Medical and Veterinary Entomology

Medical and Veterinary Entomology (2011), doi: 10.1111/j.1365-2915.2011.00969.x

Seasonal composition and temporal succession of necrophagous and predator beetles on pig carrion in central Argentina

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Abstract. Insects are the most important components of the terrestrial fauna associated with carrion because they recycle organic matter back into the ecosystem. They can be classified into four ecological categories comprising: necrophages; parasites and predators of necrophagous species; omnivores, and incidentals. To determine the composition and temporal succession of necrophagous and predator beetles on pig carrion, four experiments, one in each season, were carried out during 2004 in a rural area of Cordoba, central Argentina. Two pigs (*Sus scrofa* L.), weighing approximately 8 kg each, were used in each of the four experiments. The animals were killed by a sharp blow to the head and immediately placed in an appropriate trap. One pig was placed in the shade and the other in direct sunlight. Beetle fauna were collected daily during the first 4 weeks and thereafter every 2 or 3 days. Five stages of decomposition were observed and a total of 1586 adults and 4309 immatures of Coleoptera belonging to the Staphylinidae, Nitidulidae, Cleridae, Dermestidae, Histeridae, Anthicidae and Trogidae families were collected during the four experiments. The necrophagous community was represented by *Dermestes maculates* (De Geer), nitidulid species and members of the *Trox* genus. Staphylinidae, Cleridae and Histeridae species were considered to be the main predators of the necrophagous species.

Key words. Coleoptera, decomposition, necrophagous, predators, succession.

Introduction

Carrion is a nutritionally rich but ephemeral resource that acts as a source of shelter or food for a wide variety of fauna mainly represented by insects. Insects may play different roles in the community depending on their feeding behaviours and can be classified into four ecological categories comprising: necrophages; parasites and predators of necrophagous species; omnivores, and incidentals (Smith, 1986; Catts & Goff, 1992).

Necrophagous, parasite and predator species are very useful in investigations into unexplained deaths (Anderson & Hobischak, 2004). Forensic entomology is defined as the practice of using insects and other arthropods associated with carrion to estimate the post-mortem interval (Anderson & VanLaerhoven, 1996). The necrophagous species are represented mainly by Diptera and Coleoptera. Among the necrophagous beetles, the species belonging to the Dermestidae and Nitidulidae families are considered the most important decomposers because their adults and immature stages use carrion as a source of food that is necessary to their development. Species of the genus *Dermestes* feed on organic dry matter, such as hair or skin, and their larvae can develop on dead insects. Nitidulids can feed on decaying fruit, flowers and fungi, as well as on carrion. Several species of Staphylinidae,

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Cleridae and Histeridae beetles feed on fly larvae, thereby acting as predators. This ecological category plays a very important role in the dynamics of the community (Tantawi *et al*., 1996).

During the decomposition process, each stage is attractive to different species as a result of the particular physical and chemical conditions that prevail in the carrion, which contribute to provide a habitat ideal for certain species to lay eggs and/or feed; the changes that occur in the carrion during the decomposition process thus determine a temporal succession of insect species (Payne, 1965; Keh, 1985; Turner, 1991). The pattern of species succession can vary according to the geographical region, type of death, size of the corpse and environmental conditions such as temperature—the most important variable—and humidity, which affect the development rate of immature insects breeding on a carcass by accelerating or delaying the process of decomposition (Bornemissza, 1957; Ricklefs, 1996).

Several studies have focused on species in the coleopteran community that use carrion as a source of food and shelter, from either an ecological or a forensic perspective, in different temperate and tropical regions of the world, but studies in Cordoba and many other regions of Argentina are still scarce (Oliva, 1997; Centeno *et al.*, 2002; Battán Horenstein *et al.*, 2005). This study aimed to identify the necrophagous and predator species of Coleoptera that visit and breed on pig carcasses and to establish their successional patterns in Cordoba, Argentina.

