided with abundant *Drosophila melanogaster* Meigen every two days. For the 3rd instar, each group was provided with abundant *Drosophila virilis* Sturtevant and house cricket hatchlings *(Acheta domesticus* L.) every two days. Upon reaching the 4th instar, each nymph was isolated in a 1.6-liter ventilated container and was fed 1-2 cricket nymphs every two days until adult emergence. Upon emerging as an adult, each mantid was fed to satiation with cricket nymphs and maintained in captivity until death.

Developmental data were recorded for the isolated mantids. Starting at the 4th instar, the date of each molt was recorded, allowing for instar duration to be calculated for instars 4-7. For instars 5-7 and adults, pronotum length was measured at each stage (to 0.1 mm). For instars 6-7 and adults, Dyar's coefficient at each stage was calculated as pronotum length (mm) at stage/pronotum length (mm) at the immediately preceding stage (Dyar 1890; Cole 1980). For adults, total developmental time (hatch-to-adult interval, in days) was calculated, as well as overall growth rate (pronotum length upon adult emergence/hatch-to-adult interval).

Field-collected females, 2011.—Late-instar female nymphs were collected via visual searching in field sites in Bishop and Big Pine, California (37°22′ N, 118°24′ W and 37°10′ N, 118°17′ W, respectively) during 16-24 Aug 2011. At these sites, *S. limbata* is univoltine, with hatching occurring in May, adults first emerging in August, egg-laying occurring in Sept-Oct, and the oothecae overwintering.

Each nymph was isolated in a ventilated 1.6-liter container kept in a shaded outdoor shelter at the Owens Valley Laboratory (University of California property, Bishop, California). Each nymph was provided with misted water and one house cricket nymph every two days. The nymphs were checked daily for molting and adult emergence. Each nymph was measured for pronotum length (0.1 mm) upon capture and after each molt. These methods resulted in 50 adult females. Each adult was measured for pronotum length. Adult females were provided a standardized diet of one house cricket nymph every two days, and were maintained in captivity until death.

To assign developmental patterns to these field-collected females, I used pronotum length data from the females reared in 1992. Because the females in 1992 were of known developmental schedules, I used their lengths in their final instars as benchmarks to apply to the field-collected females. Females reared in the laboratory in 1992 underwent either six or seven nymphal instars before emerging as adults. For each of these developmental patterns, I calculated the mean pronotum length in the final nymphal instar, and constructed 1sd and 2sd intervals around the mean *(i.e.*, 1 and 2 standard deviations, respectively). I utilized overlap between the 1sd and 2sd intervals to determine developmental patterns for the field-collected females, while minimizing the error of misassigning a given female's pattern.

Statistical analysis.—Statistical analyses were performed using SPSS 17.0 (IBM Co., Chicago, Illinois, USA). All inferential tests were two-tailed, and mean and standard error values were reported for descriptive statistics. Examination of developmental parameters *(e.g.,* hatch date, instar duration, pronotum length at stage, Dyar's coefficient; Table 1) involved comparisons among females, and between males and females collectively. For these comparisons, I performed multiple univariate tests, thereby lowering alpha (a) according to the sequential Bonferroni technique (Rice 1989). Normality of these data was assessed by the Shapiro-Wilk test for normality; data with significant departures from normality ($p < 0.05$) were subject to transformation.

Results

Laboratory-reared.—Of the 915 hatchlings, 79 reached adulthood: 36 females and 43 males (Table 1). Of the 36 females, 23 reached adulthood after six instars ("six-instar females"), while the remaining 13 reached adulthood after seven instars ("seven-instar females"). Of the 43 males, four reached adulthood after five instars ("five-instar males"), while the remaining 39 reached adulthood after six instars ("six-instar males"). The mean date of hatching was similar for the females and males, with the males tending to hatch two days earlier than the females (Table 1). Hatch date and two other developmental parameters (duration of 5th instar, duration of 6th instar) were found to significantly depart from normality. These

Table 1. Developmental parameters for laboratory-reared mantids (1992). Mean (SE) reported. Hatch-to-4th = number of days from hatching to emergence at 4th instar. Dyar's coefficient = pronotum length at stage (mm) / pronotum length at immediately preceding stage (mm). Hatch-to-adult = number of days from hatching to adult emergence. Growth rate = pronotum length at adult (mm) / hatch-to-adult (d).

