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Postembryonic Development and Food Consumption of *Dichroplus elongatus* Giglio-Tos and *Dichroplus maculipennis* (Blanchard) (Orthoptera: Acrididae: Melanoplinae) under Laboratory Conditions

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Abstract

Dichroplus maculipennis (Blanchard) and *D. elongatus* Giglio-Tos are two of the most important melanoplines in Argentina, both ecologically and economically. The postembryonic development and forage loss (consumption of *Bromus brevis* Ness + fallen material) caused by older nymphs (instars IV, V, VI) and adults of both species were studied under controlled conditions (30°C, 14L:10D, 40% RH). Five nymphal instars were recorded in *D. elongatus*, and six in *D. maculipennis*. Total nymphal development was similar in both species (*D. elongatus*: 32 ± 0.70 days; *D. maculipennis*: 34.5 ± 0.37 days). Daily consumption increased from nymphal instars to pre-reproductive adult stage. In both species, pre-reproductive females had higher consumption rates than other stages considered (*D. elongatus*: 30.6 ± 0.56 mg dry weight/day; *D. maculipennis*: 48.7 ± 0.74 mg dry weight/day). In the reproductive stage, consumption decreased significantly in both sexes. When feeding, *D. maculipennis* let some plant material to drop, increasing total loss. The percentage of fallen material was greater in reproductive adults, representing 3.9% and 2.9% of the total daily loss for males and females, respectively. Females and males of *D. maculipennis* were heavier than those of *D. elongatus* ($P < 0.05$), and daily consumption was significantly higher ($P < 0.05$). Regardless sex and reproductive status, adults of *D. maculipennis* consumed 29.1 ± 0.64 mg dry weight/day on average, while one of *D. elongatus* 20.0 ± 0.3 mg dry weight/day.

Introduction

Grasshoppers are among the major groups of herbivorous insects in most grassland ecosystems (Hewitt & Onsager 1983, O'Neill *et al* 2003). In many situations, they are considered harmful insects because they compete with livestock for available forage (De Wysiecki & Sánchez 1992, Onsager 2000, O'Neill *et al* 2003, Branson 2008). At high densities, grasshoppers can destroy entire plants or large portions of them, producing not only forage loss,

but also decreasing photosynthetic area and inhibiting vegetative reproduction (Hewitt & Onsager 1983). Comparisons of the feeding patterns of different species coexisting in a community are required to understand the potential impact of grasshoppers (Joern 1989), as the loss of forage due to grasshoppers largely depends on the density of their populations, the species involved, and their consumption rates and average longevity (Hewitt & Onsager 1983).

The melanoplines selected for this study are two of

the most economically important grasshopper species of Argentina. *Dichroplus maculipennis* (Blanchard) is considered historically one of the most damaging grasshoppers in the country, especially in areas of the Pampas (Buenos Aires province) and Patagonia (particularly western Chubut and Neuquén provinces) (Liebermann 1972, Carbonell *et al* 2006). In Argentina, *D. maculipennis* is distributed in a triangle that stretches from Buenos Aires and Entre Ríos provinces in the East to southern San Juan province in the West, and to Santa Cruz province in Patagonia (Lange *et al* 2005). Apart from Argentina, *D. maculipennis* occurs in Uruguay, South-central Chile and in the southernmost state of Brazil (Rio Grande do Sul) (COPR 1982, Carbonell *et al* 2006). While studies conducted during the 90s' in the region of the Argentina's Pampas suggested an apparent decrease in the abundance of their populations (Cigliano *et al* 1995, Cigliano *et al* 2000, De Wysiecki *et al* 2000, 2004, Torrusicio *et al* 2002), in the 2008-09 and 2009-10 seasons an outbreak of historical magnitude (densities of up to 50 ind/m² and development of adult mass displacements) occurred in the southern part of the region.

Dichroplus elongatus Giglio-Tos is another species of economic importance in Argentina (Lieberman 1972, COPR 1982, Carbonell *et al* 2006). In recent years, damage caused by its feeding activity appears to have increased, as suggested by various studies in different areas (Salto & Beltramé 1999, Cigliano *et al* 2002, Torrusicio *et al* 2002, De Wysiecki *et al* 2004). The wide geographic distribution of this species throughout Argentina except Tierra del Fuego, and neighboring Uruguay, most of Chile and southern Brazil (Lange *et al* 2005), and its apparent ubiquity (De Wysiecki *et al* 1997), seem to have allowed it to somewhat benefit from the development of disturbed environments associated with agroecosystems (De Wysiecki *et al* 2004, Lange *et al* 2005). Currently, in most grasshopper outbreaks that occur in Argentina, *D. elongatus* tends to be the numerically dominant or co-dominant species (Cigliano *et al* 2002, Lange *et al* 2005).

