



## Non-parasitic life cycle of the cattle tick *Rhipicephalus (Boophilus) microplus* in *Panicum maximum* pastures in northern Argentina



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### ABSTRACT

The aim of this work was to study the non-parasitic phase of the *Rhipicephalus microplus* life cycle in *Panicum maximum* grasses from northern Argentina, in order to provide ecological information for designing methods of tick control. Four localities were chosen as replicates. The biological parameters measured were proportion of females ovipositing, the pre-oviposition period, the proportion of egg clusters hatching, the incubation period of eggs, larval longevity, and the total non-parasitic period (time from the exposure of the female to the date of death of the last larva) (TNPP). The following general trends were observed: I) a longer TNPP occurred when female ticks were exposed in mid- and late summer and early spring; II) the shortest TNPP occurred when female ticks were exposed from late winter to late spring; III) larvae that were active in early and mid-summer had the shortest longevity; IV) incubation periods of eggs, which originated from females exposed in late summer, early autumn and mid-spring, were longer than the incubation period of eggs produced by females exposed in late spring and early summer; V) eggs did not hatch when the engorged females were exposed in the pastures in mid- and late autumn and winter. The spelling period of the *P. maximum* grasses that is needed to ensure total control of *R. microplus* consists of 19–20 weeks if the spelling starts in late spring and early summer, and 27–28 weeks if the spelling begins in mid- and late summer or in autumn.

### 1. Introduction

*Rhipicephalus (Boophilus) microplus* is the most important tick species affecting cattle in the world. The effects caused by the parasitism of *R. (B.) microplus* ticks and the haemoparasites they transmit constitute a major constraint on cattle production in tropical and subtropical areas (Jongejan and Uilenberg, 2004). The deleterious effects on cattle production caused by the parasitism of *R. (B.) microplus* are associated with a reduction in weight gain and milk production, hide damage, mortality, morbidity, control costs (acaricides, man power, maintaining plunge dips) and also contribute to the development of screwworm myiasis in cattle (Späth et al., 1994; Reck et al., 2014b). An additional and significant problem associated with chemically controlling *R. (B.) microplus* is the spread of tick populations resistant to several of the available acaricides, to the accumulation of chemical residues in meat or milk and the contamination by release of chemical compounds to the environment (Frisch, 1999; George et al., 2008; Nari Henrioud, 2011; Guerrero et al., 2012; Reck et al., 2014a).

Much of the knowledge about ecology of *R. (B.) microplus* was

generated in Australia (Hitchcock, 1955; Snowball, 1957; Wilkinson and Wilson, 1959; Wilkinson, 1961; Harley, 1966; McCulloch and Lewis, 1968; Wilkinson, 1970; Sutherst et al., 1978, 1988; Mount et al., 1991; Sutherst and Bourne, 2006, among others) and then extrapolated and applied to American and African countries, where it was used for ecological inferences and the formulation of tick control strategies. But currently, after the reinstatement of *Rhipicephalus (Boophilus) australis* by Estrada-Peña et al. (2012), it is recognized that the distribution of *R. (B.) microplus* comprises America, Africa, and south-eastern Asia but not Australia, where the tick species that is present is *R. (B.) australis* (Estrada-Peña et al., 2012; Burger et al., 2014). Therefore, all information obtained in Australia applies to *R. (B.) australis* but not to *R. (B.) microplus*. Second, progress in the technology of crop production in Central Argentina has displaced the cattle industry towards the north of the country (Paruelo et al., 2005), where 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 exotic grass species extensively used in grazing systems in the north of Argentina is *Panicum maximum* (Brizuela and Cangiano, 2011), which provide a

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more suitable environment for *R. (B.) microplus* than the forested areas because pastures of *P. maximum* allow a higher stocking rate (cows/ha), increasing in this way the tick-host encounter rate (Nava et al., 2013).

*Rhipicephalus microplus* has a one-host life cycle divided in parasitic and non-parasitic phases (Nuñez et al., 1982). The parasitic phase includes larvae, nymphs and adults feeding, moulting (larvae and nymphs) and mating (adults) on the same host, after which the engorged females drop off the host to oviposit in the environment. The non-parasitic phase comprises preovipositional development and oviposition of engorged females, incubation of eggs, and host-seeking larvae. The duration of the parasitic phase is relatively constant with a mode of approximately 23 days (Nuñez et al., 1982), but not the period of the non-parasitic phase which is strongly influenced by environmental factors such as climate and vegetation. This phase of the life cycle determines the number of annual generations and the tick population abundance.