Materials and methods

Study area

One experiment was performed in each of the four seasons during 2004. The experiments were undertaken to the south of Cordoba city, Argentina, in an area basically characterized by the presence of algarrobo trees (*Prosopis alba* and *Prosopis nigra*). However, over the last 100 years, this vegetation has been partially replaced by cultures of citrus, soybean and alfalfa. The weather is predominantly dry and cold between March and September (autumn and winter) and warm and wet from September to March (spring and summer). Annual rainfall ranges between 800 mm and 1000 mm. The area can be defined as rural and is characterized by dense vegetation and isolated houses (Schnack *et al*., 1998). This site was chosen because it constitutes an area of transition between natural and urban regions, and we believe that the biodiversity in this area is increased by the contributions of species from both environments.

Equipment and procedures

Two domestic pigs (*Sus scrofa* L.), each weighing approximately 8 kg, were used in each experiment. The animals were killed by a sharp blow to the head with a blunt metallic object and immediately placed in a variant of the trap designed by Schoenly *et al*. (1991) measuring 120 × 90 × 60 cm. One trap was placed in direct sunlight and the other in the shade, approximately 300 m apart. The trap is designed to collect a large proportion of arthropods, including those attracted to the carcass and those leaving it. Each experiment lasted until the entire carcass was consumed, which took approximately 7 weeks. Samples were taken daily during the first 4 weeks in order to collect beetle species and then every 2 or 3 days over the following weeks until the end of the experiment. Relative humidity and temperature, both in the traps and in their vicinity, were recorded daily with a portable thermo hygrometer (Hygro/In/Out Thermometer HT05; TFA Dostmann GmbH, Wertheim-Reicholzheim, Germany). Carcass temperature was taken with a thermometer. Meteorological data for each season were obtained from the local weather station, located approximately 15 km from the study area.

Stage of decomposition

Five stages of decomposition were observed in the carcasses, according to Anderson & VanLaerhoven (1996): fresh (F); bloat (B); decay (D); advanced decay (AD), and dry remains (DR). The F stage of decomposition begins at the moment of death and continues until bloat is evident. The B stage, also known as putrefaction, is the main component of decomposition. During this stage gas is gradually produced by the activity of anaerobic bacteria, which results in the definitive bloated appearance of the entire carcass. During this stage a strong odour of putrefaction is evident. The onset of stage D is characterized by the complete deflation of the carcass as the skin breaks. A strong smell is emitted by the carcass during this stage. The AD stage is characterized by the reduction of the corpse to bones, cartilage and skin. Towards the end of the process of decomposition, during the DR stage, the remains are completely reduced to bones. In all experiments, except in autumn in the carcass kept in the shade, the decomposition process was complete.

Statistical analysis

Frequencies of beetle families and species collected in the traps placed under the two insolation regimens were compared using a one-way analysis of variance (ANOVA). Another one-way ANOVA was performed to compare the abundance of each family over the four seasons. Both statistical analyses were performed using InfoStat Version 1.1 (Grupo InfoStat, National University of Cordoba, Cordoba, Argentina). The Duncan multiple comparisons F-test (overall error $\alpha = 0.05$) was used to compare the means for each parameter.

Results

Community composition and temporal succession of beetle species

A total of 1586 coleopteran adults and 4309 immature stages belonging to the Staphylinidae, Nitidulidae, Cleridae,

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Table 1. Abundances and relative abundances of necrophagous and predaceous beetles collected from pig carcasses in Cordoba during 2004, by season.

		Season					
Family	Genus/species	Summer	Autumn	Winter	Spring	*n*	%
Staphylinidae	Staphylinidae sp.	205	59	67	148	479	30.20
	Creophilus maxillosus	7	9	26	24	66	4.16
Dermestidae	*Dermestes maculates*	48	8	11	48	115	7.25
Histeridae	*Hister* sp.	27	2	7	11	47	2.96
	Saprinus sp.	22	4	11	45	82	5.17
Cleridae	*Necrobia rufipes*	204	27	4	42	277	17.47
	Necrobia violaceae	1	0	0	4	5	0.32
Nitidulidae	Nitidulidae sp.	82	5	36	250	373	23.52
Anthicidae	Anthicidae sp.	23	8	9	15	55	3.47
Tenebrionidae	Tenebrionidae sp.	2	0	3	2	7	0.44
Trogidae	*Trox* sp.	8	11	4	16	39	2.46
Otros	Otros	16	9	5	11	41	2.59
Seasonal abundance		645	142	183	616	1586	100

