

SHORT COMMUNICATION

Longevity and fecundity of *Dichroplus maculipennis* (Orthoptera, Acrididae) at non-outbreaking and outbreaking situations

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ABSTRACT. Longevity and fecundity of *Dichroplus maculipennis* (Orthoptera, Acrididae) at non-outbreaking and outbreaking situations. *Dichroplus maculipennis* is one of the most characteristic and damaging grasshopper species of Argentina, mainly in areas of the Pampas and Patagonia regions. We estimated and compared the longevity and fecundity of adult female *D. maculipennis* under controlled conditions (30°C, 14L:10D, 40% RH) from individuals collected as last instar nymphs (VI) in the field and with a known recent history of low and high density conditions. Densities of *D. maculipennis* at the collecting sites were 0.95 individuals per m² in 2006 and 46 ind/m² in 2009, representing non-outbreaking and outbreaking situations, respectively. Adult female longevity in 2006 (67.96 ± 3.2 days) was significantly higher ($p < 0.05$) than in 2009 (37.44 ± 1.98 days). The number of egg-pods per female was 3.32 ± 0.44 for 2006 and 1.62 ± 0.26 for 2009. The average fecundity in 2006 (89.29 ± 11.9 eggs/female) was significantly greater ($p < 0.05$) than that in 2009 (36.27 ± 5.82 eggs/female). While it was observed that the oviposition rate was higher in 2006, this difference was not significant ($p > 0.05$). The fecundity curves showed that the highest values were at weeks 11 and 13 for the 2006 females, and at week 6 for those of 2009. Since the daily oviposition rate at low and high densities was not significantly different, the diminished fecundity rate at high density is attributable to their reduced longevity.

KEYWORDS. Fecundity; grasshopper; longevity; Melanoplinae.

RESUMO. Longevidade e fecundidade de *Dichroplus maculipennis* (Orthoptera: Acrididae: Melanoplinae) em situações de “non-outbreaking” e “outbreaking”. O gafanhoto *Dichroplus maculipennis* é um dos mais característicos e prejudiciais da Argentina, principalmente nas regiões das Pampas e da Patagonia. O objetivo deste estudo foi estimar e comparar a longevidade e fecundidade das fêmeas adultas do *D. maculipennis* sob condições controladas (30°C, 14 luz: 10 obscuridad, 40% RH) a partir do indivíduos coletados em campo como último estadio ninfal (VI) e con historia recente conocida de baixas e altas densidades. As densidades de *D. maculipennis* nos locais de coleta foram de 0.95 indivíduos por m² em 2006 e 46 indivíduos/m² em 2009, representando situações de “non-outbreaking” e “outbreaking”, respectivamente. A longevidade das fêmeas adultas em 2006 (67.96 ± 3.2 dias) foi significativamente maior ($p < 0.05$) do que as de 2009 (37.44 ± 1.98 dias). O número de oviposições por fêmea foi de 3.32 ± 0.44 para 2006 e 1.62 ± 0.26 para 2009. A fecundidade média em 2006 (89.29 ± 11.9 ovos/fêmea) foi significativamente maior ($p < 0.05$) do que a das fêmeas de 2009 (36.27 ± 5.82 ovos/fêmea). As curvas de fecundidade mostraram que os valores mais elevados ocorreram nas 11ª e 13ª semanas de 2006, e na 6ª semana para aquelas de 2009. Comparando a taxa diária de oviposição para altas e baixas densidades, não apresentaram diferenças significativas ($p > 0.05$). No entanto, as baixas taxas de fecundidade das fêmeas em densidades elevadas, se devem, provavelmente à longevidade reduzida.

PALAVRAS-CHAVE. Fecundidade; gafanhoto; longevidade; Melanoplinae.

