



## Effect of deforestation and introduction of exotic grasses as livestock forage on the population dynamics of the cattle tick *Rhipicephalus (Boophilus) microplus* (Acari: Ixodidae) in northern Argentina



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### ABSTRACT

The effect of deforestation and the introduction of exotic grasses on the population dynamics of *Rhipicephalus (Boophilus) microplus* in northern Argentina was analysed. Biological parameters that were measured included proportion of females ovipositing, pre-oviposition period, incubation period of eggs, proportion of egg clusters hatching, larval longevity and total non-parasitic period. No significant differences were observed in proportion of females ovipositing and in pre-oviposition period between forested and grassland areas. Regarding the other parameters, in the majority of the temporal series there were no significant differences. In the cases where differences with statistical significance were detected, they were not unidirectional. The replacement of native forest by grasses can potentially increase tick abundance not by the modification of microclimatic conditions, but by increasing the tick-host encounter rate due to a higher cattle density. The hypothesis that deforestation and introduction of exotic grasses affects the non-parasitic phase of *R. microplus* in northern Argentina was not supported.

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### 1. Introduction

The cattle tick *Rhipicephalus (Boophilus) microplus* (Canestrini, 1888) is the most economically important tick species in the world. The direct effects caused by the parasitism of *R. (B.) microplus* and the pathogens transmitted to cattle constitute a major constraint on cattle production in tropical and subtropical areas (Jongejan and Uilenberg, 2004). *R. (B.) microplus* is responsible for economic losses in cattle production associated to depression on weight gain and milk production, hide damage, mortality, morbidity and control costs (acaricides, man power, maintenance of the plunge dips) (Spath et al., 1994). Moreover, the wide use of chemical acaricides for tick control has also resulted in increasing problems of multi-drug resistance for several ecto-parasiticides (Frisch, 1999; Guerrero et al., 2012).

Traditionally, *R. (B.) microplus* was described as a tick species distributed in tropical and subtropical areas of Asia and America, north-eastern Australia, New Caledonia, Madagascar, South Africa (from the coastal lowlands to the equator) and West Africa in the Ivory Coast and Benin (Estrada-Peña et al., 2006a; Madder et al., 2012), but the reinstatement of *R. (Boophilus) australis* Fuller,

1899 by Estrada-Peña et al. (2012) has produced a strong modification. The current distribution of *R. (B.) microplus* comprises America, Africa, and south-eastern Asia, while *R. (B.) australis* is present in Australia, New Caledonia and also in south-eastern Asia (Estrada-Peña et al., 2012). The consequences of the separate specific status of these two taxa have made an impact on ecological, epidemiological and economic subjects, as it was discussed in Estrada-Peña et al. (2012). For example, much of the relevant information about ecology of *R. (B.) microplus* was generated in Australia (Hitchcock, 1955; McCulloch and Lewis, 1968; Mount et al., 1991; Snowball, 1957; Sutherst and Bourne, 2006; Sutherst et al., 1978, 1988; Wilkinson, 1961; Wilkinson and Wilson, 1959; Wilkinson, 1970, among others) and then extrapolated to American and African countries, where it was used for ecological inferences and formulation of tick control strategies, but all these Australian information applied only to *R. (B.) australis*. This fact clearly imposes the necessity of new studies about the ecology of *R. (B.) microplus* in America and other parts of the world.

*R. (B.) microplus* has a one-host life cycle divided in parasitic and non-parasitic phases (Nuñez et al., 1982). During the parasitic phase, larvae, nymphs and adults feed, moult (larvae and nymphs) and mate (adults) on the same host, and the engorged females drop off the host to oviposit in the environment. The non-parasitic phase includes preovipositional development and oviposition of

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engorged females, incubation of eggs, and host-seeking of larvae. The parasitic phase occurs entirely on the host and its duration is relatively constant with a mode of approximately 23 days (Nuñez et al., 1982). Contrarily, the period of the non-parasitic phase is strongly influenced by environmental factors as climate and vegetation, and is the key phase in determining the population dynamics of *R. (B.) microplus* in a given area. Taking into account that cattle, the principal host of *R. (B.) microplus*, are a ubiquitous entity along the distribution of this tick, the constraints to the presence and abundance of *R. (B.) microplus* are related to environmental conditions to which the free-living stages are exposed. For instance, Guglielmone (1992) determined six areas with differential ecological aptitude in Argentina that sustain populations of *R. (B.) microplus* and are directly linked to climatic factors. They are as follows: (1) favourable, water deficit <200 mm,  $\leq 1$  month yearly with mean temperature <14.5 °C; (2) intermediate area A, water deficit <200 mm, 3–4 months per year with mean temperatures <14.5 °C; (3) intermediate area B, water deficit between 200 and 500 mm, <3 months per year with mean temperature <14.5 °C; (4) unfavourable area B, water deficit <500 mm, <4 months per year with mean temperatures <14.5 °C; (5) unfavourable area B, water deficit <200 mm, >4 months per year with mean temperatures <14.5 °C; (6) natural tick free zone. Thus, the dynamic of environmental conditions is the principal cause of the variation in the suitability of a given area to sustain populations of *R. (B.) microplus* on a temporal scale (Estrada-Peña, 2001; Guglielmone et al., 2003; Estrada-Peña et al., 2006b; Racelis et al., 2012).

Anthropogenic modifications of land surface due to economic activities such as agriculture or the conversion of forested areas into pastureland for cattle have altered the structure and functioning of ecosystems (Vitousek et al., 1997). The creation of pastures with the introduction of non-native grasses in tropical and subtropical areas of America represents an extensive and significant human-caused land cover change (Williams and Baruch, 2000). Particularly in Argentina, changes in land-use patterns in relation to farm productivity have produced a rapid deforestation in the Chaco forest over the last four decades, but more intensely in the post 2001 period (Gasparri and Grau, 2009; Zak et al., 2008). Progress in technology applied to crop production in Central Argentina has displaced cattle industry towards marginal zones in the north of this country (Paruelo et al., 2005). In semiarid areas belonging to the Chaco Phytogeographic Province of Argentina (as defined by Cabrera (1994)), much of the previously forested landscape has been converted into grassland for livestock forage (Boletta et al., 2006; Zak et al., 2008). One of the principal grasses used in extensive grazing systems in the north of Argentina is the non-native *Panicum maximum* Jacq (Brizuela and Cangiano, 2011). This species is a warm season-grass originated from Africa, and currently found in tropical and subtropical regions around the world, where it is so well adapted that it can overwhelm native grasses (Muir and Jank, 2004). Growth of *P. maximum* occurs at the beginning of the rainy season, and it is used for both pasture and hay.

Because habitat modification has impact on tick ecology and on the dynamics of tick-borne pathogens (Allan et al., 2010; Civitello et al., 2008; Elias et al., 2006; Garris et al., 1990; Lubelczyk et al., 2004; Mangold et al., 1994; Meyer et al., 1982; Ostfeld et al., 2006; Racelis et al., 2012; Rizzoli et al., 2009), the situation described above for northern Argentina could influence the population dynamics of *R. (B.) microplus*, with consequent implications for control strategies and epidemiology of diseases caused by *R. (B.) microplus*-borne pathogens. Therefore, a longitudinal comparative study was performed to test the hypothesis that deforestation and the introduction of exotic grasses have a significant effect on oviposition, fecundity and longevity of the free-living stages of *R. (B.) microplus* and, as a result, on its population dynamics.