	6-instar Females	7-instar Females	All Females	t-test [a] (6i *vs* 7i)	5-instar Males	6-instar Males	All Males	t-test [b] (F *vs* M)
n	23	13	36		4	39	43	
Hatch date (mean)	May 15 (2)	May 15 (2)	May 15 (1)	t_{34} = 0.03 ^ p > 0.9	May 12 (1)	May 13 (1)	May 13 (1)	t_{75} = -1.14 ^ p > 0.2
4th instar								
Hatch-to-4th (d)	33 (1)	30 (1)	32 (1)	t_{22} = 3.28 p = 0.003*	36 (1)	34 (1)	34 (1)	t_{46} = -3.10 p = 0.003*
Instar duration (d)	13 (1)	10 (1)	12 (1)	t_{22} = 3.53 p = 0.002*	18 (1)	13 (1)	13 (1)	t_{46} = -2.05 p = 0.047
5th instar								
Pronotum length (mm)	10.6 (0.1)	9.5 (0.2)	10.2 (0.1)	t_{33} = 7.63 p < 0.001*	10.8 (0.2)	9.6 (0.1)	9.7 (0.1)	t_{74} = 3.65 p < 0.001*
Instar duration (d)	14 (1)	10 (1)	13 (1)	t_{34} = -7.73 ^ p < 0.001*	25 (1)	15 (1)	16 (1)	t_{77} = 4.40 ^ p < 0.001*
6th instar								
Pronotum length (mm)	14.7 (0.2)	13.1 (0.2)	14.1 (0.2)	t_{28} = 6.62 p < 0.001*	—	12.5 (0.1)	—	t_{60} = 7.08 p < 0.001*
Instar duration (d)	20 (1)	12 (1)	17 (1)	t_{34} = -9.43 ^ p < 0.001*	—	24 (1)	—	t_{73} = 7.25 ^ p < 0.001*
Dyar's coefficient	1.38 (0.01)	1.37 (0.01)	1.38 (0.01)	t_{27} = 0.78 p > 0.4	—	1.31 (0.01)	—	t_{58} = 6.47 p < 0.001*
7th instar								
Pronotum length (mm)	—	17.0 (0.3)	—	—	—	—	—	—
Instar duration (d)	—	20 (1)	—	—	—	—	—	—
Dyar's coefficient	—	1.31 (0.01)	—	—	—	—	—	—
adult								
Adult emergence date	Aug 3 (2)	Aug 5 (2)	Aug 4 (1)	t_{34} = -0.54 p > 0.5	Jul 29 (2)	Aug 7 (1)	Aug 6 (1)	t_{77} = -1.24 p > 0.2
Hatch-to-adult (d)	80 (2)	82 (2)	81 (1)	t_{34} = -0.70 p > 0.4	77 (2)	86 (1)	85 (1)	t_{75} = -2.54 p = 0.013
Pronotum length (mm)	19.4 (0.3)	22.0 (0.4)	20.4 (0.3)	t_{33} = -5.59 p < 0.001*	13.6 (0.1)	15.2 (0.1)	15.0 (0.1)	t_{76} = 17.39 p < 0.001*
Dyar's coefficient	1.33 (0.01)	1.30 (0.02)	1.32 (0.01)	t_{26} = 1.78 p > 0.05	1.26 (0.02)	1.22 (0.01)	1.22 (0.01)	t62 = 9.33 p < 0.001*
Growth rate (mm/d)	0.246 (0.008)	0.270 (0.009)	0.255 (0.006)	t_{33} = -2.00 p = 0.054	0.176 (0.005)	0.178 (0.003)	0.178 (0.003)	t_{74} = 11.93 p < 0.001*

[a] t-test comparison of 6-instar females *vs* 7-instar females.

[b] t-test comparison of all females *vs* all males.

* significant at adjusted α level by the sequential Bonferroni technique.

^ t-test results for reciprocal-transformed data ($X' = 1/X$).