Knowledge of the dynamics of non-parasitic phase of the *R. (B.) microplus* life cycle in a given area is instrumental in designing methods of tick control by pasture spelling or based on the strategic application of chemical acaricides. Because the use of *P. maximum* grasses in cattle production systems is widespread in areas of northern Argentina where *R. (B.) microplus* prevails, the aim of this work was to perform a study on the dynamics of the non-parasitic phase of *R. (B.) microplus* life cycle in *P. maximum* grasses across an area of northern Argentina where this grass species is extensively used in cattle grazing systems, in order to

provide ecological information which could be useful for designing methods of tick control based on a minimum use of chemical acaricides.

## 2. Materials and methods

The fieldwork was conducted between December 2009 and July 2012 within the dry area of the Chaco Biogeographic Province sensu Morrone (2006) (= Chaco Seco sensu Burkart et al. (1999)) in northern Argentina (Fig. 1). Four localities were chosen as replicates: I) Avia Terai (AT) (26° 40' S, 60° 46' W), Chaco Province; II) Los Pirpintos (LP) (26° 06' S, 62° 08' W), Santiago del Estero Province; III) Ceibalito (CE) (25° 07' S, 64° 17' W), Salta Province; and IV) Pozo Hondo (PH) (27° 03' S, 64° 35' W), Santiago del Estero Province. The paddocks, where *R. (B.) microplus* ticks were exposed to measure biological variables of the non-parasitic phase of their life cycle, were entirely covered by pastures of *P. maximum* var. *Gatton panic*. In the study area the climate is markedly seasonal with an annual rainfall of 600–700 mm, which is concentrated from October to March (spring–summer).

In each locality 24 series of 20 engorged *R. (B.) microplus* females were exposed in stainless steel wire mesh envelopes placed under the grass and protected from direct solar irradiation (see details in Nava et al. (2013)) following this temporal pattern: Series 1, 22 December 2009; Series 2, 23 February 2010; Series 3, 10 March 2010; Series 4, 24 March 2010; Series 5, 27 April 2010; Series 6, 12 May 2010; Series 7, 16 November 2010; Series 8, 26 November 2010; Series 9, 9 February