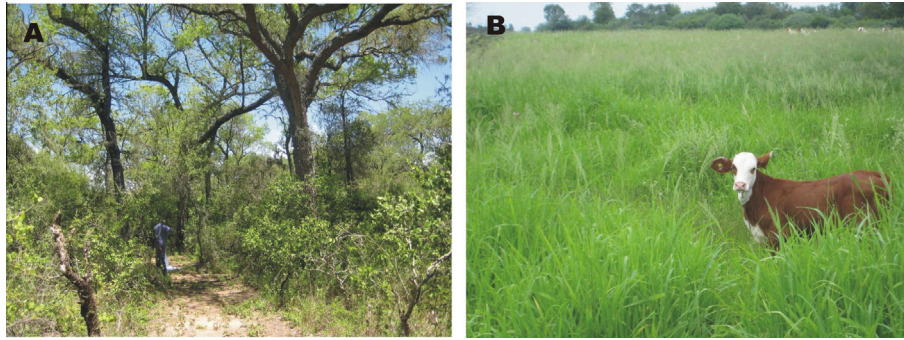
## 2. Materials and methods

The study was conducted between November 2010 and October 2012 in two localities, 400 km apart, representatives of the dry area of the Chaco Phytogeographic Province in the north of Argentina, Avia Terai (L1) (26° 40' S, 60° 46' W) in the Chaco Province, and El Tunal (L2) (25° 13' S, 64° 22' W) in the Salta Province. The area presents human disturbance as manifested by partial deforestation, livestock grazing and the introduction of exotic pastures. At both localities pairs of comparable environments were chosen as replicates: forested areas (FA) and grassland areas (GA). FA is characterized by thorny, semi-deciduous forests formed principally by *Schinopsis lorentzii* Engl., *Aspidosperma quebracho-blanco* Schltldl., *Ziziphus mistol* Griseb., *Prosopis nigra* Hieron and *Prosopis kuntzei* Harms (Fig. 1a). A variable percentage of the total area of the forest is occupied by shrubs which are originated as a consequence of overgrazing by cattle. GA was entirely covered by pastures of *P. maximum* var. *Gatton panic* throughout the period of the study (Fig. 1b). In both L1 and L2 the climate is markedly seasonal with an annual rainfall of 600–700 mm, which is concentrated from October to March (spring–summer).

Eighteen series of 20 engorged females of *R. (B.) microplus* were exposed in each of the four sites (L1GA, L1FA, L2GA, L2FA). The temporal pattern of the exposures was designed in order to obtain data from each season throughout the year. The dates of each exposure are as follow: Series 1, 16 November 2010; Series 2, 26 November 2010; Series 3, 9 February 2011; Series 4, 4 March 2011; Series 5, 9 April 2011; Series 6, 12 May 2011; Series 7, 16 June 2011; Series 8, 18 August 2011; Series 9, 15 September 2011; Series 10, 13 October 2011; Series 11, 10 November 2011; Series 12, 20 December 2011; Series 13, 4 January 2012; Series 14, 9 February 2012; Series 15, 6 March 2012; Series 16, 12 April 2012; Series 17, 11 May 2012; Series 18, 14 July 2012. Ticks were obtained from naturally parasitized cattle in the study area or by artificial infestation with unfed larvae in six- to eight-month old calves when an insufficient number of ticks were collected on the examined animals. In the field, engorged females were enclosed in stainless steel wire mesh envelopes (5 × 5 cm) (Fig. 2) placed under the grass and protected from direct solar irradiation. The mesh opening was small enough to avoid the escape of larvae. Only one female was used per envelope. As a control of the field exposures, some females were kept in the laboratory at 25 °C and 83–86% relative humidity to check for normal oviposition and egg hatching.

Climate data were recorded using HOBO® data loggers (U23-002 Pro v2) in the four exposure sites during the complete period of study. The sensors of the data loggers were placed at the ground level in the same place where the ticks were exposed. Thus, ground level temperatures and the relative humidity to which the ticks placed in the field were exposed were recorded. Temperature and relative humidity were measured daily once every hour, and they were used to calculate saturation deficit according to the formula presented by Randolph and Storey (1999). Saturation deficit is a measure of the atmosphere's drying power, which integrates temperature and relative humidity, and it is a key factor in the modulation of the life span of free-living stages of ticks (Perret et al., 2000; Randolph and Storey, 1999; Sutherst and Bourne, 2006; Teel, 1984). Consequently, saturation deficit and temperature were considered in order to compare the microclimatic conditions among the four sites. Relationships among sites for temperature and saturation deficit were compared by using a one-way analysis of variance (ANOVA) ( $P < 0.01$ ) with Tukey's post hoc test.

Biological parameters of *R. (B.) microplus* measured in each exposure included proportion of females ovipositing, pre-oviposition period (time from female exposure until beginning of oviposi-



**Fig. 1.** The two type of environments where the study was conducted. (A) Forested area; (B) grassland area.



**Fig. 2.** Stainless steel wire mesh envelopes (5 × 5 cm) employed to expose the engorged females of *Rhipicephalus (Boophilus) microplus* in both forested and grassland areas.

tion), incubation period of eggs (time from the laying of the first egg until first egg hatched), proportion of egg clusters hatching, larval longevity (time from the first egg hatched until date of death of the last larva), and total non-parasitic period (time from the exposure of the female to the date of death of the last larva). For each series, the non-parametric Mann–Whitney *U* test was employed to compare the values of the biological parameters (incubation period of eggs and larval longevity) between FA and GA within each locality, while comparison of total longevity among the four exposure sites was carried out through Kruskal–Wallis' test with Dunn's multiple comparison in order to detect statistically significant differences within (GA and FA) and among (L1 and L2) localities. The *Z*-test was used to compare proportions, and Spearman's rank correlation analysis was carried out to assess the extent of co-variation of the biological parameter between FA and GA along the year. In all cases,  $P < 0.05$  was considered statistically significant.

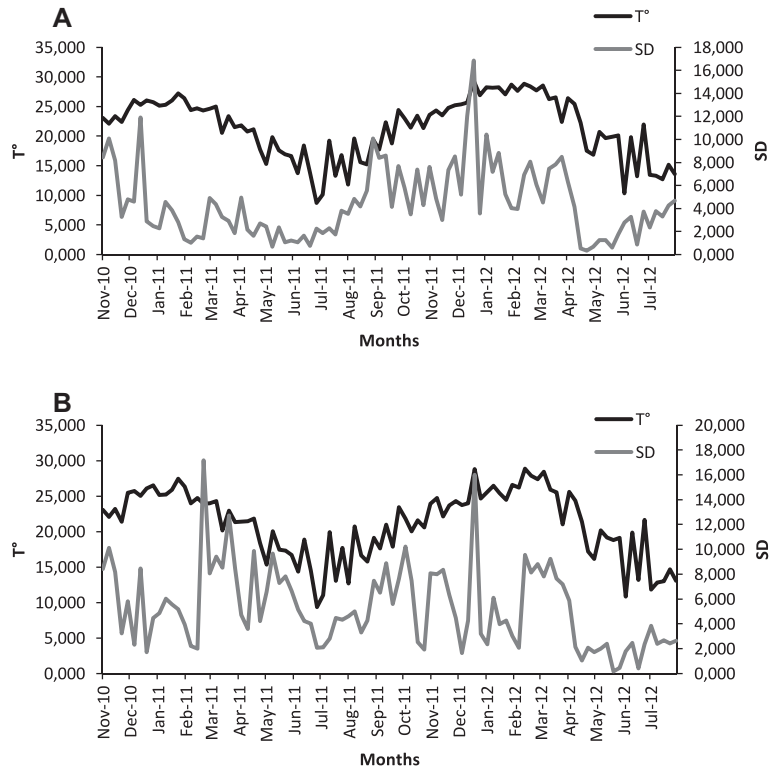
### 3. Results

Weekly mean ground-level temperatures ( $^{\circ}\text{C}$ ) and saturation deficits (mmHg) obtained for L1GA, L1FA, L2GA and L2FA during the entire study period are presented in Fig 3 (a–b) and Fig. 4 (a–b). Table 1 shows average values of temperature and saturation deficit during the period in which the free-living stages were exposed in each series. These periods were calculated from the date of tick exposure to the date of death of the last larva. For most of the series, the differences of both temperature and saturation deficit among the four sites were not significant. Differences that