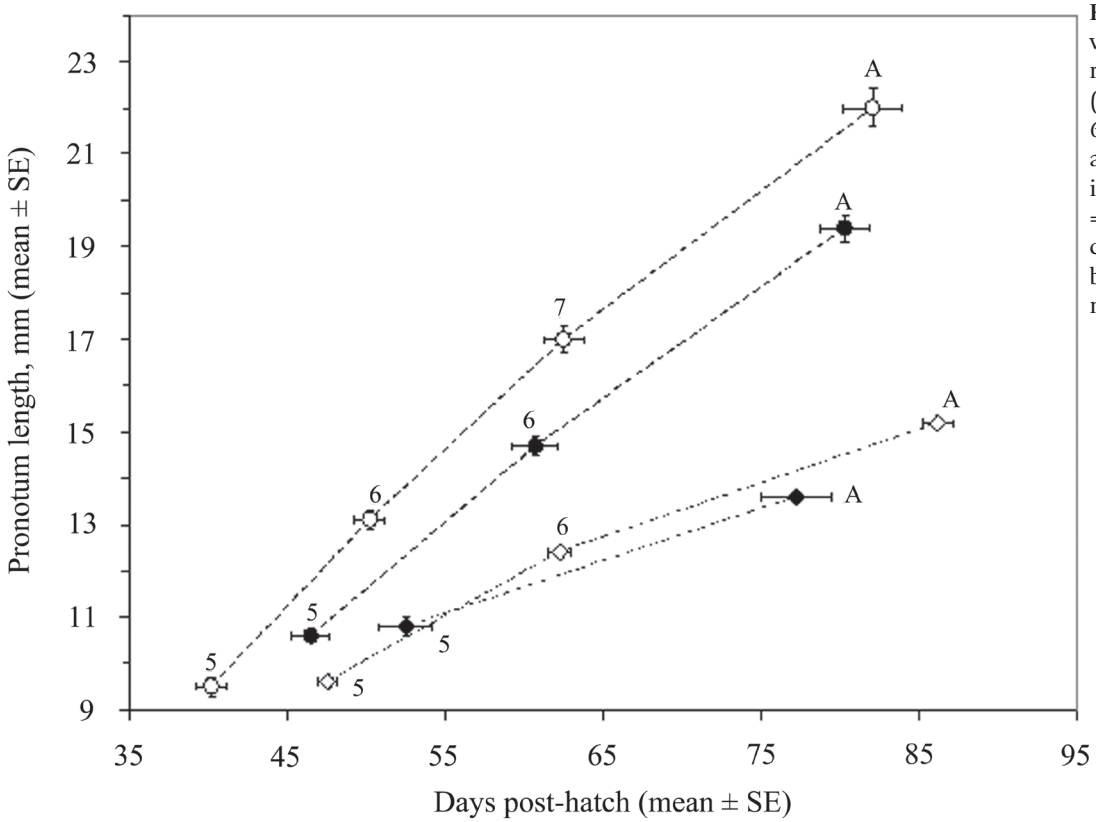

Fig. 1. Pronotum length at various stages for laboratory-reared females and males (1992). 5 = 5th instar; 6 = 6th instar; 7 = 7th instar; A = adult. White circles = seven-instar females; black circles = six-instar females; white diamonds = six-instar males; black diamonds = five-instar males.

data were subject to reciprocal-transformation ($X' = 1/X$). Results for the statistical tests of transformed data are presented in Table 1; statistical significance did not differ between transformed and non-transformed data in any case.

Males and females differed in development (Fig. 1, Table 1). Males took longer than females to reach the 4th instar, the durations of the 5th and 6th instars were longer for males than females, and average hatch-to-adult interval was four days longer for males than females. Yet, females and males had similar adult emergence dates: August 4 and August 6, respectively. The sexes differed in pronotum length and Dyar's coefficient (Fig. 1, Table 1). On average, females were longer than males at the 5th and 6th instars, as well as adulthood. Similarly, females exhibited higher Dyar's coefficients at 6th instar and adulthood.

Within-sex differences in development were evident for females (Fig. 1; Table 1). By the 4th instar, the seven-instar females already showed accelerated development, reaching this instar more quickly than the six-instar females. Seven-instar females completed the 4th, 5th, and 6th instars more quickly than six-instar females. Interestingly, the time to reach adulthood and the actual date of adult emergence did not significantly differ between the two groups of females. The shorter durations of the 4th and 5th instars for the seven-instar females compromised their body size, as they were shorter than the six-instar females at the 5th and 6th instars (Table 1). The extra 7th instar, however, enabled the seven-instar females to attain larger adult size than the six-instar females (Table 1). Growth was similar between both groups of females throughout development, whether measured by Dyar's coefficient at 6th instar and adulthood or by overall growth rate to adulthood (Table 1).

Among females, the date of adult emergence was positively correlated with the date of hatching (Pearson correlation: $r = 0.63$, $p < 0.001$, all females combined). Differentiating females by developmental pattern did not change this positive relationship (Linear regression: adjusted $r^2 = 0.37$, $F_{2,33} = 11.42$, whole-model $p < 0.001$; Date of hatching $p < 0.001$, Developmental pattern $p > 0.4$). Thus, females that hatched later in the calendar emerged as adults later, regardless of developmental pattern.

Comparison of developmental parameters is somewhat difficult among males, as the small number of five-instar males ($n = 4$) precludes statistical analysis. Despite the small sample size, these five-instar males showed shorter time to adulthood and shorter prontoum length than the six-instar males (Fig. 1, Table 1). For all males combined, the date of adult emergence was positively correlated with the date of hatching (Pearson correlation: $r = 0.62$, $p < 0.001$). This relationship persisted when only examining six-instar males (Pearson correlation: $r = 0.67$, $p < 0.001$).

Regarding adult pronotum length and the calendar date of adult emergence, no correlation was evident for all females combined (Fig. 2a; Pearson correlation: $r = -0.17$, $p > 0.3$). Differentiating females by developmental pattern revealed a negative relationship between adult pronotum length and adult emergence date (Linear regression: adjusted $r^2 = 0.53$, $F_{2,32} = 20.01$, whole-model $p < 0.001$; Date of emergence $p = 0.032$, Developmental pattern $p < 0.001$), with the regression coefficient for Date of emergence = -0.06 (SE = 0.03). For all males combined, adult pronotum length did not correlate with emergence date (Fig. 2a; Pearson correlation: $r = 0.08$, $p > 0.5$); restricting analysis to six-instar males did not change this result (Pearson correlation: $r = -0.16$, $p > 0.3$).