Dermestidae, Histeridae, Anthicidae and Trogidae families were collected during the four experiments. The most abundant family during summer and spring was the Staphylinidae ($F = 7.87$, $P < 0.0001$), which showed a preference for the carcass in the sunlit condition ($F = 4.48$, $P = 0.035$) (Tables 1 and 2). In summer, insects in this family arrived at the sunlit carcass during decomposition stage B, but arrived later at the shaded carcass. Larvae of this family were observed mainly during the DR stage (Table 3). In autumn, the staphylinids arrived at both corpses at the same time, but only the sunlit carcass yielded adults of this family during all stages of decomposition. Several larvae were collected during stages D and AD (Table 4). This family showed the same patterns of succession in winter and spring (Tables 5 and 6). The staphylinids were represented by *Creophilus maxillosus* (Linneus) and although adults of this species were present in low numbers, immatures were

Table 2. Mean abundances of Coleoptera families.

	Season				Insolation regime	
Family	Summer	Autumn	Winter	Spring	Sunlit	Shaded
Staphylinidae	0.86^{b}	0.39^{a}	0.44^{a}	0.73^{b}	0.69^{b}	0.52^{a}
Dermestidae	0.37^{b}	0.05^{a}	0.07^{a}	0.32^{b}	0.26^{b}	0.15^{a}
Histeridae	0.34^{b}	0.04^{a}	0.10^{a}	0.40^{b}	0.27^{b}	0.17^{a}
Cleridae	0.72^{c}	0.17^{ab}	0.03^{a}	0.29^{b}	0.54^{b}	0.07^{a}
Nitidulidae	0.53^{b}	0.04^{a}	0.14^{a}	1.02^{c}	0.61^{b}	0.26^{a}
Anthicidae	0.20^{b}	0.06^{a}	0.06^{a}	0.12^{a}	0.15^{b}	0.07^{a}
Tenebrionidae	0.02^{b}	0^{a}	0.02^{a}	0.02^{a}	0.005^{a}	0.03^{a}
Trogidae	0.07^{ab}	0.08^{ab}	0.03^{a}	0.13^{b}	0.10^{a}	0.06^{a}

Means in the same column followed by the same letter do not differ significantly, according to Duncan's multiple comparisons ($\alpha = 0.05$).

Table 3. Temporal succession of necrophagous and predaceous beetles collected from sunlit and shaded carcasses during summer in 2004.

		Sunlit carcass, stage of decay					Shaded carcass, stage of decay				
Family	Genus/species	F	B	D	AD	DR	F	B	D	AD	DR
Staphylinidae	Staphylinidae sp. (A)		●		●	●				●	●
	Staphylinidae sp. (I)					⬤			○		⬤
	Creophilus maxillosus (A)					●					●
	Creophilus maxillosus (I)										○
Dermestidae	*Dermestes maculates* (A)			●	●	●				●	●
	Dermestes maculates (I)			○	⬤	■			○	○	■
Histeridae	*Hister* sp. (A)				●	●				●	●
	Saprinus sp. (A)				●	●				●	●
Cleridae	*Necrobia rufipes* (A)			●	●	●				●	●
	Necrobia rufipes (I)			○		⬤					□
	Necrobia violaceae (A)					●					
Nitidulidae	Nitidulidae sp. (A)			●	●	●					●
Tenebrionidae	Tenebrionidae sp. (A)					●					●
Trogidae	*Trox* sp. (A)	●			●	●					●
	Trox sp. (I)					○					
Anthicidae	Anthicidae sp. (A)					●				●	●

○, 1-10; ● (grey), 11–40; ⬤ (black), 41–70; □, 71–100; ■, >300.
F, fresh; B, bloat; D, decay; AD, advanced decay; DR, dry remains; A, adults; I, immatures.

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Table 4. Temporal succession of necrophagous and predaceous beetles collected from sunlit and shaded carcasses during autumn in 2004.