Given the economic and ecological importance of *D. maculipennis* and *D. elongatus* in Argentina, we have studied their postembryonic development and have estimated the forage losses caused by older nymphs (instars IV, V, VI) and adults under laboratory conditions.

Material and Methods

Individuals used in this study belonged to the first laboratory generation (F1) of specimens originally collected in the southern Pampas regions (Laprida county, Buenos Aires province, 37° 32' 60''S, 60° 49' 00''O), and maintained in a rearing room under controlled conditions (30°C, 14L: 10D, 40% RH) as described in previous studies

(De Wysiecki *et al* 1997, Mariottini *et al* 2006, 2009). All individuals that hatched from the same egg-pod were considered as a cohort (Sánchez *et al* 2001). Four cohorts of *D. elongatus* with 33, 19, 37, and 21 individuals each, and five cohorts of *D. maculipennis* with 26, 22, 20, 23, and 23 individuals each were monitored. Each cohort was maintained separately in the same room in clear acetate tubes (45 cm long x 10 cm diameter) with removable wire-screened ends (Henry 1985) until they reached the last nymphal instar, when they were transferred to aluminum-framed cages with wire-screened walls and transparent acrylic slide opening (20 x 20 x 30 cm).

All cohorts were daily monitored until death of the last individual, recording for both species the number of nymphal instars, the duration of each instar, and the total duration of the nymphal cycle. Adult longevity was measured for *D. maculipennis* only because De Wysiecki *et al* (1997) had already estimated such parameter for *D. elongatus* under the same rearing conditions.

Estimation of forage losses (plant material consumed + destroyed) was carried out with fourth, fifth and sixth instars, and adults (males and females in both pre-reproductive and reproductive stages). These developmental stages were selected because in most grasshoppers they tend to produce a most significant damage (Putnam 1962, 1963, Hewitt & Onsager 1983). The trials were performed following Sánchez & De Wysiecki (1990). For each feeding trial, ten individuals of a given stage were placed in each one of the cages already described. In each feeding trial, a fresh ration of *Bromus brevis*, a native Poaceae species of important forage value (Ragonese 1985), was offered to the grasshoppers in each cage. After 24h, the remains were collected, sorted into fallen and standing material, and oven dried at 60°. Ten control rations per trial were prepared and oven-dried. The average dry weight of control rations was used as a correction factor, and applied to the initial fresh weight of each of the offered rations to calculate the dry weight of the food offered. The difference in weight between the offered rations and the remaining material after a trial represented the consumption during the test. The number of feeding trials conducted was 155 for *D. elongatus* (31 fourth instars, 33 fifth instars, 18 pre-reproductive females, 24 reproductive females, 25 pre-reproductive males, 24 reproductive males) and 90 for *D. maculipennis* (9 fifth instars, 9 sixth instars, 20 pre-reproductive females, 18 reproductive females, 17 pre-reproductive males, 17 reproductive males).

Feeding trials in the pre-reproductive state were performed within the first week after grasshoppers entered adulthood (Sánchez & De Wysiecki 1990). Subsequently, adults of both sexes were placed in the same cage until mating was observed. Afterwards, individuals were separated by sex, and consumption in the reproductive state was estimated.

Parameters estimated were daily average consumption per individual, average individual total loss (consumption + fallen material) and total consumption of an individual during each stage of development. The consumption during adulthood was estimated by averaging the consumption of the pre-reproductive and reproductive states and then multiplied by the average longevity.

Additionally, the average biomass (dry weight) of nymphs and adults of both species was determined by direct weighting of individuals, and the relative consumption rate (mg/mg individual/day) was estimated.

Results were analyzed using the Kruskal-Wallis test followed by Mann-Whitney. All analyses were conducted using XLSTAT 7.5.3.

Results

Postembryonic development

Males and females of *D. maculipennis* had six nymphal instars, with the nymphal development period totaling 34.5 ± 0.37 d (ranging from 27 to 40 d) (Table 1). Average adult longevity was 66.9 ± 1.75 d (range: 32-90 d) for females and 74.3 ± 2.1 d (range: 38-108 d) for males. Males lived significantly longer than females ($Z = -2.62 = 0.009$). *Dichroplus elongatus* had only five nymphal instars (Table 1) with a nymphal development period of 32.2 ± 0.73 days (range: 31-34 d).