The melanopline grasshopper *Dichroplus maculipennis* (Blanchard, 1851) is one of the most widely distributed species of the genus, occurring in southernmost Brazil (Rio Grande do Sul), much of Argentina and Chile, and Uruguay. In Argentina, *D. maculipennis* is distributed in a triangle that stretches from Buenos Aires and Entre Rios provinces in the East to southern Catamarca province in the North, and southern Santa Cruz province in Patagonia (Carbonell *et al.* 2006). The species is considered one of the most characteristic and damaging of Argentina, mainly in areas of the Pampas and Patagonia regions (Liebermann 1972; Lange *et al.* 2005). According to the categories employed for defining the pest

status of grasshopper species (COPR 1982), Carbonell *et al.* (2006) have categorized *D. maculipennis* as a major pest of several crops (barley, rye, oats, wheat, flax, lucerne) and forage on natural pastures. It is a polyphagous and univoltine species that presents obligatory embryonic diapause (COPR 1982).

Although some studies conducted in the Pampas during the 90s' suggested a possible decrease in the abundance of *D. maculipennis* (Cigliano *et al.* 1995; Cigliano *et al.* 2000), starting in 2008 an outbreak occurred in parts of the southern Pampas, where densities reached up to 50 individuals per m² and en masse flights were widespread. Unlike other

melanoplinae of Argentina, adults of *D. maculipennis* at high densities are historically known to show significant aggregation behavior and dispersal flights, covering distances that can exceptionally reach 50 kilometers (Joan 1927; Schiuma 1938; Daguerre 1940; Liebermann 1972; COPR 1982).

Different aspects of the life cycle of grasshoppers, such as longevity and fecundity, may vary in relation to a great variety of factors, including population density (Joern and Gaines 1990). Life histories may also vary because of genetic and environmental factors acting on previous and present generations (Chapuis *et al.* 2010). The goal of this study was to estimate and compare the longevity and fecundity of adult female *D. maculipennis* under controlled conditions, but from individuals collected in the field as juveniles just immediately preceding adulthood (nymphal instar VI) with a known recent history of low and high density conditions, respectively.

Individuals of *D. maculipennis* employed in the experiences were collected with entomological nets as last instar nymphs (VI) in natural and improved pastures at the locality of Laprida (36°02'S, 59°06'W), Buenos Aires province, in the southern Pampas region as defined by Morrone (2006). Collecting times were late December 2006 and 2009. The state of the *D. maculipennis* population (non-outbreaking versus outbreaking) at collecting times was determined by estimating density (individuals/m²) through the rings method developed by Onsager and Henry (1977) and by field observations of aggregation and dispersal behavior. Since *D. maculipennis* is univoltine and the outbreak appeared to begin in November 2008, the individuals collected in 2009 corresponded to the second generation of the outbreaking state.

Once in the laboratory, individuals of both collections received the same treatment. Immediately after entering adulthood, 25 couples (one male, one female) were formed corresponding to each of both collecting times. Each couple was placed in a wire-screened, aluminium cage (12x12x16 cm) in a rearing room under controlled conditions (30°C, 14L:10D, 40% RH) of wide use (Henry 1985; Hinks & Erlandson 1994; Mariottini *et al.* 2010). The grasshoppers were fed daily with thoroughly washed, fresh leaves of a variety of grasses, lettuce, cabbage, and wheat bran flakes. Each cage was provided with a substrate for egg-pod laying that consisted of a plastic container (10 cm deep) filled with sterilized sand. Thermoregulation and mating was stimulated with 75W bulbs suspended 15 cm above each cage. Couples were maintained until death. Once a week the containers were sifted, the egg-pods recovered, and the number of eggs per pod counted. We recorded longevity of females, number of egg-pods per female, and number of eggs per pod, and estimated the average fecundity (number of eggs/female), the oviposition rate (eggs/female/day), and the fecundity curve (m_x = mean number of eggs per female of x age). In order to compare longevity of females, fecundity, and oviposition rate the parametric test of ANOVA by ranks was employed. Statistical tests were performed using the XLSTAT 7.5.3 program (Addinsoft, 2005). Results are expressed as mean value \pm SE.