		Sunlit carcass, stage of decay					Shaded carcass, stage of decay				
Family	Genus/species	F	B	D	AD	DR	F	B	D	AD	DR
Staphylinidae	Staphylinidae sp. (A)	◍	◍	◍	◍	◍	◍				◍
	Staphylinidae sp. (I)			○	●					○	○
	Creophilus maxillosus (A)		◍	◍	◍					◍	◍
	Creophilus maxillosus (I)					●					○
Dermestidae	*Dermestes maculates* (A)			◍	◍	◍				◍	
	Dermestes maculates (I)					●					
Histeridae	*Hister* sp. (A)				◍						
	Saprinus sp. (A)			◍	◍						
Cleridae	*Necrobia rufipes* (A)			◍	◍	◍					
Nitidulidae	Nitidulidae sp. (A)			◍	◍					◍	◍
Trogidae	*Trox* sp. (A)	◍	◍	◍	◍	◍	◍		◍	◍	◍
Anthicidae	Anthicidae sp. (A)	◍	◍	◍		◍					

○, 1-10; ◍, 11–40; ●, 41–70.
F, fresh; B, bloat; D, decay; AD, advanced decay; DR, dry remains; A, adults; I, immatures.

Table 5. Temporal succession of necrophagous and predaceous beetles collected from sunlit and shaded carcasses during winter in 2004.

		Sunlit carcass, stage of decay					Shaded carcass, stage of decay				
Family	Genus/species	F	B	D	AD	DR	F	B	D	AD	DR
Staphylinidae	Staphylinidae sp. (A)		◍	◍	◍	◍		◍	◍	◍	◍
	Staphylinidae sp. (I)				●	●				●	○
	Creophilus maxillosus (A)			◍	◍	◍				◍	◍
	Creophilus maxillosus (I)				●	□		○		●	○
Dermestidae	*Dermestes maculates* (A)				◍	◍				◍	◍
	Dermestes maculates (I)			○	●	■				○	□
Histeridae	*Hister* sp. (A)			◍	◍						◍
	Saprinus sp. (A)			◍	◍	◍				◍	◍
Cleridae	*Necrobia rufipes* (A)					◍					◍
	Necrobia rufipes (I)					○					○
Nitidulidae	Nitidulidae sp. (A)			◍	◍	◍				◍	◍
Trogidae	*Trox* sp. (A)			◍	◍	◍					
	Trox sp. (I)				○						
Anthicidae	Anthicidae sp. (A)	◍				◍				◍	◍
Tenebrionidae	Tenebrionidae sp. (A)									◍	

○, 1-10; ◍, 11–40; ●, 41–70; □, 71–100; ■, 101–300.
F, fresh; B, bloat; D, decay; AD, advanced decay; DR, dry remains; A, adults; I, immatures.

very abundant (Table 7). Immature stages of *C. maxillosus* were collected later in the decay process.

The Nitidulidae represented the second most abundant family, showing a clear numerical predominance in the spring ($F = 50.1$, $P < 0.0001$) and preference for the carrion in the shade ($F = 30.99$, $P < 0.0001$) (Tables 1 and 2). This family appeared in the carcasses mainly during decomposition stage D and remained until the end of the decomposition process (Tables 3–5).

The Cleridae were represented by two species of the genus *Necrobia*, of which *Necrobia rufipes* (De Geer) was the most abundant and was collected as both adults and larvae (Tables 1 and 7). Although this species was collected in all four experiments, its frequency was highest in summer ($F = 32.29$, $P < 0.0001$), particularly in the sunlit carcass ($F = 81.32$, $P < 0.0001$) (Table 2). In summer, autumn and spring, *N. rufipes* arrived at the sunlit carcass early in the decomposition process (Tables 3, 4 and 6), but in winter it was observed only during the advanced stages of decay (Table 5). *Necrobia rufipes* larvae were collected during the final stages of decay.

The Dermestidae were represented only by *Dermestes maculatus*, which were collected as adults in very low frequencies during the four experiments ($F = 14.92$, $P < 0.0001$) and mainly from the shaded carcass ($F = 6.35$, $P = 0.0122$). However, this species was the most abundant as larvae (Table 7). Adults of *D. maculatus* arrived at the carcasses during decomposition stages B (Table 6), D (Tables 3 and 4) and AD (Tables 3, 5 and 6) and their larvae were very abundant during the final stages of decay (Tables 3–6). *Dermestes maculatus* larvae were collected in high frequencies in summer, winter and spring, from stage D until the end of the decomposition process. In autumn, larvae of this species were collected in low frequencies.