Consumption

Daily consumption of individuals at different stages of development was significantly different for both species (*D. elongatus*: $H = 474.9$, $df = 5$, $P < 0.0001$; *D. maculipennis*: $H = 483.9$, $df = 5$, $P < 0.0001$). Consumption increased significantly with the successive instars up to the pre-reproductive adult stage in both sexes, but

Table 1 Number and duration in days (Mean \pm SE) of nymphal instars of *Dichroplus elongatus* and *Dichroplus maculipennis* at 30°C and 14:10 (L:D) photoperiod.

<i>D. elongatus</i>		<i>D. maculipennis</i>	
Stages	Duration	Stages	Duration
I	5.8 ± 0.44 (n = 110)	I	6.1 ± 0.09 (n = 134)
II	6.0 ± 0.83 (n = 107)	II	5.7 ± 0.14 (n = 129)
III	5.4 ± 0.62 (n = 101)	III	5.1 ± 0.12 (n = 125)
IV	8.1 ± 1.04 (n = 97)	IV	6.1 ± 0.22 (n = 119)
V	7.0 ± 0.91 (n = 97)	V	5.9 ± 0.27 (n = 119)
-	-	VI	5.5 ± 0.33 (n = 116)
Nymphal development		32.2 ± 0.73	
		34.5 ± 0.37	

declined afterwards at the reproductive stage for both species of grasshoppers.

Fourth instars of *D. elongatus* consumed 13.0 ± 0.46 mg/day, while fifth instars consumed significantly more (21.3 ± 0.48 mg/day) ($Z = -10.6$, $P < 0.0001$) (Table 2). Consumption by the pre-reproductive females was significantly higher than that of nymphs (Table 2). In the reproductive stages, females consumed 19.1 ± 0.05 mg/day, significantly less than the pre-reproductive females ($Z = 12.9$, $P < 0.0001$). The consumption of reproductive females was similar to that of pre-reproductive males ($Z = 0.157$, $P = 0.875$).

Pre-reproductive males consumed 20.4 ± 0.37 mg/day (Table 2), significantly more than fourth instars

Table 2 Forage losses by *Dichroplus elongatus* (Mean \pm ES) at 30°C and 14:10 (L: D) photoperiod.

Stage	n	Consumption rate (mg/individual/day)	Total losses per stage (mg/estage)	Relative consumption rate (mg/mg grasshopper/day)
Fourth instar	310	13.0 ± 0.46 c	104.2 ± 3.73	0.47
Fifth instar	330	21.3 ± 0.48 b	149.4 ± 3.42	0.35
Adult female				
Pre-reproductive	180	30.6 ± 0.56 a	1002.5 ± 19.33 a	0.23
Reproductive	240	19.1 ± 0.05 b		0.15
Adult male				
Pre-reproductive	250	20.4 ± 0.37 b	832.2 ± 15.9 b	0.28
Reproductive	240	12.9 ± 0.31 c		0.18

Values from the same column with different letters are significantly different (Mann-Whitney test, $P < 0.05$).

Table 3 Forage losses by *Dichroplus maculipennis* (Mean \pm ES) at 30°C and 14:10 (L:D) photoperiod.

Stage	n	Consumption rate (mg/individual/day)	Destruction rate (mg/individual/day)	Total losses (mg/individual/day)	Total losses per Stage (mg/estage)	Relative consumption Rate (mg/mg grasshopper/day)
Fifth instar	90	24.5 \pm 1.23 c	0	24.5 \pm 1.23	145.5 \pm 7.34	0.47
Sixth instar	90	34.2 \pm 2.40 b	0.3 \pm 0.05	34.5 \pm 2.42	186.5 \pm 13.25	0.38
Adult female						
Pre-reproductive	200	48.7 \pm 0.74 a	0.4 \pm 0.064	49.1 \pm 0.70	2360.8 \pm 63.61 a	0.15
Reproductive	180	18.4 \pm 0.79 d	0.5 \pm 0.085	18.9 \pm 0.80		0.06
Adult male						
Pre-reproductive	170	32.3 \pm 0.88 b	0.1 \pm 0.025	33.5 \pm 0.91	1760.4 \pm 56.71 b	0.17
Reproductive	170	11.7 \pm 0.43 e	0.5 \pm 0.077	12.8 \pm 0.45		0.06

Values from the same column with different letters are significantly different (Mann-Whitney test, $P < 0.05$).