Densities of *D. maculipennis* at the collecting sites were 0.95 individuals per m² in 2006 and 46 ind/m² in 2009, representing non-outbreaking and outbreaking situations, respectively. As shown in table I, adult female longevity was 67.96 ± 3.2 (range = 32–90) and 37.44 ± 1.98 (25–59) days in 2006 and 2009, respectively, a significant difference ($F = 64.25$, $df = 49$, $p = 0.0001$). The number of egg-pods per female was 3.32 ± 0.44 (range = 0–8) for 2006 and 1.62 ± 0.26 (0–4) for 2009. The average fecundity of females in 2006 (Table I) was significantly greater than that of females in 2009 ($F = 13.045$, $df = 49$, $p = 0.001$). While it was observed that the oviposition rate was higher in females of 2006, this difference was not significant ($F = 0.652$, $df = 49$, $p = 0.423$). The fecundity curves (Fig. 1) showed that the highest values were at weeks 11 and 13 for the 2006 females, and at week 6 for those of 2009.

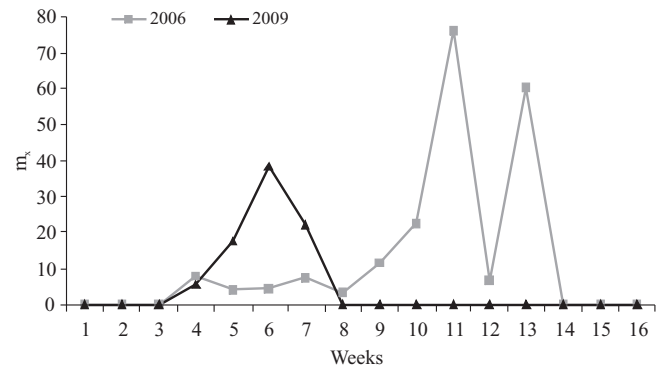


Fig. 1. Fecundity curves (m_x) of *Dichroplus maculipennis* under controlled conditions (30°C, 14L:10D, 40% RH) and field-collected as VI instar nymphs at low (2006) and high density (2009).

Table I. Adult female longevity and reproductive attributes of *Dichroplus maculipennis* under controlled conditions (30°C, 14L:10D, 40% RH) and field-collected as VI instar nymphs at low (2006) and high density (2009).

<i>Dichroplus maculipennis</i>	Low density (2006)	High density (2009)
Longevity (days)	67.96 ± 3.2	37.44 ± 1.98
Number egg-pods per female	3.32 ± 0.44	1.62 ± 0.26
Number of eggs per pod	26.9 ± 1.94	22.4 ± 1.3
Fecundity (eggs per female)	89.29 ± 11.9	36.27 ± 5.82
Daily oviposition rate (eggs per female per day)	1.22 ± 0.15	1.036 ± 0.176

Results of this study show that adult females of *D. maculipennis* collected at high density had significant lower longevity and fecundity than adult females collected at low density. Since the daily oviposition rate of females at low and high densities was not significantly different, the diminished fecundity rate of females at high density is attributable to their reduced longevity. Some authors have reported similar results in other species. Antoniou (1973, 1978) observed under laboratory conditions that females of *Ornithacris turbida* (Walker, 1870) and *Humbe tenuicornis* (Schaum,

1853) reared at low density lived longer, laid more egg-pods, and had a greater fecundity than those reared in crowded conditions, but also displaying a similar weekly rate of oviposition at both densities. Smith (1970, 1972) reported that the number of egg-pods lay by the females of *Melanoplus sanguinipes* (Fabricius, 1798) decreased with crowding within a generation because females lived a shorter time and had a lower oviposition rate.

Grasshoppers exhibit life history variation in response to a variety of factors (Stauffer & Whitman 1997; Branson 2003). Increased population density frequently leads to physiological changes that are expressed in coloration, morphology, development rate, metabolism, and behavior (Applebaum & Heifetz 1999; Sword 2005; Chapuis *et al.* 2008; Song & Wenzel 2008). The phase polyphenism observed in locusts, an extreme case of phenotypic plasticity, is attributed to changes in population densities of both parents and offspring (Song & Wenzel 2008; Chapuis *et al.* 2008; Chapuis *et al.* 2010). Unlike locusts, grasshoppers do not exhibit phase polyphenism (Song & Wenzel 2008), but may express various changes (including those affecting reproductive output) in response to population density that differ in different species, some responding intensely to crowding, others only partially (Applebaum & Heifetz 1999).