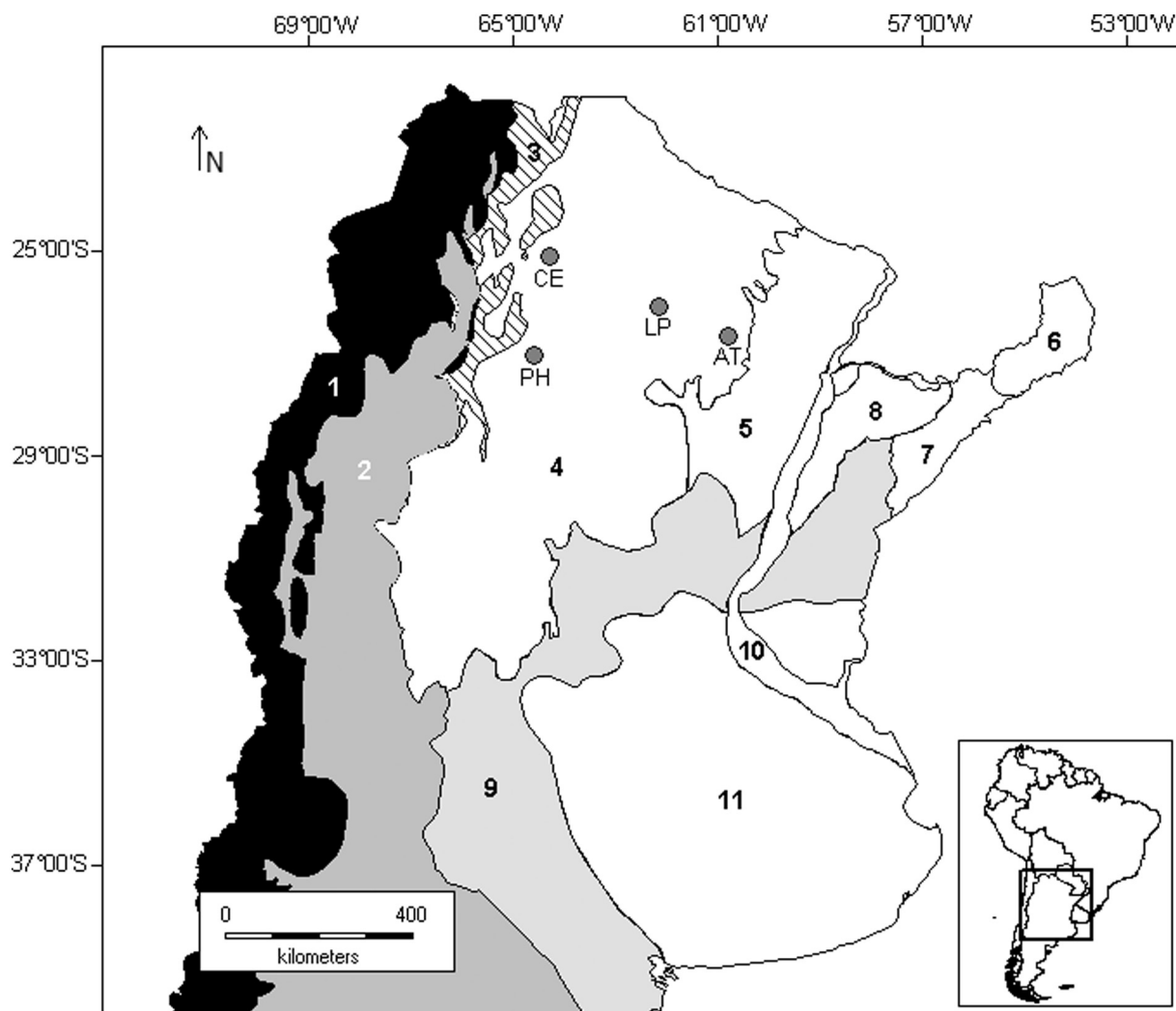


Fig. 1. Ecoregions of Argentina modified from Burkart et al. (1999): (1) Andes and Patagonia, (2) Monte, (3) Selva de las Yungas, (4) Chaco Seco, (5) Chaco Húmedo, (6) Selva Paranaense, (7) Campos y Malezales, (8) Esteros del Iberá, (9) Espinal, (10) Delta e Islas del Paraná, (11) Pampa. AT: Avia Terai; CE: Ceibalito; LP: Los Pirpintos; PH: Pozo Hondo.

2011; Series 10, 4 March 2011; Series 11, 9 April 2011; Series 12, 12 May 2011; Series 13, 16 June 2011; Series 14, 18 August 2011; Series 15, 15 September 2011; Series 16, 13 October 2011; Series 17, 10 November 2011; Series 18, 14 December 2011; Series 19, 4 January 2012, Series 20, 9 February 2012; Series 21, 6 March 2012; Series 22, 12 April 2012; Series 23, 11 May 2012; Series 24, 14 July 2012. Ticks were obtained from naturally parasitized cattle in the study area or by an artificial infestation of unfed larvae on six- to eight-month old calves when an insufficient number of ticks had been collected on the examined animals. Only one female was used per envelope.

The temperature and relative humidity were recorded daily at every hour with HOBO® data loggers (U23-002 Pro v2) at the ground level where the ticks were exposed. Additionally, saturation deficit (a measure of the atmosphere's drying power which integrates temperature and relative humidity) was calculated by using the formula presented by Randolph and Storey (1999). Comparisons among ground temperatures and saturation deficits of the four sites were made by using a one-way analysis of variance (ANOVA) ( $P < 0.01$ ) with Tukey's post hoc test (Zar, 1999).

The biological parameters of the non-parasitic phase of *R. (B.) microplus* life cycle measured during each exposure included the proportion of females ovipositing (PFO), the pre-oviposition period (time from female exposure until beginning of oviposition) (POP), the proportion of egg clusters hatching (PECH), the incubation period of eggs (the time beginning when the first egg was laid until the first egg hatched) (IP), larval longevity (time from the first egg hatched until date of death of the last larva) (LL), and total non-parasitic period (time from the exposure of the female to the date of death of the last larva) (TNPP). The envelopes containing ticks were weekly examined in the field. A statistical comparison of IP, LL and TNPP among localities was performed using Kruskal–Wallis' test with Dunn's multiple comparison (Zar, 1999).

Stepwise multiple regressions were generated to determine the relationship between free-living developmental phases of *R. (B.) microplus* ticks and microclimate variables. The incubation period of eggs and larval longevity were the criterion variables, and temperature, relative humidity and saturation deficit at the ground level were the predictor variables. Data were log-transformed and the relationship with the highest coefficient of determination ( $R^2$ ) was chosen as the best descriptor. The mean values of microclimatic variables to which egg masses and hatched larvae were exposed, were calculated from the date when the first egg was laid to the date when the first egg hatched in the first case, and from the date when the first egg hatched to the date of the last larva's death in the second case.

