Seasonal Polymorphism in Elytral Coloration Pattern of *Anomala flavipennis* Burmeister (Coleoptera: Scarabaeidae) in Mexico[1]

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Abstract Elytral polychromatism in *Anomala flavipennis* Burmeister was detected in both spring and fall generations in northeastern Mexico from 2000 to 2002. Four distinctive coloration patterns were observed: (a) immaculated, (b) one-spotted, (c) two-spotted, and (d) striped. These categories were represented by 0, 1.4, 7.8, and 28.0% respective levels of melanization of elytral area. A significant interaction was detected between elytral pattern and generation, with melanized forms occurring more commonly during the spring and clearer forms during the fall. Weighted mean of elytral melanized area in the population ranged from 1.46% for fall to 7.80% for spring generations. Linear regression models suggested ($R^2 \geq 0.93$) an inverse association between temperature during pupation-adult ecdysis and elytral melanized area. The rationale and advantage for *A. flavipennis* responding to temperature by elytral melanization remain unknown, particularly because of the crepuscular-nocturnal habits of adults.

Key Words *Anomala flavipennis,* polychromatism, melanization, bivoltinism, seasonality

The white grub, *Anomala flavipennis* Burmeister, ranges from the eastern half of the United States south of the Great Lakes, towards the Southwest, and into northeastern Mexico (Potts 1977, Rodríguez-del-Bosque et al. 1995). Larvae and adults of *A. flavipennis* damage maize, sorghum, wheat, potato, and forage grasses (Hayes and McColloch 1924, Forschler and Gardner 1991, Ratcliffe 1991, Rodriguez-del-Bosque et al. 1995, Rodriguez-del-Bosque 1996a). *Anomala flavipennis* is univoltine in the United States (Hayes and McColloch 1924, Forschler and Gardner 1991, Ratcliffe 1991) but bivoltine in northeastern Mexico, which is attributed to the warmer climate in the southern distribution of the this scarab (Rodríguez-del-Bosque 1998).

Potts (1977) separated *A. flavipennis* into five subspecies, based mainly on color pattern. However, Ratcliffe (1991) notes the color patterns most likely represent variation within the species and should be treated as a single taxon. During a previous study (Rodríguez-del-Bosque 1998), preliminary observations showed a differential elytral coloration pattern within and between spring and fall generations of *A. flavipennis,* thus prompting this investigation. The objective of this study was to determine if variation in *A. flavipennis* elytral coloration was a random event or if those differences were affected by environmental changes during its bivoltine life cycle in Mexico.

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Materials and Methods

This investigation was conducted at the INIFAP Rio Bravo Experiment Station, near Rio Bravo, Tamaulipas, Mexico (25°58′N, 98°01′W). The station (100 ha) is surrounded by agricultural fields planted mainly with grain sorghum. Other crops, including maize and some vegetables, are planted in limited areas. Most of the agricultural activity occurs during the spring growing season (January-July), although a small proportion of the area is planted for a second crop or fall growing season (August-December).

Adults of *A. flavipennis* were monitored daily during the spring (April-May) and fall (August-September) generations from 2000 to 2002 using a standard 15-W black light trap (Harding et al. 1966). Black light traps have proven to be effective for capturing abundant populations of *A. flavipennis* at this site (Rodríguez-del-Bosque et al. 1995, Rodríguez-del-Bosque 1998) and elsewhere (Forschler and Gardner 1991). Adults were divided into groups based on four distinctive elytral coloration patterns: (a) immaculated, (b) one-spotted, (c) two-spotted, and (d) striped, representing levels of melanization in the elytral area (Fig. 1). Specimens with intermediate color patterns were grouped within the closest category as possible. Percentage of the elytra that was melanized was estimated in five replicates for each elytral coloration pattern by using a Polar Planimeter (Lasico, Los Angeles, CA) based on enlarged images similar to Figure 1. Weighted percent (WP) of elytral melanized area of the population was calculated for each generation and year as follows:

$$WP = Pa^{*} Aa + Pb^{*} Ab + Pc^{*} Ac + Pd^{*}Ad,$$

where P is the proportion captured having each coloration pattern, A is the percent of the melanized area of each coloration pattern, and a-d are the respective coloration patterns (Fig. 1).