One possible explanation for the decrease in longevity and fecundity of females that were found at high density could be the existence of a “trade-off” between early reproduction and longevity. Although in our experiments females of both groups began to oviposit after the fourth week of adulthood, the fecundity curves show that at high density the higher values of fecundity were at week 6 while at low density they were at weeks 11–13. Reproduction is assumed to carry a cost, in terms of future survival, growth or fecundity (De Souza Santos & Begon 1987; Forsman 2001). Insects can accelerate the reproduction or maturation if they inhabit seasonal environments with relatively short growing seasons. However, early reproduction has costs, such as reduced longevity or diminished investment in the number of eggs (De Souza Santos & Begon 1987; Homeny & Juliano 2007). Chapuis *et al.* (2010) recorded that female *Locusta migratoria* (Linnaeus, 1758) with a crowding history reproduced earlier (by reducing oviposition times) than females with an isolation history.

Another hypothesis that could explain the decrease in longevity and fertility in *D. maculipennis* at high density might be related to en masse dispersal. In several species of Acrididae, significant increases in population size trigger flight dispersal or migratory capabilities (Farrow 1990; Sword 2005). One of the costs that have been associated to en masse flight dispersal is that migrants often have a decrease in reproductive fitness in relation to non-migrants (Rankin & Burchsted 1992). As it was already mentioned, *D. maculipennis* readily becomes migratory in outbreak situations (COPR 1982).

Results of this study represent a considerable advance in understanding the biology of *D. maculipennis*. However, given the ecological and economic importance of the species in

Argentina, further research is envisaged, particularly regarding the central factors that govern the conspicuous size fluctuations of its populations.

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REFERENCES

- Addinsoft. 2005. XLSTAT Pro version 7.5.3 available at <http://www.xlstat.com/en/home>.
- Antoniou, A. 1973. The life history of the grasshopper *Ornithacris turbida* (Walker) (Orthoptera: Acrididae: Cyrtacanthacridinae) in a laboratory. **Journal of Natural History** 7: 461–469.
- Antoniou, A. 1978. Laboratory studies on the life-history of the grasshopper *Humbe tenuicornis* Schaum (Orthoptera: Acrididae: Oedipodinae) in relation to density and phase. **Journal of Natural History** 12: 185–93.
- Applebaum, S. W. & Y. Heifetz. 1999. Density-dependent physiological phase in insects. **Annual Review of Entomology** 44: 317–41.
- Branson, D. H. 2003. Reproduction and survival in *Melanoplus sanguinipes* (Orthoptera: Acrididae) in response to resource availability and population density: the role of exploitative competition. **The Canadian Entomologist** 135: 415–426.
- Carbonell, C.; M. M. Cigliano & C. E. Lange. 2006. **Acridomorph species of Argentina and Uruguay**. CD-ROM. Publications on Orthopteran Diversity, The Orthopterists Society at the “Museo de La Plata”, Argentina.
- Chapuis, M.-P.; A. Estoup; A. Augé Sabatier; A. Foucart; M. Lecoq & Y. Michalakis. 2008. Genetic variation for parental effects on the propensity to gregarise in *Locusta migratoria*. **BMC Evolutionary Biology** 8: 37.
- Chapuis, M.-P.; L. Crespín, A. Estoup; A. Augé-Sabatier; A. Foucart; M. Lecoq & Y. Michalakis. 2010. Parental crowding influences life-history traits in *Locusta migratoria* females. **Bulletin of Entomological Research** 100: 9–17.
- Cigliano, M. M.; M. L. De Wysiecki & C. E. Lange. 1995. Disminución de la abundancia de *Dichroplus maculipennis* (Acrididae) en comunidades del Sudoeste de la provincia de Buenos Aires. **Revista de la Sociedad Entomológica Argentina** 54: 41–42.
- Cigliano, M. M.; M. L. De Wysiecki & C. E. Lange. 2000. Grasshopper species diversity in the Pampas, Argentina. **Diversity and Distributions** 6: 81–91.
- COPR, 1982. **The locust and grasshopper agricultural manual**. London, Centre for Overseas Pest Research, p. 690.
- Daguerré, J. B. 1940. Observaciones biológicas sobre *Dichroplus arrogans* (Stal). **Revista de la Sociedad Entomológica Argentina** 10: 341–346.
- De Souza Santos, P. & M. Begon. 1987. Survival costs of reproduction in grasshoppers. **Functional Ecology** 1: 215–221.
- Farrow, R. A. 1990. Flight and migration in acridoids, p. 227–314. In: Chapman, R. F.; Joern, A. (eds). **Biology of grasshoppers**. New York, John Wiley & Sons, 563 p.
- Forsman, A. 2001. Clutch size versus clutch interval: life history strategies in the colour-polymorphic pygmy grasshopper *Tetrix subulata*. **Oecologia** 129: 357–366.
- Henry, J. E. 1985. *Melanoplus* spp., p. 451–464. In: P. Singh & R. F. Moore (eds). **Handbook of Insect Rearing**. Vol. 1, 488 p.
- Hinks, C. F. & M. A. Erlandson. 1994. Rearing grasshoppers and locusts: Review, rationale and update **Journal of Orthoptera Research** 3: 1–10.