As the hatching period spanned one month (29 April to 27 May), hatching date can be standardized for all adults by examining the total developmental period (hatch-to-adult, in days). For all females combined, a negative correlation was detected between developmental period and adult pronotum length (Fig. 2b; Pearson corrleation: $r = -0.37$, $p < 0.05$). This negative relationship persisted when differentiating females by developmental pattern (Linear regression: adjusted $r^2 = 0.68$, $F_{2,32} = 37.73$, whole-model $p < 0.001$; Developmental period $p < 0.001$, Developmental pattern $p < 0.001$), with the regression coefficient for Developmental

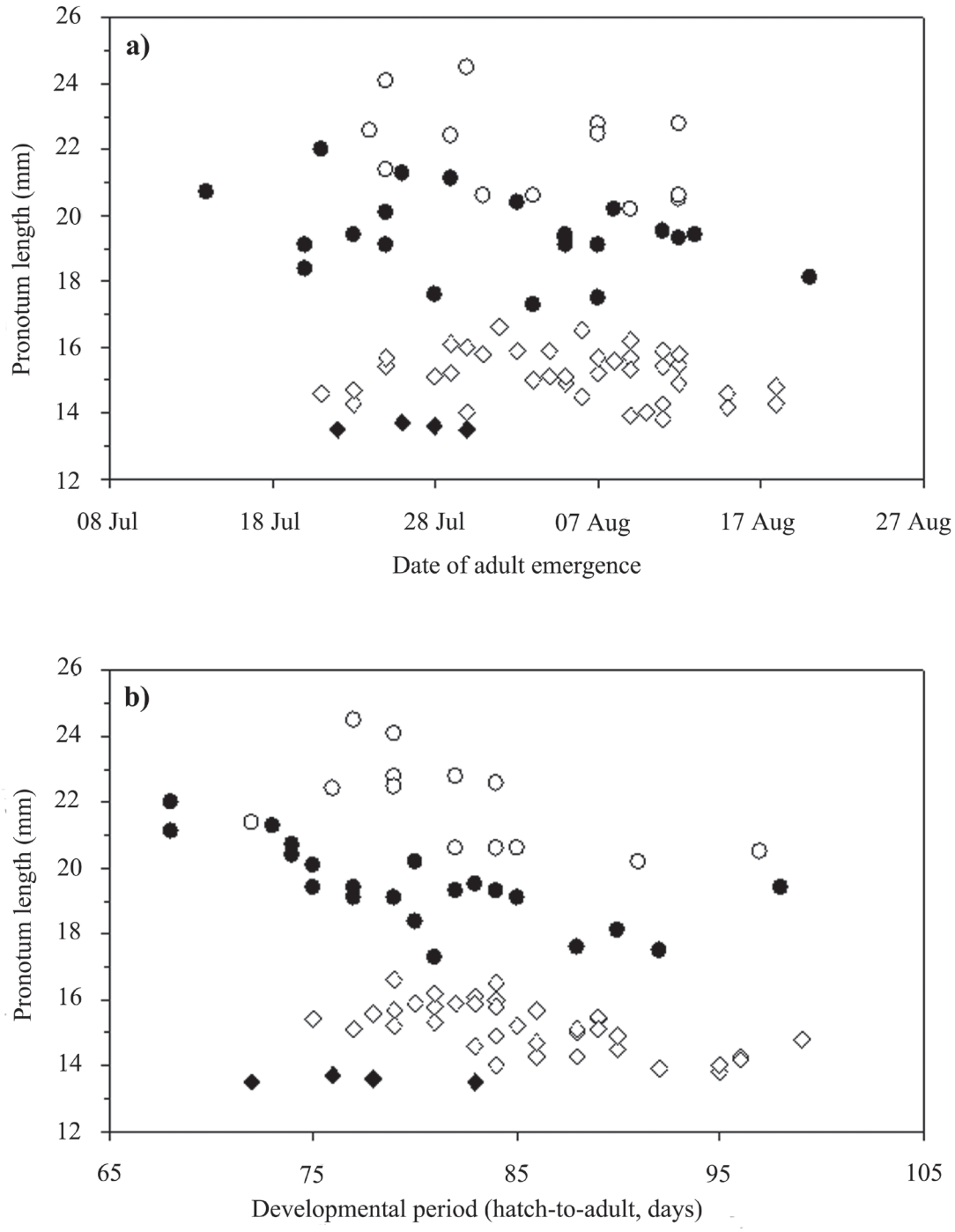

Fig. 2. Adult pronotum length *vs* time for laboratory-reared females and males (1992). White circles = seven-instar females; black circles = six-instar females; white diamonds = six-instar males; black diamonds = five-instar males. a) Calendar date of adult emergence. b) Developmental period (hatch-to-adult), in days.

period = -0.12 (SE = 0.03). For all males combined, developmental period did not correlate with pronotum length (Fig. 2b; Pearson correlation: $r = -0.24$, $p > 0.1$). Examination of six-instar males, however, showed a negative relationship (Pearson correlation: $r = -0.63$, $p < 0.001$), as the shorter five-instar males tended to develop more quickly, thereby weakening the overall negative relationship.