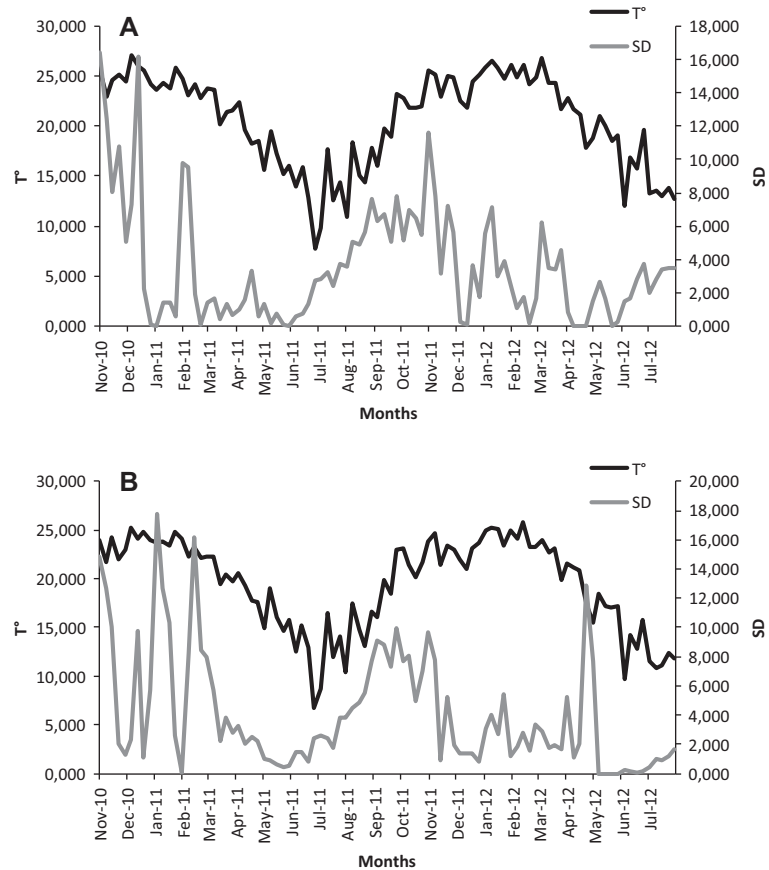
proved to be statistically significant were found in three of the 18 series for temperature and in six of the 18 series for saturation deficit (Table 1). In the case of temperature, the differences were significant among localities, but not between FA and GA within each locality. In series 3, 4, 5 and 6 (summer and autumn 2011), the saturation deficit in L1FA was significantly higher than the saturation deficit in L1GA, L2GA and L2FA, and in series 13 and 14 (summer 2012) the difference in the mean values of saturation deficit was significant between localities but not within localities when FA and GA were compared. The major difference of temperature was  $4.16\text{ }^{\circ}\text{C}$  between L1GA and L2FA in series 13, while the major difference of SD was  $5.86\text{ mmHg}$  between L1FA and L2GA in series 3.

A total of 360 engorged females of *R. (B.) microplus* were exposed in each of the four exposure sites. In all series, the proportion of females ovipositing was never inferior to 0.80, independently of the series (Table 2). The differences among sites were not significant ( $P > 0.05$ ). In the same way, no significant differences were observed in the pre-oviposition period among the four sites. The pre-oviposition period never was superior to 7 days, and this value was considered for all exposures as the pre-oviposition period in order to calculate the total longevity. The proportions of egg cluster hatching for each series and the respective statistical significances are shown in Table 3. In L1, there was no hatch observed in the series 6, 7, 8, 17 and 18, while in L2 there was no hatch observed in 6, 7, 8, 9, 17 and 18. These series corresponded to exposures of late autumn and winter. Statistically significant differences were only found in four of the 13 series in L1, and in four of the 12 series in L2 (Table 3). In some series the proportion of egg cluster hatching was higher in GA than in FA, but in others the opposite was true (Table 3).

Data on the incubation period of eggs are shown in Table 4. Three of 12 pairs of comparisons were statistically different in L1, and three of 10 in L2. The maximum difference in the mean values between GA and FA was 11.3 days in L1, and 25.9 in L2. In the four points, the incubation periods of the summer exposures were shorter than those corresponding to the remaining seasons (Table 4 and Figs. 5a, b, 6a, 6b). The results on larval longevity showed a similar pattern that the other biological parameters, because significant differences were only observed in three of the 12 series in L1, and in three of 10 series in L2 (Table 5). The maximum difference in the mean values of larval longevity between GA and FA was 40.6 days in L1, and 44.3 in L2. The longest periods of larval longevity were observed in those larvae produced by females exposed in February and March, whilst the shortest period was detected for larvae produced by females exposed in September, October, November and December. As it was observed for the proportions of egg cluster hatching, the differences were not all in the same direction. The incubation period and larval longevity were significantly greater in GA than in FA in some series, but in others they were significantly greater in FA than in GA (Tables 4 and 5).



**Fig. 3.** Weekly mean ground-level temperatures (°C) and saturation deficits (mmHg) registered during the study period in Avia Terai, Chaco Province, Argentina. (A) Grassland area; (B) forested area. T°: temperature; SD: Saturation deficit.



**Fig. 4.** Weekly mean ground-level temperatures (°C) and saturation deficits (mmHg) registered during the study period in El Tunal, Salta Province, Argentina. (A) Grassland area; (B) forested area. T°: Temperature; SD: Saturation deficit.

**Table 1**  
Average of values of temperature in °C (T°) and saturation deficit in mmHg (SD) of the period in which the free-living stages of *Rhipicephalus (Boophilus) microplus* were exposed in each series, calculated from the date of female exposition to the date of death of the last larva. L1FA: Avia Terai, forested area; L2GA: El Tunal, grassland area; L2FA: El Tunal, forested area. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	T° L1GA	T° L1FA	T° L2GA	T° L2FA	SD L1GA	SD L1FA	SD L2GA	SD L2FA
Series 1	16 Nov 2010 (SP)	25.45 <sup>a</sup>	25.50 <sup>a</sup>	24.61 <sup>a</sup>	24.09 <sup>a</sup>	4.14 <sup>a</sup>	4.76 <sup>a</sup>	5.55 <sup>a</sup>	6.46 <sup>a</sup>
Series 2	26 Nov 2010 (SP)	25.41 <sup>a</sup>	25.40 <sup>a</sup>	24.36 <sup>a</sup>	23.96 <sup>a</sup>	3.49 <sup>a</sup>	5.35 <sup>a</sup>	4.26 <sup>a</sup>	6.43 <sup>a</sup>
Series 3	9 Feb 2011 (SU)	18.90 <sup>a</sup>	19.05 <sup>a</sup>	18.09 <sup>a</sup>	17.18 <sup>a</sup>	2.27 <sup>a</sup>	7.27 <sup>b</sup>	1.41 <sup>a</sup>	3.78 <sup>a</sup>
Series 4	4 Mar 2011 (SU)	17.47 <sup>a</sup>	17.81 <sup>a</sup>	16.61 <sup>a</sup>	15.79 <sup>a</sup>	2.29 <sup>a</sup>	6.05 <sup>b</sup>	1.52 <sup>a</sup>	2.21 <sup>a</sup>
Series 5	9 Apr 2011 (AU)	16.60 <sup>a</sup>	16.99 <sup>a</sup>	15.54 <sup>a</sup>	14.88 <sup>a</sup>	3.00 <sup>a</sup>	5.27 <sup>b</sup>	2.63 <sup>a</sup>	2.84 <sup>a</sup>
Series 6	12 May 2011 (AU)	15.13 <sup>a</sup>	15.66 <sup>a</sup>	14.05 <sup>a</sup>	13.63 <sup>a</sup>	1.61 <sup>a</sup>	4.65 <sup>b</sup>	1.43 <sup>a</sup>	1.45 <sup>a</sup>
Series 7	16 Jun 2011 (AU)	14.74 <sup>a</sup>	15.44 <sup>a</sup>	13.54 <sup>a</sup>	12.99 <sup>a</sup>	2.67 <sup>a</sup>	3.69 <sup>a</sup>	3.02 <sup>a</sup>	2.85 <sup>a</sup>
Series 8	18 Aug 2011 (WI)	19.77 <sup>a</sup>	19.26 <sup>a</sup>	18.90 <sup>a</sup>	18.48 <sup>a</sup>	6.52 <sup>a</sup>	6.38 <sup>a</sup>	6.24 <sup>a</sup>	7.40 <sup>a</sup>
Series 9	15 Sep 2011 (WI)	23.37 <sup>a</sup>	22.35 <sup>a</sup>	22.76 <sup>a</sup>	21.94 <sup>a</sup>	6.41 <sup>a</sup>	6.09 <sup>a</sup>	5.66 <sup>a</sup>	5.88 <sup>a</sup>
Series 10	13 Oct 2011 (SP)	24.27 <sup>a</sup>	23.30 <sup>a</sup>	23.42 <sup>a</sup>	22.46 <sup>a</sup>	6.11 <sup>a</sup>	6.23 <sup>a</sup>	5.80 <sup>a</sup>	6.01 <sup>a</sup>
Series 11	10 Nov 2011 (SP)	24.28 <sup>a</sup>	23.53 <sup>a</sup>	23.63 <sup>a</sup>	22.57 <sup>a</sup>	7.32 <sup>a</sup>	6.27 <sup>a</sup>	5.28 <sup>a</sup>	5.01 <sup>a</sup>
Series 12	20 Dec 2011 (SP)	27.07 <sup>a</sup>	25.53 <sup>ab</sup>	24.76 <sup>bc</sup>	23.63 <sup>c</sup>	4.46 <sup>a</sup>	4.13 <sup>a</sup>	3.93 <sup>a</sup>	2.87 <sup>a</sup>
Series 13	4 Jan 2012 (SU)	27.33 <sup>a</sup>	26.01 <sup>ab</sup>	24.90 <sup>bc</sup>	23.17 <sup>c</sup>	6.81 <sup>a</sup>	6.13 <sup>a</sup>	3.19 <sup>b</sup>	2.82 <sup>b</sup>
Series 14	9 Feb 2012 (SU)	26.26 <sup>a</sup>	25.18 <sup>ab</sup>	24.03 <sup>abc</sup>	22.77 <sup>c</sup>	4.13 <sup>a</sup>	4.76 <sup>a</sup>	1.74 <sup>b</sup>	2.70 <sup>b</sup>
Series 15	6 Mar 2012 (SU)	23.61 <sup>a</sup>	22.94 <sup>a</sup>	22.10 <sup>a</sup>	21.50 <sup>a</sup>	3.30 <sup>a</sup>	3.23 <sup>a</sup>	2.36 <sup>a</sup>	2.15 <sup>a</sup>
Series 16	12 Apr 2012 (AU)	19.37 <sup>a</sup>	18.81 <sup>a</sup>	18.59 <sup>a</sup>	16.65 <sup>a</sup>	2.32 <sup>a</sup>	1.93 <sup>a</sup>	1.80 <sup>a</sup>	1.73 <sup>a</sup>
Series 17	11 May 2012 (AU)	16.45 <sup>a</sup>	16.10 <sup>a</sup>	16.01 <sup>a</sup>	14.09 <sup>a</sup>	2.60 <sup>a</sup>	1.99 <sup>a</sup>	2.24 <sup>a</sup>	1.44 <sup>a</sup>
Series 18	14 Jul 2012 (WI)	13.63 <sup>a</sup>	13.08 <sup>a</sup>	13.28 <sup>a</sup>	12.14 <sup>a</sup>	3.28 <sup>a</sup>	2.38 <sup>a</sup>	3.07 <sup>a</sup>	2.04 <sup>a</sup>