Minimum and maximum air temperatures were obtained daily from a weather station located 310 m from the light trap; mean daily temperatures were calculated. Interaction between elytral pattern (a-d) and generation (spring and fall) was tested using a two-way analysis of variance (ANOVA, $P < 0.01$) with years as replicates (SAS Institute 1996). To test the influence of temperature (x) on the weighted percent

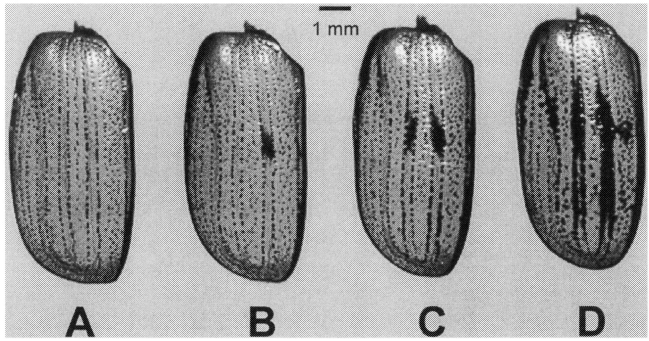

Fig. 1. Left elytron of four color patterns in *A. flavipennis:* (A) immaculated; (B) one-spotted; (C) two-spotted; and (D) striped. Rio Bravo, Tamaulipas, Mexico.

of elytral melanized area of the population (y), simple linear regression ($y = a + bx$) analyses were developed (SAS Institute 1996) for temperatures during two periods: (x_1) pupation, 15 March-15 April for spring and 15 July-15 August for fall; and (x_2) imaginal eclosion, 16 April-15 May for spring and 16 August-15 September for fall (Rodríguez-del-Bosque 1996b, 1998). Weighted percents of elytral melanized area of the population were normalized using an arcsine square-root transformation before regression analysis (Ott 1984).

Results

Total captures of *A. flavipennis* ranged from 7,572 in the spring 2001 to 25,164 in fall 2001 (Table 1). During the 3 yrs of the study, *A. flavipennis* fall captures were 2.4 times higher than spring captures. Data in this study indicated that the relative proportions of the four elytral coloration pattern in both generations was not random. A significant interaction was detected between elytral pattern and generation ($F = 24.46$; df = 3; $P < 0.01$). Data were pooled for the 3-yr period because there was no significant difference among years ($F = 0.30$; df = 2; $P = 0.75$) (Fig. 2). The more highly melanized forms tended to be more abundant during the spring generation. In contrast, the clearer forms were more common during the fall (Fig. 2).

Melanized area in the elytra averaged 0 for immaculated, 1.4% for one-spotted, 7.8% for two-spotted, and 28.0% for striped. Weighted average population estimates of elytral melanized area ranged from 1.46 to 1.76% for the fall generation, and from 6.25 to 7.80% for spring generation, respectively (Table 2).

Temperature prior to emergence appears to play an important role in melanization of *A. flavipennis* elytra (Table 2). Both linear regression models for pupal and imaginal eclosion periods suggested a close association ($R^2 \geq 0.93$) between temperature and elytral melanized area in a given *A. flavipennis* population (generation and year).

Discussion

Total captures of *A. flavipennis* in relation to generation (spring and fall) was similar to previous reports for this location (Rodríguez-del-Bosque et al. 1995, Rod-

Table 1. Numbers of *A. flavipennis* in relation to elytral coloration pattern and generation. Rio Bravo, Tamaulipas, Mexico, 2000-2002

Generation	Year	Elytral coloration pattern				
		Immaculated	One-spotted	Two-spotted	Striped	Total
Spring	2000	505	2,258	4,103	906	7,772
	2001	1,063	3,374	2,633	505	7,572
	2002	1,547	4,362	3,594	1,863	11,366
	Total	3,115	9,994	10,330	3,271	26,710
Fall	2000	9,618	10,259	1,613	166	21,656
	2001	13,199	10,310	1,277	378	25,164
	2002	8,760	6,508	2,162	181	17,611
	Total	31,577	27,077	5,052	725	64,431

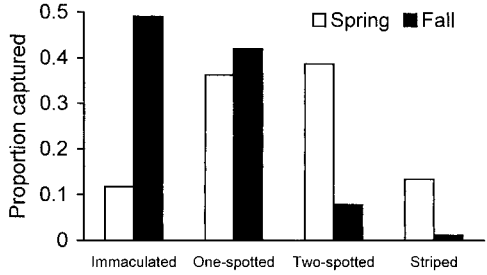

Fig. 2. Proportions of four elytral color patterns of *A. flavipennis* captured in spring and fall. Rio Bravo, Tamaulipas, Mexico, 2000-2002 (pooled data).