Variation in development was evident within sibling groups *(i.e.*, within a single ootheca). With regard to females, six of the nine oothecae produced both six-instar and seven-instar adults. Three such oothecae are illustrated in Fig. 3, each producing 6-8 adult females in total. Within each ootheca, the females typically hatched on the same calendar day, but showed considerable variation in pronotum length at adulthood, hatch-to-adult interval, and hatch-to-adult growth rates (indicated by individual lines in Fig. 3). Variation in growth rates (slope of lines) was evident for females of the same developmental schedule within an ootheca *(e.g.*, seven-instar females in Fig. 3a, and six-instar females in Fig. 3b). With regard to males, the 4 five-instar adults emerged from the same ootheca; this ootheca produced 6 six-instar males as well.

Final-instar pronotum lengths for the laboratory-reared females

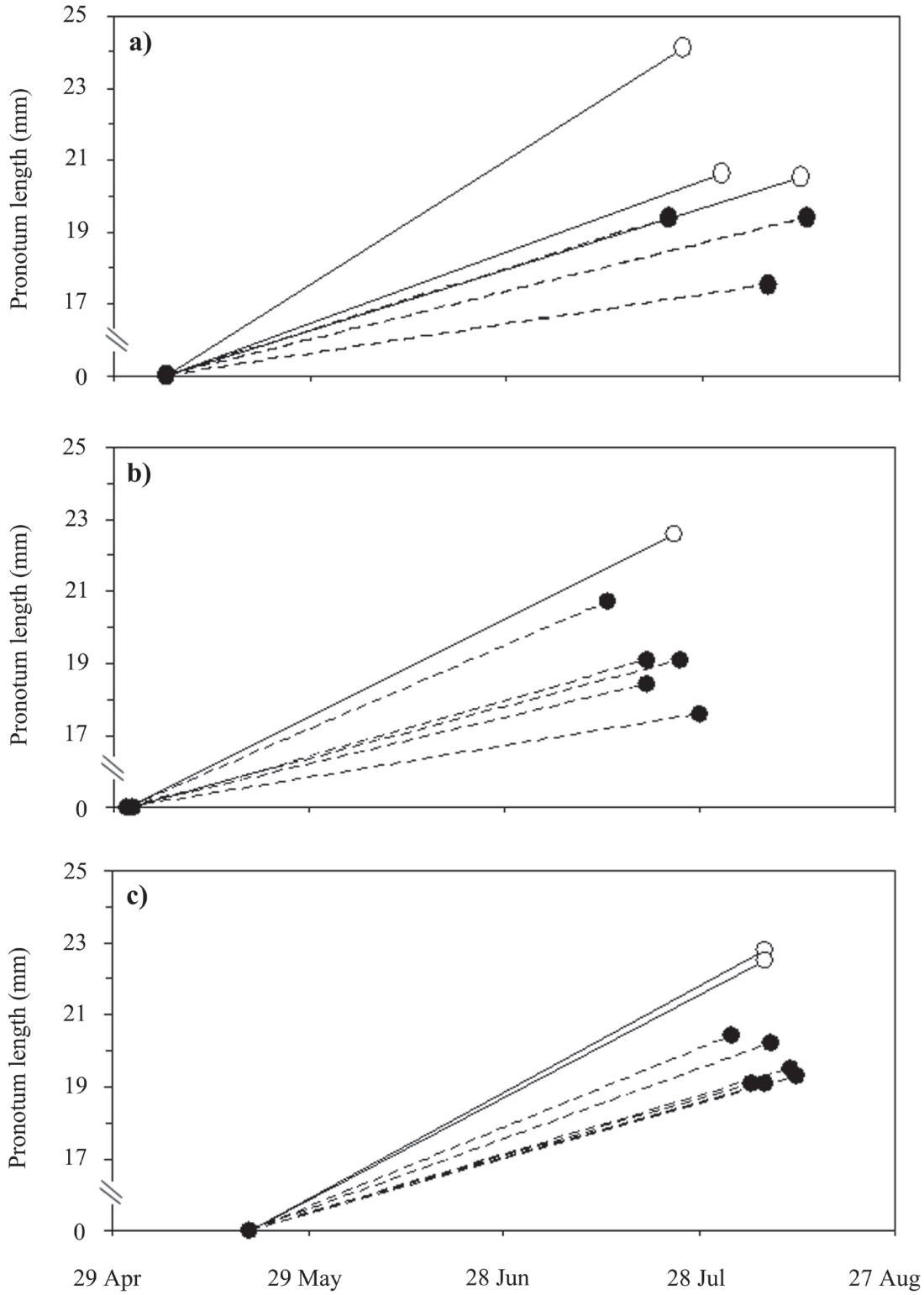

Fig. 3. Variation in developmental pattern among females within oothecae (1992). Each panel (a, b, c) is a different ootheca. Lines indicate growth rates for individual females. Data points on the x-axis represent the date of hatching (pronotum length at hatching is set to 0.0 mm). Data points above the x-axis depict the date of adult emergence and corresponding adult pronotum length. White circles and solid lines = seven-instar females; black circles and dashed lines = six-instar females.