ANOVA. Numbers not sharing superscripts are significantly different ( $P < 0.05$ ). Comparisons were done among the four points of exposures for each series.

**Table 2**  
Proportion of *Rhipicephalus (Boophilus) microplus* females ovipositing. L1FA: Avia Terai, forested area; L2GA: El Tunal, grassland area; L2FA: El Tunal, forested area. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	L1GA	L1FA	L2GA	L2FA
Series 1	16 Nov 2010 (SP)	1	0.95	0.90	0.90
Series 2	26 Nov 2010 (SP)	1	0.90	1	1
Series 3	9 Feb 2011 (SU)	0.80	1	1	1
Series 4	4 Mar 2011 (SU)	0.95	1	0.80	0.90
Series 5	9 Apr 2011 (AU)	1	0.95	0.95	1
Series 6	12 May 2011 (AU)	1	0.95	1	0.95
Series 7	16 Jun 2011 (AU)	1	1	0.85	1
Series 8	18 Aug 2011 (WI)	0.95	1	1	1
Series 9	15 Sep 2011 (WI)	0.95	1	1	0.95
Series 10	13 Oct 2011 (SP)	0.80	1	0.85	0.80
Series 11	10 Nov 2011 (SP)	1	0.80	1	1
Series 12	20 Dec 2011 (SP)	0.90	1	1	1
Series 13	4 Jan 2012 (SU)	1	0.80	0.85	1
Series 14	9 Feb 2012 (SU)	0.80	0.90	1	1
Series 15	6 Mar 2012 (SU)	1	1	1	1
Series 16	12 Apr 2012 (AU)	0.85	0.85	1	1
Series 17	11 May 2012 (AU)	1	1	0.95	0.95
Series 18	14 Jul 2012 (WI)	1	1	0.95	0.90

**Table 3**  
Proportions of egg cluster hatching of *Rhipicephalus (Boophilus) microplus*. L1GA: Avia Terai, grassland area; L1FA: Avia Terai, forested area; L2GA: El Tunal, grassland area; L2FA: El Tunal, forested area. Differences between proportions were tested with the Z-test. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	L1GA	L1FA	P-value	L2GA	L2FA	P-value
Series 1	16 Nov 2010 (SP)	0.15	0.75	0.0001	0.44	0.61	0.31
Series 2	26 Nov 2010 (SP)	0.60	0.70	0.63	0.60	1	0.02
Series 3	9 Feb 2011 (SU)	1	0.95	0.31	0.95	0.95	1
Series 4	4 Mar 2011 (SU)	0.95	1	0.31	1	1	1
Series 5	9 Apr 2011 (AU)	1	0.85	0.14	0.21	0	0.03
Series 6	12 May 2011 (AU)	0	0	–	0	0	–
Series 7	16 Jun 2011 (AU)	0	0	–	0	0	–
Series 8	18 Aug 2011 (WI)	0	0	–	0	0	–
Series 9	15 Sep 2011 (WI)	0.80	0.70	0.46	0	0	–
Series 10	13 Oct 2011 (SP)	0.80	0.90	0.53	0.18	0.20	0.46
Series 11	10 Nov 2011 (SP)	0.75	0.87	0.36	0.60	0.73	0.43
Series 12	20 Dec 2011 (SP)	0.26	0.46	0.06	0.80	1	0.13
Series 13	4 Jan 2012 (SU)	0	0.72	–	0.85	0.95	0.31
Series 14	9 Feb 2012 (SU)	0.90	1	0.15	0.40	0.95	0.0001
Series 15	6 Mar 2012 (SU)	0.55	1	0.001	1	0.90	0.14
Series 16	12 Apr 2012 (AU)	0.30	0.16	0.001	0.53	0	–
Series 17	11 May 2012 (AU)	0	0	–	0	0	–
Series 18	14 Jul 2012 (WI)	0	0	–	0	0	–

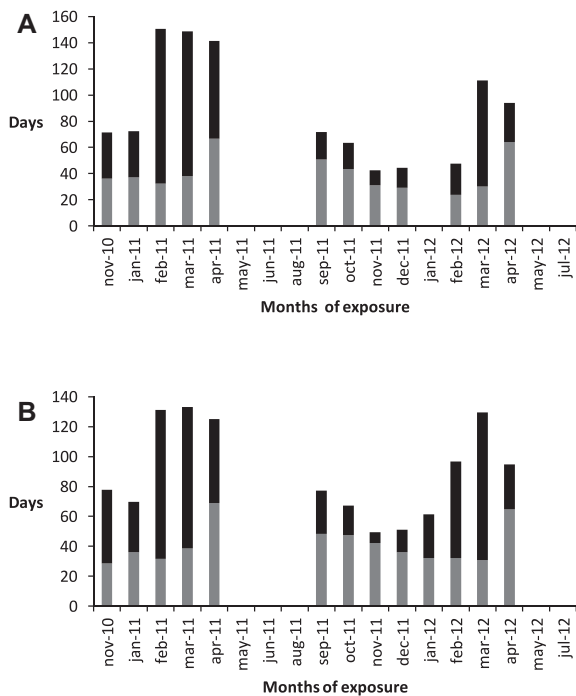
Results corresponding to total non-parasitic period are shown in Table 6. A multiple comparison of this parameter among the four sites of exposures was performed by applying a Kruskal–Wallis test. Statistically significant differences between FA and GA were only found in series 3, 5, 13 and 14 (summer and early autumn). However, the differences were not unidirectional. In series 3 and 5 the total longevity was higher in GA, but in series 13 and 14 the values were higher in FA. In some cases the differences between FA and GA arose within a locality, but not between GA and FA of different localities, as for example in series 15. Additionally, in exposures such as that of series 16, the total non-parasitic period in FA and GA was similar within a locality, but significant differences among localities in the values recorded for GA were found.