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Table 6. Temporal succession of necrophagous and predaceous beetles collected from sunlit and shaded carcasses during spring in 2004.

		Sunlit carcass, stage of decay					Shaded carcass, stage of decay				
Family	Genus/species	F	B	D	AD	DR	F	B	D	AD	DR
Staphylinidae	Staphylinidae sp. (A)		◍	◍	◍	◍		◍	◍	◍	◍
	Staphylinidae sp. (I)				○	●		○	○	●	●
	Creophilus maxillosus (A)			◍	◍	◍	◍	◍	◍	◍	◍
	Creophilus maxillosus (I)				○	□			□	▩	●
Dermestidae	*Dermestes maculates* (A)				◍	◍		◍	◍	◍	◍
	Dermestes maculates (I)				●	■		○	●	▩	▩
Histeridae	*Hister* sp. (A)				◍	◍				◍	
	Saprinus sp. (A)			◍	◍	◍		◍	◍	◍	◍
Cleridae	*Necrobia rufipes* (A)				◍	◍		◍	◍	◍	◍
	Necrobia rufipes (I)					●				○	●
	Necrobia violaceae (A)					◍				◍	
Nitidulidae	Nitidulidae sp. (A)		◍	◍	◍	◍			◍	◍	◍
Trogidae	*Trox* sp. (A)		◍			◍	◍	◍	◍	◍	
	Trox sp. (I)					○					
Anthicidae	Anthicidae sp. (A)					◍				◍	◍
Tenebrionidae	Tenebrionidae sp. (A)							◍		◍	

○, 1-10; ◍, 11–40; ●, 41–70; □, 71–100; ▩, 101–300; ■, >300.
F, fresh; B, bloat; D, decay; AD, advanced decay; DR, dry remains; A, adults; I, immatures.

Table 7. Abundances and relative abundances of necrophagous and predaceous beetle larvae collected from pig carcasses in Cordoba during 2004, by season.

		Season					
Family	Genus/species	Summer	Autumn	Winter	Spring	*n*	%
Dermestidae	*Dermestes maculates*	1467	25	297	1713	3502	81.27
Staphylinidae	Staphylinidae sp.	48	35	47	64	194	4.50
	Creophilus maxillosus	8	18	103	301	430	9.98
Cleridae	*Necrobia rufipes*	90	0	6	80	176	4.08
Trogidae	Trogidae sp.	3	1	1	2	7	0.16

The Histeridae, represented by the genera *Hister* and *Saprinus*, were collected only as adults, mainly in the spring and summer months ($F = 15.82$, $P < 0.0001$), and showed preference for the carcass in the sun ($F = 4.32$, $P = 0.0384$). Both genera showed similar abundances except in spring, when species of the genus *Saprinus* were clearly more abundant than species of *Hister*. The adults of this genus showed different patterns of arrival at the carcasses, but in general were present during the intermediate phases of the decay process.

Other families such as the Anthicidae and Trogidae were present during the four seasons, but at low frequencies (Tables 1 and 2). The Trogidae were represented by the genus *Trox*, collected both as adults and larvae. Adults of *Trox* appeared early in the decay process, but larvae, present only in the sunlit carcasses, appeared later in the process when most of the carrion had already been consumed. Trogidae larvae were collected during summer, winter and spring (Tables 3, 5 and 6) from carcasses in the final stages of decay, but were observed in carcasses from the F stage onwards in autumn (Table 4).

Discussion

Beetles are an important component of the fauna associated with decaying organic matter (Johnson, 1975; Morón & López-Méndez, 1985; Early & Goff, 1986; Anderson & VanLaerhoven, 1996; Moura *et al*., 1997).

The family Dermestidae, which is characteristic of the necrophagous community, has been widely cited in association with decaying animal matter (Anderson & VanLaerhoven, 1996; Tantawi *et al*., 1996; Oliva, 1997; Souza & Linhares, 1997; Carvalho *et al*., 2000). Members of this family feed on products containing animal protein or animal or vegetable matter, showing notably necrophagous behaviour (Smith, 1986). In general, the dermestids are associated with the last stages of decay, in which the remains are dry (Souza & Linhares, 1997). In this study, larvae of *D. maculatus* were collected during the later stages of decay, as they were by Souza and Linhares (1997) in Brazil and Centeno *et al.* (2002) in Buenos Aires.