($Z = 8.09$, $P < 0.001$). In the reproductive male, daily consumption was 12.9 ± 0.31 mg, significantly lower than that of fifth instars ($Z = -11.9$, $P < 0.0001$), and was not different from fourth instars ($Z = -0.79$, $P = 0.424$). The average adult consumption of *D. elongatus*, regardless sex and reproductive state of maturity, was 20.0 ± 0.30 mg/day. During testing with *D. elongatus*, fallen material was never observed, so it was then considered that total loss was equal to consumption. The loss caused by a female throughout the adult stage was $1,002.5 \pm 19.33$ mg, significantly higher than that caused by a male ($Z = 7.74$, $P < 0.0001$) (Table 2).

Fifth instars of *D. maculipennis* consumed significantly less (24.5 ± 1.23 mg/day) than sixth instars (34.2 ± 2.4 mg/day) (Table 3) ($Z = -4.15$, $P < 0.0001$). But pre-reproductive females were the ones to consume the most (48.7 ± 0.74 mg/day) (Table 3). Food consumption declined significantly for both sexes at the reproductive stage (females: $Z = 15.3$, $P < 0.0001$; males: $Z = 14.6$, $P < 0.0001$) (Table 3). There was no significant difference between the daily consumption of pre-reproductive males and sixth instars ($Z = -1.18$, $P = 0.238$). The average adult consumption of *D. maculipennis* regardless of sex and reproductive maturity was 29.1 ± 0.64 mg/day.

Unlike *D. elongatus*, *D. maculipennis* let plant material to drop when eating. The percentage of fallen plant material was higher for adults of both sexes at their reproductive stage, accounting for 3.9% and 2.9% of the daily loss, respectively. Fallen material was not observed in tests with fifth instars. The total loss by a female during the adult stage was significantly higher ($2,360.8 \pm 63.6$ mg) than that of a male ($1,760.4 \pm 56.7$) ($Z = 6.98$, $P < 0.0001$).

In both species, the consumption per weight unit decreased with successive stages of development, with a slightly higher value for adult males (Tables 2 and 3).

Females of both species were significantly heavier than males (Table 4) (*D. elongatus*: $Z = 8107$, $P < 0.0001$; *D. maculipennis*: $Z = 6.9$, $P < 0.0001$), and *D. maculipennis* adults were larger than those of *D. elongatus* (females: $Z = -8.73$, $P = 0.0001$; males: $Z = -8.76$, $P < 0.0001$). Females of *D. maculipennis* consumed a much higher daily amount of food than females of *D. elongatus* ($Z = -8.03$, $P < 0.0001$). On average, a female *D. elongatus* consumed 24.04 ± 0.46 mg/day, while a female of *D. maculipennis* 34.8 ± 0.9 mg/day. Males of *D. maculipennis* consumed more than *D. elongatus* ($Z = -5.95$, $P < 0.0001$). The average consumption of an adult male of *D. maculipennis* was 23.4 ± 0.76 mg/day and of a male of *D. elongatus* was 16.4 ± 0.31 mg/day.

Discussion

The variation observed in the duration of the nymph development for *D. elongatus* in this study as compared to data available in the literature (Liebermann 1949) might be due to the different geographic origin of the grasshoppers studied or to the rearing conditions (not stated by Liebermann). This type of intraspecific

Table 4 Biomass (dry weight) of *Dichroplus elongatus* and *Dichroplus maculipennis*.

Stage	<i>D. elongatus</i>	<i>D. maculipennis</i>
Fourth instar (n = 30)	27.7 \pm 1.81	-
Fifth instar (n = 30)	61.7 \pm 3.05	51.8 \pm 3.21
Sixth instar (n = 30)	-	89.9 \pm 4.10
Adult female (n = 50)	131.0 \pm 6.83 a	326.5 \pm 8.70 a
Adult male (n = 50)	72.2 \pm 2.55 b	192.9 \pm 5.60 b

Values from the same column with different letters are significantly different (Mann-Whitney test, $P < 0.05$).

variation has been already reported mentioned for other melanopline species with wide distribution ranges (COPR 1982). Although *D. elongatus* developed into adulthood with one instar less than *D. maculipennis*, the total duration of their nymph stage was similar.