- Homeny, R. H. & S. A. Juliano. 2007. Developmental response to a seasonal time constraint: the effects of photoperiod on reproduction in the grasshopper *Romalea microptera*. **Ecological Entomology** **32**: 559–566.
- Joan, T. 1927. Nota preliminar sobre la evolución de la tucura. **Revista de la Sociedad Entomológica Argentina** **3**: 7–11.
- Joern, A. & S. B. Gaines. 1990. Population dynamics and regulation in grasshoppers. p. 415–482. *In*: Chapman, R. F. & A. Joern (Eds.), **Biology of grasshoppers**. New York, John Wiley & Sons, 563 p.
- Lange, C. E.; M. M. Cigliano & M. L. De Wysiecki. 2005. Los acridoideos de importancia económica en la Argentina, p. 93–135. *In*: Barrientos Lozano, L. y P. Almaguer (Eds). **Manejo integrado de la langosta centroamericana y acridoideos plaga en América Latina**. Tamaulipas, Instituto Tecnológico de Ciudad Victoria, 302 p.
- Liebermann, J. 1972. The current state of the locust and grasshopper problem in Argentina, p. 191–198. *In*: Proceedings of the International Study Conference on the current and future problems of Acridology, London.
- Mariottini, Y.; M. L. De Wysiecki & C. E. Lange. 2010. The biology and population parameters of the grasshopper *Ronderosia bergi* (Stål) (Orthoptera: Acrididae: Melanoplineae), under laboratory conditions. **Journal of Insect Science** **10**: 109.
- Morrone, J. J. 2006. Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. **Annual Review of Entomology** **51**: 467–94.
- Onsager, J. O. & J. E. Henry. 1977. A method for estimating the density of rangeland grasshoppers (Orthoptera: Acrididae) in experimental plots. **Acrida** **6**: 231–237.
- Rankin, M. A. & J. C. A. Burchsted. 1992. The cost of migration in insects. **Annual Review of Entomology** **37**: 533–559.
- Schiuma, R. 1938. Informe sobre “Tucuras”, **Publicacion Miscelanea N° 43**, Buenos Aires, Dirección de Sanidad Vegetal del Ministerio de Agricultura y Ganadería de la Nación. 1 p.
- Smith, D. S. 1970. Crowding in Grasshoppers. 1. Effect of crowding within one generation on *Melanoplus sanguinipes*. **Annals of the Entomological Society of America** **63**: 1775–1776.
- Smith, D. S. 1972. Crowding in Grasshoppers II. Continuing effects of crowding on subsequent generations of *Melanoplus sanguinipes* (Orthoptera: Acrididae). **Environmental Entomology** **1**: 314–317.
- Song, H. & J. W. Wenzel. 2008. Phylogeny of bird-grasshopper subfamily Cyrtacanthacridinae (Orthoptera: Acrididae) and the evolution of locust phase polyphenism. **Cladistics** **24**: 515–542.
- Stauffer, T.W. & D. W. Whitman. 1997. Grasshopper oviposition. p 231–267. *In*: S. Gangwere (ed). **The Bionomics of grasshoppers**. New York, CABI, 528 p.
- Sword, G. 2005. Local population density and the activation of movement in migratory band-forming Mormon crickets **Animal Behaviour** **69**: 437–444.