showed separation between six-instar and seven-instar females, with some overlap in the range 15.2-16.5 mm (Fig. 4a). The 1sd and 2sd intervals for six-instar and seven-instar females are indicated in Fig. 4a. While 1sd intervals for six-instar and seven-instar females do not overlap, using these intervals as the bases for assigning developmental schedules to field-collected females risks assignment error. For example, two seven-instar females from the laboratory lay within the 1sd interval for six-instar females *(i.e.*, seven-instar

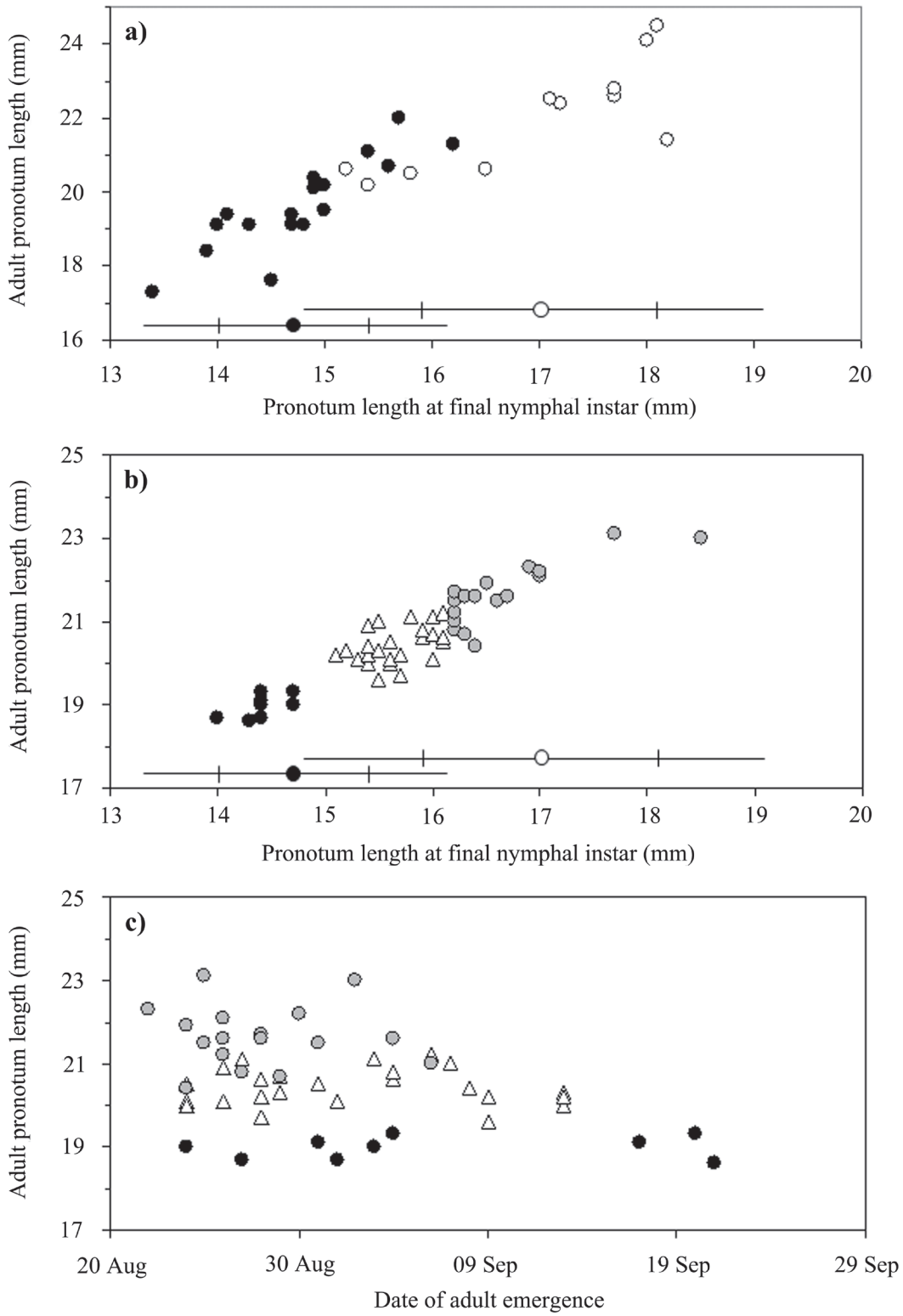

Fig. 4. Female pronotum length. a) Laboratory-reared (1992). x-axis = pronotum length at final nymphal instar. Black circles = six-instar females; white circles = seven-instar females. At bottom of panel are shown mean final instar pronotum length for six-instar females (black) and seven-instar females (white), with ±1 standard deviation (vertical tick marks) and ±2 standard deviations (ends of horizontal lines) shown for each mean. b) Field-collected (2011). x-axis = pronotum length at final nymphal instar. Black circles = females assigned to six-instar pattern; gray circles = females assigned to seven-instar pattern; white triangles = females not assigned to developmental pattern. As reference for the criteria for assigning females to developmental patterns, at bottom of panel are shown mean final instar pronotum lengths for six-instar females (black) and seven-instar females (white) from 1992, with ±1 standard deviation and ±2 standard deviations shown for each mean. c) Field-collected (2011). x-axis = date of adult emergence. Black circles = females assigned to six-instar pattern; gray circles = females assigned to seven-instar pattern; white triangles = females not assigned to developmental pattern.