The longevity of adults of *D. elongatus*, as estimated by De Wysiecki *et al* (1997) under the same conditions, was 41.7 ± 4.13 days in females and 49.9 ± 4.07 in males, with no significant differences between the sexes. Under the same rearing conditions, adults of *D. maculipennis* were found to be longer-lived than *D. elongatus*, and the longevity of males was significantly higher than that of females.

Hewitt & Onsager (1983) indicated that the amount of forage consumed by grasshoppers tends to increase as development progresses. *Dichroplus elongatus* and *D. maculipennis* significantly increased their consumption from the nymph stage to the pre-reproductive adult stage. However, reproductive adults significantly decreased their daily food consumption. Sánchez & de Wysiecki (1990) demonstrated under field conditions the same pattern for the melanopline *Dichroplus pratensis* Bruner, another species of economic importance in Argentina (Lange *et al* 2005). Consumption increased from fourth instars to the pre-reproductive stage, and then decreased during the reproductive stage. Akman Gündüz & Gülel (2002) estimated the consumption of the Desert locust, *Schistocerca gregaria* Forsk, under laboratory conditions, and showed that consumption significantly increased from first nymphal instars to the first week of adult life (in coincidence with sexual maturation), after which consumption began to decline. An explanation on why food consumption tends to decline as adults reach maturity has not been put forward, and our study was not designed at that end. However, it might be possible that simply the nutritional requirements just diminish after full development is attained.

Unlike *D. elongatus*, consumption of pre-reproductive males of *D. maculipennis* was not significantly higher than that of last instars (VI), probably due to the fact that sixth instars were not discriminated by sex. Sánchez & de Wysiecki (1990) found a similar trend between fifth instars and pre-reproductive males of *D. pratensis*.

Pre-reproductive females of both species showed the highest consumption, a fact that may relate to the nutritional requirements necessary for oogenesis (Lockwood *et al* 1996). Hill *et al* (1968) studied the relationship between somatic growth and the development of the ovaries with food consumption in *S. gregaria*. They recorded during the first 10 d of adulthood that females strongly increased their food consumption, reaching 112% by weight, to obtain required amount of proteins for oogenesis.

The food consumption per unit of weight recorded for adults of *D. elongatus* and *D. maculipennis* was slightly

higher for males, as observed for *Melanoplus scudderi* Uhler (Gangwere 1959) and contrary to that reported for *D. pratensis* (Sánchez & De Wysiecki 1990). Gangwere (1959) also suggested that although females consumed more than males, their lower consumption per weight unit as compared to males was due to their lower activity and metabolic rate.

Nymphs and pre-reproductive adults of *D. maculipennis* consumed a greater amount of food than *D. elongatus* per day. The daily consumption of reproductive adults of *D. elongatus* declined less than that of *D. maculipennis*. Reproductive females of *D. elongatus* consumed 1.6 times less than pre-reproductives, while males 0.5 times less. In *D. maculipennis*, reduction in food consumption in the reproductive stage was higher, with reproductive females consuming 2.64 times less than pre-reproductive females, while males had a reduction of 2.76 times. The reduction observed in food consumption in laboratory conditions was half of that reported under natural conditions for *D. pratensis*, with a 5.77 and a 4.17 fold reduction in food consumption for females and males when comparing insects at the reproductive and pre-reproductive stages, respectively (Sánchez & De Wysiecki 1990).

As in most grasshoppers, females of both studied species were significantly larger than males. In addition to the requirements for oogenesis, probably the differences in size between the sexes explain why females have a higher consumption as indicated elsewhere (Johnson & Pavlikova 1986, Johnson & Mündel 1987). Holmberg & Hordman (1984) estimated that daily consumption rates of adults of several species of grasshoppers were 20% higher than the consumption of individuals of stage V. Compared with the species used in this study, daily consumption of *D. elongatus* (20.0 ± 0.30 mg) would resemble that of *M. sanguinipes*, and that of *D. maculipennis* (29.1 ± 0.64 mg) to *Melanoplus packardii* Scudder.

Integrating our results with the framework by Hewitt & Onsager (1983) where they mentioned that the forage loss produced by grasshoppers is basically governed by the population density of the species involved, the rates of consumption, and adult longevity, one might conclude that, at equal densities, *D. maculipennis* would cause significantly higher losses than *D. elongatus*, as *D. maculipennis* has a higher daily consumption, drops plant material when feeding, and adults live longer than those of *D. elongatus*.

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