Table 2. Relationship between weighted percent of elytral melanized area (y) and average temperature during *A. flavipennis* pupation (x_1) and adult ecdysis (x_2). Rio Bravo, Tamaulipas, Mexico, 2002-2002

			Average temperature (°C) during:	
Generation	Year	% Elytral melanization (y)	Pupation (x_1)	Imaginal eclosion (x_2)
Spring	2000	7.80	22.6	24.4
	2001	6.25	23.8	24.8
	2002	7.59	23.3	25.8
Fall	2000	1.46	31.0	29.4
	2001	1.39	30.7	30.4
	2002	1.76	30.3	29.4
		R^2 =	0.99	0.93
	Linear regression model =		$y = 25.0 - 0.77\ x_1$	$y = 34.8 - 1.11\ x_2$

ríguez-del-Bosque 1998), and much greater than numbers captured in Kansas (Hayes and McColloch 1924) and Georgia (Forschler and Gardner 1991). Apparently, the greater abundance of *A. flavipennis* in northeastern Mexico, the most southern distribution of the species, is favored by bivoltinism, in contrast to univoltinism of the same species in northern latitudes (Rodríguez-del-Bosque 1998).

Many insects exhibit seasonal patterns of change in color and/or structure for adaptation to seasonal environmental factors. Nondiapause seasonal polymorphism may be controlled by one or several interacting factors, including temperature, photoperiod, food quality, crowding, and non-random mating (Tauber et al. 1986, Osawa and Nishida 1992). Temperature has been reported to influence seasonal coloration polymorphism in coleopterans (Komai 1956, Brakefield and Wilmer 1985, Ouedraogo et al. 1991, Lamana and Miller 1995) and other taxa (Lewis 1985, Berry and Willmer 1986, Tauber et al. 1986, Goulson 1994). It is frequently interpreted as "thermal melanism", an adaptation to varying thermal environments within the geographic

distribution of the species (Brakefield and Willmer 1985). Conversely, Turner and Lombard (1990) found no thermal significance when comparing two sympatric desert beetles, one white and the other black, and concluded that color variations of these beetles are cryptic or aposematic rather than thermoregulatory. However, Wlodkowic et al. (1999) and Thompson et al. (2002) noted that temperature during pupation and imaginal eclosion may influence melanization of adults.

Variation in elytral coloration pattern in *A. flavipennis* has been reported previously (Ratcliffe 1991). However, proportions of such patterns have not been documented, and the factors involved in such variations have not been discussed, particularly in relation to its geographic distribution. For instance, the completely black pattern is the most common in Kansas; however, immaculated and other forms may occasionally occur (Hayes and McColloch 1924).

In addition to the four *A. flavipennis* coloration patterns described in this paper (a-d), at least two more patterns could be identified according to reports on elytral color variation in northern latitudes (Hayes and McColloch 1924, Potts 1977, Ratcliffe 1991). These are (e) dark striped and (f) black, which represent levels of elytral melanized areas near to 50 and 100%, respectively. Those high melanization levels were never observed in this study or in previous reports from the same locality (Rodríguez-del-Bosque et al. 1995, Rodríguez-del-Bosque 1998). The darker morphs observed in northern latitudes may further confirm the impact of temperature on elytral melanization in *A. flavipennis* as observed in this study. Lower temperatures, particularly at night, occurring in northern latitudes during pupation and adult eclosion are probably associated with darker morphs, as compared to southern latitudes.

The rationale and advantage for *A. flavipennis* responding to temperature by elytral melanization remain unknown. Evolution towards thermal melanization is not likely to be the case for *A. flavipennis,* particularly because of the crepuscular-nocturnal habits of adults.

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