The variation of total non-parasitic period in relation to the month when females were exposed is depicted in Fig. 7. The four exposure sites showed the same seasonal pattern. The longer period was observed for the series with females exposed in summer and early autumn (series 3, 4, 5, 13, 14, 15), which implies larvae active in late summer, autumn and winter. The shortest period

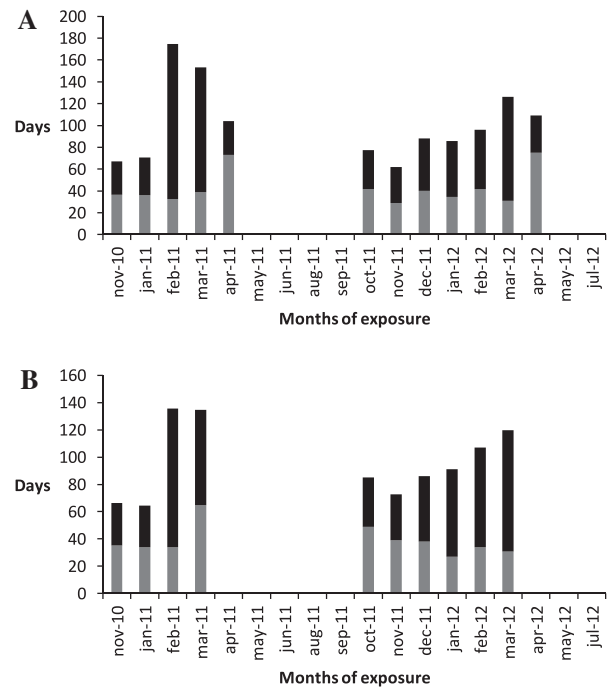
**Table 4**

Incubation period (days) of eggs of *Rhipicephalus (Boophilus) microplus*. L1GA: Avia Terai, grassland area; L1FA: Avia Terai, forested area; L2GA: El Tunal, grassland area; L2FA: El Tunal, forested area. Differences between GA and FA were tested with Mann–Whitney *U* test. Values correspond to the mean followed by the range in parenthesis. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	L1GA	L1FA	<i>P</i> -value	L2GA	L2FA	<i>P</i> -value
Series 1	16 Nov 2010 (SP)	36 (24–39)	28.6 (24–39)	0.06	36.5 (24–39)	35.2 (24–39)	0.75
Series 2	26 Nov 2010 (SP)	37 (33–39)	36 (33–39)	0.57	36.2 (34–38)	34 (32–36)	0.50
Series 3	9 Feb 2011 (SU)	32.4 (28–35)	31.7 (28–35)	0.56	32.6 (28–35)	33.8 (28–35)	0.42
Series 4	4 Mar 2011 (SU)	38.2 (38–42)	38.5 (38–42)	0.69	38.8 (38–42)	64.7 (59–74)	<0.0001
Series 5	9 Apr 2011 (AU)	66.7 (64–73)	68.8 (64–76)	0.29	73.0 (64–76)	–	–
Series 6	12 May 2011 (AU)	–	–	–	–	–	–
Series 7	16 Jun 2011 (AU)	–	–	–	–	–	–
Series 8	18 Aug 2011 (WI)	–	–	–	–	–	–
Series 9	15 Sep 2011 (WI)	50.8 (45–54)	48.2 (45–52)	0.10	–	–	–
Series 10	13 Oct 2011 (SP)	43.5 (40–49)	47.5 (40–50)	0.13	41.5 (34–49)	49.0 (34–49)	0.09
Series 11	10 Nov 2011 (SP)	31.0 (24–45)	42.3 (24–45)	0.01	29.0 (20–32)	39.1 (32–40)	0.001
Series 12	20 Dec 2011 (SP)	29.3 (24–40)	36.0 (24–40)	0.03	40.0 (40–40)	38.0 (24–40)	0.24
Series 13	4 Jan 2012 (SU)	–	32.8 (26–38)	–	34.6 (26–34)	26.9 (26–34)	0.001
Series 14	9 Feb 2012 (SU)	23.8 (18–34)	32.3 (18–34)	0.001	41.5 (34–49)	35.9 (34–49)	0.06
Series 15	6 Mar 2012 (SU)	30.1 (30–31)	30.9 (30–31)	0.64	30.9 (30–31)	30.6 (30–31)	0.62
Series 16	12 Apr 2012 (AU)	64.0 (64–64)	64.8 (64–65)	0.14	75.0 (75–75)	–	–
Series 17	11 May 2012 (AU)	–	–	–	–	–	–
Series 18	14 Jul 2012 (WI)	–	–	–	–	–	–



**Fig. 5.** Variation of eggs incubation period and larval longevity of *Rhipicephalus (Boophilus) microplus* in relation to the months in which engorged females were exposed in Avia Terai, Chaco Province, Argentina. (A) Grassland area; (B) forested area. Grey: Egg incubation period. Black: Larval longevity.



**Fig. 6.** Variation of eggs incubation period and larval longevity of *Rhipicephalus (Boophilus) microplus* in relation to the months in which engorged females were exposed in El Tunal, Salta Province, Argentina. (A) Grassland area; (B) forested area. Grey: Egg incubation period. Black: Larval longevity.

corresponded to the series with females exposed in spring (series 1, 2, 10, 11 and 12), whose progenies were active in early and mid-summer.

Spearman's rank correlation among any seasonal variation in the biological parameter between FA and GA was significant for both localities (L1: incubation of eggs  $r_s = 0.81$  and  $P = 0.001$ , larval longevity  $r_s = 0.92$  and  $P < 0.0001$ , total non-parasitic period  $r_s = 0.95$  and  $P < 0.0001$ ; L2: incubation of eggs  $r_s = 0.76$  and  $P = 0.005$ , larval longevity  $r_s = 0.92$  and  $P < 0.001$ , total non-parasitic period  $r_s = 0.96$  and  $P < 0.0001$ ). These results indicate that these biological parameters co-vary in a similar way during the year in both FA and GA (Figs. 5–7).

#### 4. Discussion

The hypothesis that deforestation and introduction of exotic grasses significantly affects the non-parasitic phase of *R. (B.) microplus* was not supported, at least under the observed microclimatic conditions. There were not differences among the exposure sites when comparing proportion of females ovipositing and pre-oviposition period. Regarding the other parameters (incubation period of eggs, proportion of egg clusters hatching, larval longevity and total non-parasitic period), in the majority of the series there were no significant differences. In the cases where differences with

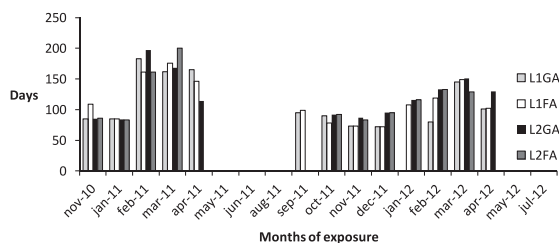
**Table 5**  
Larval longevity (days) of *Rhipicephalus (Boophilus) microplus*. L1GA: Avia Terai, grassland area; L1FA: Avia Terai, forested area; L2GA: El Tunal, grassland area; L2FA: El Tunal, forested area. Differences between GA and FA were tested with Mann–Whitney *U* test. Values correspond to the mean followed by the range in parenthesis. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	L1GA	L1FA	<i>P</i> -value	L2GA	L2FA	<i>P</i> -value
Series 1	16 Nov 2010 (SP)	35.3 (28–39)	49.3 (16–63)	0.06	30.7 (28–39)	31.2 (28–40)	0.65
Series 2	26 Nov 2010 (SP)	35.3 (28–39)	33.8 (27–39)	0.58	34.6 (28–39)	30.4 (28–40)	0.21
Series 3	9 Feb 2011 (SU)	118.3 (107–141)	99.6 (64–119)	0.002	142.2 (120–155)	101.8 (44–119)	<0.0001
Series 4	4 Mar 2011 (SU)	110.3 (64–113)	94.7 (36–127)	0.06	114.4 (114–119)	70.1 (62–119)	<0.0001
Series 5	9 Apr 2011 (AU)	74.6 (63–113)	56.2 (36–63)	<0.0001	31 (31–31)	–	–
Series 6	12 May 2011 (AU)	–	–	–	–	–	–
Series 7	16 Jun 2011 (AU)	–	–	–	–	–	–
Series 8	18 Aug 2011 (WI)	–	–	–	–	–	–
Series 9	15 Sep 2011 (WI)	20.8 (15–34)	29.1 (16–36)	0.09	–	–	–
Series 10	13 Oct 2011 (SP)	20.0 (15–34)	19.7 (15–21)	0.49	36 (36–36)	36 (36–36)	1
Series 11	10 Nov 2011 (SP)	11.4 (6–21)	7.1 (6–21)	0.48	32.8 (11–48)	33.5 (11–36)	0.29
Series 12	20 Dec 2011 (SP)	15 (15–15)	15 (15–15)	1	48 (48–48)	48 (48–48)	1
Series 13	4 Jan 2012 (SU)	–	29.1 (13–63)	–	51.2 (13–75)	64.2 (48–75)	0.06
Series 14	9 Feb 2012 (SU)	23.8 (21–39)	64.4 (45–78)	<0.0001	54.5 (12–77)	73.1 (54–77)	0.005
Series 15	6 Mar 2012 (SU)	80.9 (27–107)	98.7 (77–111)	0.08	95.5 (50–113)	89 (81–91)	0.16
Series 16	12 Apr 2012 (AU)	30 (30–30)	30 (30–30)	1	34 (32–48)	–	–
Series 17	11 May 2012 (AU)	–	–	–	–	–	–
Series 18	14 Jul 2012 (WI)	–	–	–	–	–	–