females of final-instar lengths 15.2 and 15.4 mm in Fig. 4a). Using the non-overlapping regions within the 2sd intervals largely avoids misassignment, as follows. With regard to the six-instar females from the laboratory, the region of the 2sd interval that does not overlap with the seven-instar 2sd interval is 13.3-14.7; this region only includes six-instar females. Similarly, the non-overlapping region of the 2sd interval for seven-instar females is 16.2-19.2 mm (Fig. 4a). All but one of the females in this region are seven-instar females; the lone six-instar female lies at the minimum value of this range (16.2 mm).

Field-collected females.—For the field-collected female nymphs, final-instar pronotum lengths spanned 14.0-18.5 mm (n = 50; Fig. 4b). This range was contained within the 2sd intervals of the six-instar and seven-instar females from the laboratory (indicated in Fig. 4b). Applying the criterion of non-overlapping 2sd intervals to the field-collected nymphs, distinguishable six-instar females (14.7 mm or less in pronotum length, n = 9) and seven-instar females (16.2 mm or greater in pronotum length, n = 17) were revealed, with the remaining females not being assigned to developmental patterns (Fig. 4b). A negative relationship was observed between date of adult emergence and adult pronotum length for the field-collected females (Pearson correlation: $r = -0.39$, $p < 0.01$, n = 50; Fig. 4c).

Seven-instar females emerged as adults within the period 22 Aug - 06 Sep (mean ± SE = Aug 28 ± 1, n = 17). While a substantial proportion of six-instar females also emerged as adults within this period (67%), a number of particularly late-emerging six-instar females resulted in the mean date of emergence being significantly later than seven-instar females (six-instar mean ± SE date of emergence = Sep 6 ± 4, n = 9; t-test: $t_{24} = 3.2$, $p < 0.01$).

For all field-collected females combined, mean ± SE Dyar's coefficient = 1.31 + 0.01 (n = 50). This value was very similar to the overall mean for the 1992 laboratory-reared females (mean ± SE = 1.32 ± 0.01; Table 1). For the field-collected females, Dyar's coefficient at adulthood did not significantly differ between six-instar females (1.32 ± 0.01, n = 9) and seven-instar females (1.30 ± 0.01, n = 17; $t_{24} = 1.68$, $p > 0.1$).

Discussion

The present study answers several questions regarding developmental patterns and body size in *Stagmomantis limbata*. For the laboratory-reared mantids (1992), females showed the most variation in developmental pattern. The majority of females underwent a six-instar pattern to adulthood (64%), with the remaining 36% following a seven-instar pattern. Differences between these two patterns were evident by the 4th instar. Seven-instar females showed an accelerated developmental pace, reaching the 4th instar more quickly than six-instar females, as well as shortening the durations of the 4th, 5th, and 6th instars. This quickened pace allowed for the additional 7th instar to be completed without substantially delaying the total time taken to reach adulthood, as the developmental period from hatching to adult emergence did not significantly differ between seven-instar and six-instar females. The shorter times taken to reach the 4th, 5th, and 6th instars in the laboratory compromised body size for the seven-instar females, as these females were shorter than six-instar females at the 5th and 6th instars. The additional 7th instar, however, resulted in seven-instar females being significantly longer than six-instar females at adulthood. Growth rate was similar between seven-instar and six-instar females, whether measured as Dyar's coefficient or as overall growth rate to adulthood.

Most of the lab-reared males followed a six-instar pattern (91%), with the remaining 9% following a five-instar pattern. Six-instar males required more days to reach adulthood than five-instar males, and emerged as longer adults. In the laboratory, clear and persistent differences were evident between the sexes by the 4th and 5th instars. From the 4th instar onwards, females typically took less time to reach each instar. From the 5th instar onwards, females were longer than the males, and showed higher Dyar's coefficients at the 6th instar and adulthood. In many species within the Mantodea, females are longer than males (Roy 1999; Ehrmann 2002). The present study contributes towards an understanding of the ontogeny of this sexual size dimorphism, as developmental differences between the sexes were obvious by the 4th and 5th instars. How much earlier in development that these differences can be detected remains unknown for *S. limbata*. In the mantid *P. albofimbriata*, Allen *et al.* (in press) indicate that males and females significantly differ in size as early as the second instar. The onset of sexual size dimorphism warrants further investigation, as this question is unresolved for many invertebrates (Abbott & Svensson 2008; Stillwell *et al.* 2010).