Although the Nitidulidae live mainly in flowers and fungi, they have also been found in association with carrion (Payne & King, 1970; Smith, 1986; Anderson & VanLaerhoven, 1996;

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Tantawi *et al*., 1996). Members of this family are considered to be omnivorous because the adults can feed on live prey as well as on carrion (Smith, 1986; Sánchez Piñero, 1997). This family usually arrives during the later stages of decomposition when the remains are dry (Payne & King, 1970). In this study, we did not observe any strong preference of this family for a particular stage of decomposition and recorded it mostly during the D, AD and DR stages.

It is important to point out the presence of adults of Trogidae because although they have been cited by many authors (Reed, 1958; Payne & King, 1970; Johnson, 1975; Deloya *et al*., 1987; Schoenly *et al*., 1991) as members of the necrophagous fauna, they are not mentioned in the various studies performed in Argentina (Oliva, 1997; Centeno *et al*., 2002) and Brazil (Moura *et al*., 1997; Souza & Linhares, 1997; Carvalho *et al*., 2000). This study, together with those by Diéguez & Gomez (2004) and Gómez (2005), represent the only references to Trogidae in Argentina. Both adults and larvae of Trogidae are necrophagous. They are usually found in association with the last stage of decay, when most of the carrion has already been consumed (Payne, 1965). They feed mainly on keratin; the adults are often found in fur, feather and hide of dead animals. In accordance with Payne & King (1970), in this study adults of this family were observed from the first stage of decay until the end of the process.

The high abundance of Cleridae observed confirms the usual presence of this family in association with decaying animal matter (Anderson & VanLaerhoven, 1996; Oliva, 1997; Souza & Linhares, 1997). In accordance with reports from other authors, *N. rufipes* showed a strong preference for the warmer months (Tantawi *et al*., 1996; Grassberger & Frank, 2004). The Cleridae include species that are predaceous as both adults and larvae (Smith, 1986). However, *N. rufipes* is thought to exhibit feeding patterns that differ from the usual clerid habits (Anderson & VanLaerhoven, 1996). Reed (1958) observed *N. rufipes* preying on both eggs and larvae of other insects, as well as feeding on carrion. Several authors consider this species to be clearly necrophagous (Payne & King, 1970; Anderson & VanLaerhoven, 1996), but others consider it to be predaceous (Goff & Catts, 1990). Adults of *N. rufipes* were collected from the carcasses in decomposition stages D and AD. Anderson & VanLaerhoven (1996) collected this species only when the carrion was dry. By contrast, Tantawi *et al*. (1996) observed this species during the decay stage.

Staphylinidae, a family characteristic of the saprophagous community (Smith, 1986), were collected in high numbers and were present in all four seasons. This family is considered to represent the principal predator of the community, both as adults and larvae (Smith, 1986; Sanchez Piñero, 1997). Adult and immature staphylinids are predaceous on dipteran larvae (Smith, 1986). Like other authors, we observed this family in all stages of the decay process (Chapman & Sankey, 1955; Payne & King, 1970; Goff & Catts, 1990). *Creophilus maxillosus* was present in all four experiments, but was most frequent in winter, which corroborates the findings of other authors (Tantawi *et al*., 1996). This species is predaceous and dipteran larvae represent its main food resource. Tantawi *et al*. (1996) observed the presence of *C. maxillosus* only in the dry stage, but both adults and larvae were collected throughout the decay process in the present study.

The Histeridae family was represented by the genera *Saprinus* and *Hister*, both of which were collected during the warmer months. This family is predaceous, mainly on dipteran larvae (Goff & Catts, 1990; Tantawi *et al*., 1996). The predaceous behaviour of Histeridae can have a strong impact on the abundance of the Diptera community (Nuorteva, 1970). Payne & King (1970) reported this family as being present during the early stages of the decay process. Species of the genera *Saprinus* and *Hister* were collected mainly during the D and AD stages, coinciding with the peak in abundance of dipteran larvae.

Acknowledgements

This research was supported by funding from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and the Secretaria de Ciencia y Técnica (Ministry of Science and Technology, SECyT) of Argentina.

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Accepted 8 February 2011

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