**Table 6**  
Total non-parasitic period (time from the exposure of the female to the date of death of the last larva) of *Rhipicephalus (Boophilus) microplus*. L1GA: Avia Terai, grassland area; L1FA: Avia Terai, forested area; L2GA: El Tunal, grassland area; L2FA: El Tunal, forested area. Values correspond to the mean followed by the maximum value in parenthesis. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	L1GA	L1FA	L2GA	L2FA
Series 1	16 Nov 2010 (SP)	83.33 <sup>a</sup> (85) (SU)	92.71 <sup>a</sup> (109) (SU)	82.10 <sup>a</sup> (85) (SU)	82.08 <sup>a</sup> (86) (SU)
Series 2	26 Nov 2010 (SP)	82.43 <sup>a</sup> (85) (SU)	81.85 <sup>a</sup> (85) (SU)	82.60 <sup>a</sup> (84) (SU)	79.00 <sup>a</sup> (83) (SU)
Series 3	9 Feb 2011 (SU)	165.32 <sup>a</sup> (183) (WI)	146.40 <sup>b</sup> (161) (WI)	188.62 <sup>c</sup> (197) (WI)	149.11 <sup>b</sup> (161) (WI)
Series 4	4 Mar 2011 (SU)	158.27 <sup>ab</sup> (162) (WI)	146.69 <sup>b</sup> (176) (WI)	164.03 <sup>a</sup> (168) (WI)	166.2 <sup>a</sup> (200) (SP)
Series 5	9 Apr 2011 (AU)	168.5 <sup>a</sup> (165) (SP)	139.10 <sup>b</sup> (146) (SP)	106.51 <sup>c</sup> (114) (WI)	–
Series 6	12 May 2011 (AU)	–	–	–	–
Series 7	16 Jun 2011 (AU)	–	–	–	–
Series 8	18 Aug 2011 (WI)	–	–	–	–
Series 9	15 Sep 2011 (WI)	90.42 <sup>a</sup> (95) (SP)	92.30 <sup>a</sup> (95) (SP)	–	–
Series 10	13 Oct 2011 (SP)	74.20 <sup>a</sup> (90) (SU)	69.25 <sup>a</sup> (78) (SU)	81.10 <sup>a</sup> (92) (SU)	80.23 <sup>a</sup> (92) (SU)
Series 11	10 Nov 2011 (SP)	61.26 <sup>a</sup> (73) (SU)	66.00 <sup>a</sup> (73) (SU)	76.87 <sup>a</sup> (87) (SU)	74.71 <sup>a</sup> (83) (SU)
Series 12	20 Dec 2011 (SP)	72.00 <sup>a</sup> (72) (SU)	72.00 <sup>a</sup> (72) (SU)	95.00 <sup>b</sup> (95) (SU)	95.00 <sup>b</sup> (95) (SU)
Series 13	4 Jan 2012 (SU)	–	69.14 <sup>a</sup> (108) (AU)	95.11 <sup>b</sup> (116) (AU)	100.26 <sup>b</sup> (116) (AU)
Series 14	9 Feb 2012 (SU)	59.76 <sup>a</sup> (80) (AU)	112.41 <sup>bc</sup> (119) (AU)	104.37 <sup>b</sup> (133) (WI)	121.71 <sup>c</sup> (133) (WI)
Series 15	6 Mar 2012 (SU)	118.35 <sup>a</sup> (145) (WI)	135.70 <sup>b</sup> (149) (WI)	144.50 <sup>b</sup> (151) (WI)	109.2 <sup>a</sup> (129) (WI)
Series 16	12 Apr 2012 (AU)	101 <sup>a</sup> (101) (WI)	99.78 <sup>a</sup> (102) (WI)	130 <sup>b</sup> (130) (SP)	–
Series 17	11 May 2012 (AU)	–	–	–	–
Series 18	14 Jul 2012 (WI)	–	–	–	–

Kruskal–Wallis test. Numbers not sharing superscripts are significantly different (*P* < 0.05). Comparisons were done among the four points of exposures for each series.



**Fig. 7.** Variation of total non-parasitic period (time from the exposure of the female to the date of death of the last larva) of *Rhipicephalus (Boophilus) microplus* in relation to the months in which engorged females were exposed. L1GA: Avia Terai, grassland area; L1FA: Avia Terai, forested area; L2GA: El Tunal, grassland area; L2FA: El Tunal, forested area.

statistical significance were detected, they were not unidirectional. In some series the values were higher in FA than in GA, but in others the values were higher in GA than in FA. Multiple comparisons of total non-parasitic period showed for some series a significant difference between L1 and L2 but not between FA and GA within

a locality. Additionally, all biological parameters of the *R. (B.) microplus* recorded in this work vary in the same way throughout the year, regardless of locality or habitat type (forest or grassland). A positive and significant correlation among the seasonal variations of each biological parameter between FA and GA shows that the habitat modification does not have an influence on the seasonal dynamics of the free-living stages of this tick.

Proportion of females ovipositing and pre-oviposition period were relatively constant throughout the study period. However, the results on the pre-oviposition period should be taken carefully because all engorged ticks were obtained from the same locality and then transported to the four points of exposures in a period of one or 2 days after collection. Consequently, the temperature and humidity conditions to which the ticks were exposed during the transport could have influence on the pre-oviposition period. The principal parameters which determine variation in the total non-parasitic period are egg hatchability, incubation period of eggs and larval longevity. In the four sites, incubation period of eggs decreased from late winter to summer and then increased from late summer to late autumn. When compared with other ecological

studies on the non-parasitic phase of *R. (B.) microplus* in sub-tropical and temperate localities where climate is also markedly seasonal, the seasonal pattern of incubation period of eggs was very similar to those observed in other areas of the Southern Cone of South America in Argentina, Uruguay and Paraguay (Brizuela et al., 1996; Cardozo et al., 1984; Ivancovich, 1975; Ivancovich et al., 1984; Nari et al., 1979), and in localities of USA that represent the Northern extreme range of the *R. (B.) microplus* distribution (Davey et al., 1994). A major difference concerns to the total failure of eggs to hatch in winter, which correspond to the females exposed in May, June, July and August. This cessation of the life cycle of *R. (B.) microplus* in winter was recorded in north-western Argentina (Ivancovich et al., 1984) and in Uruguay (Cardozo et al., 1984; Nari et al., 1979), but not in northeastern Argentina (Ivancovich et al., 1984), Paraguay (Brizuela et al., 1996) and USA (Davey et al., 1994). Although it was demonstrated that *R. (B.) microplus* eggs failed to hatch under prolonged exposure to low temperatures (Bennett, 1974; Davey and Cooksey, 1989), future studies are needed to determine the temperature range for which the eggs are viable under natural conditions in northwestern Argentina. With respect to larval longevity, it was higher in those larvae born in late summer and early autumn than in larvae born in spring or early summer in the four sites, coinciding with the results of previous studies in northwestern Argentina (Ivancovich 1975), Paraguay (Brizuela et al., 1996), Uruguay (Cardozo et al., 1984) and USA (Davey et al., 1994).