This study identified both six- and seven-instar patterns in females in the field, thereby demonstrating developmental variation in nature. The field results also suggested that six-instar females emerge as adults later than seven-instar females. These results tend to support the hypothesis that early-emerging adults undergo more molts in nature, albeit with some caveats. For the field-collected females, there was substantial overlap between the adult emergence dates of six-instar and seven-instar females. Yet, a small number of particularly late-emerging six-instar females resulted in the mean dates of emergence differing. This could be a statistical artifact, especially considering that, in the laboratory, the total developmental period (hatch-to-adult) and calendar date of adult emergence did not differ significantly between six-instar and seven-instar females. Furthermore, previous studies on *S. limbata* and other mantids did not report differences in the durations of developmental patterns for females (Roberts 1937a, 1937b; Matsura *et al.* 1984), and Iwasaki (1992) actually indicated longer developmental periods for seven-instar males than for six-instar males in *T. aridifolia*. Clearly, these conflicting results call for more research on this question.

One critique of the present study is that laboratory developmental patterns derived from a population of *S. limbata* from Davis, CA in 1992 may not apply to field-collected *S. limbata* from Bishop, CA in 2011. Examination of the final instar lengths of the field-collected females, however, clearly reveals the assigned six-instars as a distinct, separate cluster of the smallest individuals (*i.e.*, lower left cluster in Fig. 4b). It seems reasonable to conclude that these individuals are indeed six-instar females, even without reference to the laboratory data, thus allowing for a comparison of adult-emergence of six- *vs* seven-instar females in the field. Furthermore, the overall mean Dyar's coefficients at adulthood for the laboratory-reared and field-collected females are nearly identical (1.32 and 1.31, respectively), suggesting consistent underlying developmental physiology.

The field and laboratory data generally corroborate the negative relationship between adult female pronotum length and date of adult emergence, as documented in nature for *S. limbata* (Maxwell & Frinchaboy, in press). For the laboratory-reared females, however, this negative relationship was somewhat weak when pronotum length was examined against calendar date of adult emergence. A weak relationship may be attributable to variation in hatch dates, as later-hatching seven-instar females may push large pronotum length values towards later dates (Fig. 2a). This effect was evident in the present study. When hatching date was standardized by examining the developmental period (hatch-to-adult interval), a stronger negative correlation was found between pronotum length

and developmental period (Fig. 2b). Thus, when adults are confined to a standardized hatching date, a stronger negative relationship between pronotum length and time becomes evident. In nature, therefore, the consistent negative relationship between adult female pronotum length and adult emergence date in *S. limbata* might be a reflection of the following factors: a narrow window for hatching and, for a given developmental pattern, slowly-growing individuals emerging as adults later and smaller. A critical time in the season, by which immatures must mature in order to reproduce, might compel slow-growers to emerge at particularly small sizes, thereby generating a even stronger negative relationship between adult length and emergence date (Higgins & Rankin 1996; Higgins 2000; Maxwell & Frinchaboy, in press).

The present study raises the question of why variation in instar number exists in this species. Proximate explanations of this variation point to various environmental and genetic influences (Higgins & Rankin 1996; Esperk *et al.* 2007; González-Suárez *et al.* 2011; Chown & Gaston 2010). One such environmental influence is food availability during development (Esperk *et al.* 2007). Food availability, however, does not seem to account for the occurrence of early-emerging adult six-instar females, both in the laboratory and collected from the field. That is, such females, isolated and regularly supplied with prey, might be expected to continue feeding to undergo a 7th instar to emerge at larger adult size. Other environmental influences on the number of instars include the date of hatching and microhabitat temperature (Higgins 2000; Esperk *et al.* 2007; Chown & Gaston 2010; Dmitriew 2010). Neither hatching date nor temperature, however, appears to explain the present study's variation within oothecae, where laboratory-reared females that hatched on the same day and reared under the same temperature followed different developmental patterns (Fig. 3). Other factors, such as genetic or maternally-induced differences between individuals, remain possible explanations of this study's different developmental patterns.

A separate question is the adaptive value of the different developmental patterns (Stearns 1992; Arendt 1997; Nylin & Gotthard 1998; Whitman & Agrawal 2009). In *S. limbata*, an individual's number of instars might be a particular developmental strategy, especially if different developmental patterns entail separate costs and benefits. While seven-instar females are typically longer and are therefore expected to reap benefits such as increased fecundity (Maxwell & Frinchaboy, in press), large size most likely includes nutritional and energetic costs (Peters 1983; Blanckenhorn 2000). Furthermore, each molt involves risks to the individual, including deformities due to molting errors and vulnerability to predators (personal observations; see Whitman 2008), which potentially add costs to the seven-instar pattern. Thus, each developmental pattern might be viable, as each represents an evolutionary solution to the challenges of survival and reproduction.

Further research on environmental and genetic effects will shed light on the factors that determine the developmental pattern of a given individual. The possibility of genetically- or maternally-determined developmental patterns, together with observations of different developmental patterns among sibling females, suggests the intriguing notion of bet-hedging by egg-laying females; that is, producing variation in developmental patterns among progeny within a brood. Such an integration of the proximate factors that determine developmental pattern with considerations of the fitness consequences of body size will provide much insight into the evolution of life histories.

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