Climate determines the favourability of the environment for the development and survival of the free-living stages of ticks and also the temporal extension in which conditions are favourable (Sutherst et al., 1988). When data obtained in the four exposure sites are analyzed jointly, it is possible to conclude that the microclimatic differences associated with the replacement of forests for *P. maximum* grasses (see Table 1) are not enough to significantly alter the dynamics of the free-living stages of *R. (B.) microplus* in northern Argentina. These results are not in accordance with those obtained in previous studies that showed either positive (Elias et al., 2006; Lubelczyk et al., 2004; Racelis et al., 2012) or negative (Civitello et al., 2008) effects of invasive plants on the quality of tick's habitat. The introduction of *P. maximum* grasses does not have a significant effect (positive or negative) on the life cycle of *R. (B.) microplus* in northern Argentina. In view of this, a key factor modulating the size of *R. (B.) microplus* populations should be cattle density. Non-native species influence the population dynamics of arthropod vectors by two mechanistic pathways: (1) altering distribution, abundance or diversity of hosts; (2) altering climatic conditions which can alter vector survival (Allan et al., 2010). According with the results obtained during this study, the replacement of native forest by *P. maximum* grasses can potentially increase tick abundance not by the modification of microclimatic conditions, but by increasing the tick-host encounter rate because pastures of *P. maximum* allow a higher stocking rate (cows/ha) than the forested areas. Similar conclusions were reached by Guglielmo (1992). Thus, the lack of significant effect on the free-living stages of *R. (B.) microplus* by the introduction of *P. maximum* grasses coupled with the increase of host density (cow/ha) can result in a build-up of *R. (B.) microplus* populations.

This study highlights the effect of habitat modification on the ecology of *R. (B.) microplus* in the southernmost region of its distribution range in South America, although further researches on the relationship between microclimatic variables and development and survival of *R. (B.) microplus* ticks should be carried in the study area. Finally, these results provide empirical data to design tick control strategies. As an alternative or complement to the use of chemical acaricides in integrated control programs, tick populations can be controlled by denying host to free-living by means of pasture spelling (Norton et al., 1983; Sutherst et al., 1979). Thus,

questing larvae of *R. (B.) microplus* die by starvation and desiccation. The total non-parasitic period constitutes basic information for planning tick control by pasture spelling. The shortest period of survival of free-living stages in summer compared to other seasons, indicates that a temporal destocking pasture in late spring or summer is, from a temporal point of view, more practical. According to the results obtained for northern Argentina (see the maximum values of total non-parasitic period in Table 6), a 14-week spelling period, starting in November or December (late spring and early summer), may be sufficient to achieve a tick-free paddock. However, an important constraint to pasture spelling is that *P. maximum* thrives on summer rainfall when temperatures are optimal for its growth. Thus, the appropriate period for pasture spelling coincides with the months of higher productivity of *P. maximum* grasses. A possible option is to use the spelled paddocks for hay production during the period considered in the spelling scheme, but empirical data are needed to assess the effectiveness of this method.

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### References

- Allan, B.F., Dutra, H.P., Goessling, L.S., Barnett, K., Chase, J.M., Marquis, R.J., Pang, G., Storch, G.A., Thach, R.E., Orrock, J.L., 2010. Invasive honeysuckle eradication reduces tick-borne disease by altering host dynamics. *Proceeding of the National Academy of Science, USA* 43, 18523–18527.
- Bennett, G.F., 1974. Oviposition of *Boophilus microplus* (Canestrini) (Acaridae: Ixodidae). II. Influence of temperature, humidity and light. *Acarologia* 16, 250–257.
- Boletta, P.E., Ravelo, A.C., Planchuelo, A.M., Grilli, M., 2006. Assessing deforestation in the Argentine Chaco. *Forest Ecology and Management* 228, 108–114.
- Brizuela, M.A., Cangiano, C.C., 2011. Especies forrajeras cultivadas en Argentina. In: Cangiano, C.A., Brizuela, M.A. (Eds.), *Producción animal en pastoreo*, Ediciones del Instituto Nacional de Tecnología Agropecuaria, pp. 31–55.
- Brizuela, C.M., Ortellano, C.A., Sanchez, T.I., Osorio, O., Walker, A.R., 1996. Formulation of integrated control of *Boophilus microplus* in Paraguay: analysis of natural infestations. *Veterinary Parasitology* 63, 95–108.
- Cabrera, A.L., 1994. *Enciclopedia Argentina de Agricultura y Jardinería. Fascículo 1. Regiones fitogeográficas argentinas. Tomo II*. Editorial ACME, Buenos Aires, 85 pp.
- Cardozo, H., Nari, A., Franchi, M., López, A., Donatti, N., 1984. Estudio sobre la ecología del *Boophilus microplus* en tres áreas enzoóticas del Uruguay. *Veterinaria (Montevideo)* 20, 4–10.
- Civitello, D.J., Flory, S.L., Clay, K., 2008. Exotic grass invasion reduces survival of *Amblyomma americanum* and *Dermacentor variabilis* ticks (Acari: Ixodidae). *Journal of Medical Entomology* 45, 867–872.
- Davey, R.B., Cooksey, L.M., 1989. Effects of prolonged exposure at low temperature on *Boophilus microplus* (Acari: Ixodidae). *Journal of Medical Entomology* 26, 407–410.
- Davey, R.B., Pound, J.M., Cooksey, L.M., 1994. Comparative reproduction and nonparasitic development of *Boophilus microplus* and hybridized *Boophilus* ticks (Acari: Ixodidae) under natural field conditions in subtropical South Texas. *Experimental and Applied Acarology* 18, 185–200.
- Elias, S.P., Lubelczyk, C.B., Rand, P.W., Lacombe, E.H., Holman, M.S., Smith, R.P., 2006. Deer browse resistant exotic-invasive understory: an indicator of elevated human risk of exposure to *Ixodes scapularis* (Acari: Ixodidae) in southern coastal Maine woodlands. *Journal of Medical Entomology* 43, 1142–1152.
- Estrada-Peña, A., 2001. Climate warming and changes in habitat suitability for *Boophilus microplus* (Acari: Ixodidae) in Central America. *Journal of Parasitology* 87, 978–987.
- Estrada-Peña, A., Bouattour, A., Camicas, J.L., Guglielmo, A.A., Horak, I., Jongejan, F., Latif, A., Pegram, R., Walker, A.R., 2006a. The known distribution and ecological preferences of the tick subgenus *Boophilus* (Acari: Ixodidae) in Africa and Latin America. *Experimental and Applied Acarology* 38, 219–235.
- Estrada-Peña, A., Corson, M., Venzal, J.M., Mangold, A.J., Guglielmo, A.A., 2006b. Changes in climate and habitat suitability for the cattle tick *Boophilus microplus*



- in its southern Neotropical distribution range. *Journal of Vector Ecology* 31, 158–167.
- Estrada-Peña, A., Venzal, J.M., Nava, S., Mangold, A.J., Guglielmone, A.A., Labruna, M.B., de la Fuente, J., 2012. Reinstatement of *Rhipicephalus (Boophilus) australis* (Acari: Ixodidae) with redescription of the adult and larval stages. *Journal of Medical Entomology* 49, 794–802.
- Frisch, J.E., 1999. Towards a permanent solution for controlling cattle ticks. *International Journal for Parasitology* 29, 57–71.
- Garris, G.I., Popham, T.W., Zimmerman, R.H., 1990. *Boophilus microplus* (Acari: Ixodidae): oviposition, egg viability, and larval longevity in grass and wooded environments of Puerto Rico. *Environmental Entomology* 19, 66–75.
- Gasparri, N.I., Grau, H.R., 2009. Deforestation and fragmentation of Chaco dry forest in NW Argentina (1972–2007). *Forest Ecology and Management* 258, 913–921.
- Guerrero, F.D., Lovis, L., Martins, J.R., 2012. Acaricide resistance mechanisms in *Rhipicephalus (Boophilus) microplus*. *Revista Brasileira de Parasitologia Veterinaria* 21, 1–6.
- Guglielmone, A.A., 1992. The level of infestation with the vector of cattle babesiosis in Argentina. *Memorias do Instituto Oswaldo Cruz* 87, Suppl. III, 133–137.
- Guglielmone, A.A., Giorgi, R., Sodiro, A., Gay, R., Canal, A., Mangold, A.J., Estrada-Peña, A., 2003. Aptitud ecológica de los departamentos de Castellanos y Las Colonias, Santa Fe, para sustentar hipotéticas poblaciones de la garrapata común del vacuno, *Boophilus microplus* (Acari: Ixodidae). *Revista de Investigaciones Agropecuarias* 32, 75–92.
- Harley, K.L.S., 1966. Studies on the survival of the non-parasitic stages of the cattle tick *Boophilus microplus* in three climatically dissimilar districts of north Queensland. *Australian Journal of Agricultural Research* 17, 387–410.
- Hitchcock, L.F., 1955. Studies on the non-parasitic stages of the cattle tick, *Boophilus microplus* (Canestrini) (Acarina: Ixodidae). *Australian Journal of Zoology* 3, 295–311.
- Ivancovich, J.C., 1975. Bioecología de la garrapata del ganado *Boophilus microplus* (Canestrini, 1888). *Revista de Investigaciones Agropecuarias* 12, 1–54.
- Ivancovich, J.C., Braithwaite, G.B., Barnett, S.F., 1984. Comportamiento de los estados no-parasitarios de la garrapata del Ganado- *Boophilus microplus* (Canestrini). II-El Sombrerito (provincial de Corrientes). III-Bartolomé de las Casas (provincial de Formosa). IV. Siete diferentes localidades. *Boletín de la Estación Experimental Regional Agropecuaria Presidente Roque Sáenz Peña, Instituto Nacional de Tecnología Agropecuaria* 88, 4–109.
- Jongejan, F., Uilenberg, G., 2004. The global importance of ticks. *Parasitology* 129, 1–12.
- Lubelczyk, C.B., Elias, S.P., Rand, P.W., Holman, M.S., Lacombe, E.H., Smith, J.R.P., 2004. Habitat associations of *Ixodes scapularis* (Acari: Ixodidae) in Maine. *Environmental Entomology* 33, 900–906.
- Madder, M., Adehan, S., de Deken, R., Adehan, R., Lokossou, R., 2012. New foci of *Rhipicephalus microplus* in West Africa. *Experimental and Applied Acarology* 56, 385–390.
- Mangold, A.J., Aguirre, D.H., Gaido, A.B., Guglielmone, A.A., 1994. Seasonal variation of ticks (Ixodidae) in *Bos taurus* x *Bos indicus* cattle under rotational grazing in forested and deforested habitats in northwestern Argentina. *Veterinary Parasitology* 54, 289–395.
- McCulloch, R.N., Lewis, I.J., 1968. Ecological studies of the cattle tick, *Boophilus microplus*, in the north coast district of new South Wales. *Australian Journal of Agricultural Research* 19, 689–710.
- Meyer, J.A., Lancaster, J.L., Simco, J.S., 1982. Comparison of habitat modification, animal control, and standard spraying for control of the lone star tick. *Journal of Economic Entomology* 75, 524–529.
- Mount, G.A., Haile, D.G., Davey, R.B., Cooksey, L.M., 1991. Computer simulation of *Boophilus* cattle tick (Acari: Ixodidae) populations dynamics. *Journal of Medical Entomology* 28, 223–240.
- Muir, J., Jank, L., 2004. Guineagrass. In: Sollenberger, L.E., Moser, L., Burson, L. (Eds.), *Warm-season (C4) Grasses*, Madison, Agronomy monograph, 45, American Society of Agronomy – Crop Science Society of America- Soil Science Society of America, pp. 589–621.
- Nari, A., Cardozo, H., Berdié, J., Canabez, F., Bawden, R., 1979. Estudio preliminar sobre la ecología de *Boophilus microplus* (Can) en Uruguay. Ciclo no parasitario en un área considerada poco apta para el desarrollo. *Veterinaria (Montevideo)* 15, 25–31.
- Norton, G.A., Sutherst, R.W., Maywald, G.F., 1983. A framework for integrating control methods against the cattle tick, *Boophilus microplus* in Australia. *Journal of Applied Ecology* 20, 489–505.
- Nuñez, J.L., Muñoz, Cobeñas, M., Moltedo, H., 1982. *Boophilus microplus*: la garrapata común del ganado vacuno. Hemisferio Sur, Buenos Aires, Argentina, 184 pp.
- Ostfeld, R.S., Canham, C.D., Oggenfuss, K., Winchcombe, R.J., Keesing, F., 2006. Climate, deer, rodents and acorns as determinants of variation in Lyme-disease risk. *PLoS Biology* 4, 1058–1068.
- Paruelo, J.M., Guerschman, J.P., Verón, S.R., 2005. Expansión agrícola y cambios en el uso del suelo. *Ciencia Hoy* 15, 14–23.
- Perret, J.L., Guigoz, E., Rais, O., Gern, L., 2000. Influence of saturation deficit and temperature on *Ixodes ricinus* tick questing activity in a Lyme borreliosis-endemic area (Switzerland). *Parasitology Research* 86, 554–557.
- Racelis, A.E., Davey, R.B., Goolsby, J.A., Pérez de León, A.A., Varner, K., Duhaime, R., 2012. Facilitative ecological interactions between invasive species: *Arundo donax* stands as favorable habitat for cattle ticks (Acari: Ixodidae) along the US-Mexico border. *Journal of Medical Entomology* 49, 410–417.
- Randolph, S.E., Storey, K., 1999. Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. *Journal of Medical Entomology* 36, 741–748.
- Rizzoli, A., Hauffe, H.C., Tagliapietra, V., Neteler, M., Rosà, R., 2009. Forest structure and roe deer abundance predict tick-borne encephalitis risk in Italy. *PLoS One* 4, e4336.
- Snowball, G.J., 1957. Ecological observations on the cattle tick, *Boophilus microplus* (Canestrini). *Australian Journal of Agricultural Research* 8, 394–413.
- Spath, E.J.A., Guglielmone, A.A., Signorini, A.R., Mangold, A.J., 1994. Estimación de las pérdidas económicas directas producidas por la garrapata *Boophilus microplus* y las enfermedades asociadas en la Argentina. 1ra parte. *Therios* 23, 341–360.
- Sutherst, R.W., Bourne, A.S., 2006. The effect of desiccation and low temperature on the viability of eggs and emerging larvae of the tick, *Rhipicephalus (Boophilus) microplus* (Canestrini) (Ixodidae). *International Journal for Parasitology* 36, 193–200.
- Sutherst, R.W., Wharton, R.H., Utech, K.B.W., 1978. *Guide to studies on tick ecology. Commonwealth scientific and industrial research organization. Australia. Division of Entomology, Technical Paper No. 14, pp. 55*
- Sutherst, R.W., Norton, G.A., Barlow, N.D., Conway, G.R., Birley, M., Comins, N.H., 1979. An analysis of management strategies for cattle tick (*Boophilus microplus*) control in Australia. *Journal of Applied Ecology* 16, 359–382.
- Sutherst, R.W., Sutherland, I.D., Bourne, A.S., Maywald, G.F., Stegeman, D.A., 1988. Ecology of the cattle tick (*Boophilus microplus*) in Subtropical Australia. I. Introduction and free-living stages. *Australian Journal of Agricultural Research* 39, 285–297.
- Teel, P.D., 1984. Effect of saturation deficit on eggs of *Boophilus annulatus* and *B. microplus* (Acari: Ixodidae). *Annals of the Entomological Society of America* 77, 65–68.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of earth's ecosystems. *Science* 277, 494–499.
- Wilkinson, P.R., 1961. The use of sampling methods in studies of the distribution of larvae of *Boophilus microplus* on pastures. *Australian Journal of Zoology* 9, 752–783.
- Wilkinson, P.R., 1970. Factors affecting the distribution and abundance of the cattle tick in Australia: observations and hypotheses. *Acarologia* 12, 492–508.
- Wilkinson, P.R., Wilson, J.T., 1959. Survival of cattle ticks in central Queensland pastures. *Australian Journal of Agricultural Research* 10, 129–143.
- Williams, D.G., Baruch, Z., 2000. African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biological Invasions* 2, 123–140.
- Zak, M.R., Cabido, M., Cáceres, D., Díaz, S., 2008. What drives accelerated land cover change in central Argentina? Synergistic consequences of climatic, socioeconomic, and technological factors. *Environmental Management* 42, 181–189.