### 3. Results

Weekly mean ground level temperatures (°C) and saturation deficits (mm Hg) obtained for CE, PH, LP and AT during the study period are presented in Fig. 2. Measurements for LP start in series 3. Table 1 shows mean values for the temperature and saturation deficit during the period in which the free-living stages were exposed to each series. These periods were calculated from the date of tick exposure to the death of the last larva. Differences in temperatures which proved to be statistically significant were found in 14 of the 24 series. Most of the significant differences were around 2 °C, but in five series (1, 13, 19, 20 and 24) the significant differences were between 3.1 °C and 5.4 °C (Table 1). Significant differences in the saturation deficit's values among localities were found in each series (Table 1). However, differences in both temperature and saturation deficit were not unidirectional. The localities with the highest values of these two microclimatic parameters varied among each series.

A total of 480 engorged *R. (B.) microplus* females were exposed in each of the four localities. The PFO was never < 0.80 in most of the series for all localities. The exceptions were series 1, 7 and 16 from LP and series 16 and 20 from PH with values of 0.70, 0.50, 0.70, 0.60 and

0.70, respectively. No significant differences in the POP were observed. The POP was never longer than 7 days, and this value was considered for all exposures as the pre-oviposition period in order to calculate the TNPP. The PECH for each series is shown in Table 2. There was no hatching observed in series 5, 6, 12, 13, 14, 23 and 24 in any of the four localities, which all corresponded to exposures in autumn and winter. Additionally, there was no hatching in series 15 (winter) in CE, or in series 11, 15 and 22 (autumn and winter) in PH. In each case, the eggs clusters which did not hatch belonged to autumn and winter exposures. The failure of eggs to hatch occurred when they were exposed to weekly mean temperature values below 20 °C, regardless of the values of saturation deficit (see Fig. 2 and Table 2). In the series whereby egg hatching was observed (eggs oviposited by females exposed in spring, summer, early autumn and late winter), the values of PECH were highly variable among each series within the same locality and among localities within the same series (Table 2).

Data on the IP are shown in Table 3. The IP corresponding to exposures in late spring and early summer was usually shorter than that of exposures in late summer, mid-spring and early autumn (Table 3). No significant differences were found between localities for most of the series. The only exceptions corresponded to series 4 and 11 (late summer and early autumn), where a significantly higher value was found in LP regarding the other three localities (Table 3). The results of LL are presented in Table 4. The longest periods of LL were recorded in those larvae produced by females exposed in mid- to late summer while the shortest periods were observed in larvae produced by females exposed in spring (Table 4). Unlike that which occurs in the case of IP, statistically significant differences between localities for LL values were found for most of the series, with the only exceptions being series 7 and 18 (Table 4), but these differences were not unidirectional. For example, in the summer of 2010 (series 2, 3 and 4) the LL was higher in AT regarding LP, CE and PH, but in the summer of 2011 (series 9 and 10) the locality with the higher value of LL was CE. Finally, mean and maximum values of the TNPP are given in Table 5. The longer periods of TNPP were observed in series wherein females were exposed from mid-summer to early autumn (series, 2, 3, 4, 9, 10, 11 and 21) where the maximum values ranged from 145 to 197 days (Table 5). The shortest periods of TNPP were recorded in series formed by females exposed in spring (series 7, 8, 16, 17 and 18); the maximum TNPP values of these series ranged from 59 to 121 days (Table 5).

It was found in the regression analysis that the IP has a strong negative linear relation with the mean temperature ( $R^2 = 0.81$ ). As the temperature (T) increases, the IP decreases. The equation describing this relationship is as follows:  $IP = 4.086 - 1.849 * T$ . The LL was significantly explained ( $R^2 = 0.74$ ) by the mean temperature (T) and saturation deficit (SD). The higher the T and SD were, the shorter was the LL was. This relationship is described by the following equation:  $LL = 3.881 - 1.529 * T - 0.429 * SD$ .

### 4. Discussion

The biological parameters of the non-parasitic phase of *R. (B.) microplus* that were evaluated during this study showed the following general trends: I) a longer TNPP occurred when female ticks were exposed in mid- and late summer and early spring; II) the shortest TNPP occurred when female ticks were exposed from late winter to late spring; III) larvae that were active in early and mid-summer had the shortest longevity; IV) incubation periods of eggs, which originated from females exposed in late summer, early autumn and mid-spring, were longer than the incubation period of eggs produced by females exposed in late spring and early summer; V) females oviposited throughout the year, but the eggs did not hatch when the engorged females were exposed in the pastures in mid- and late autumn and winter. This ecological pattern is similar to that previously described by Nava et al. (2013) and Canevari et al. (2017) in both dry and subhumid areas of northern Argentina, which also belong to the Chaco Biogeo-

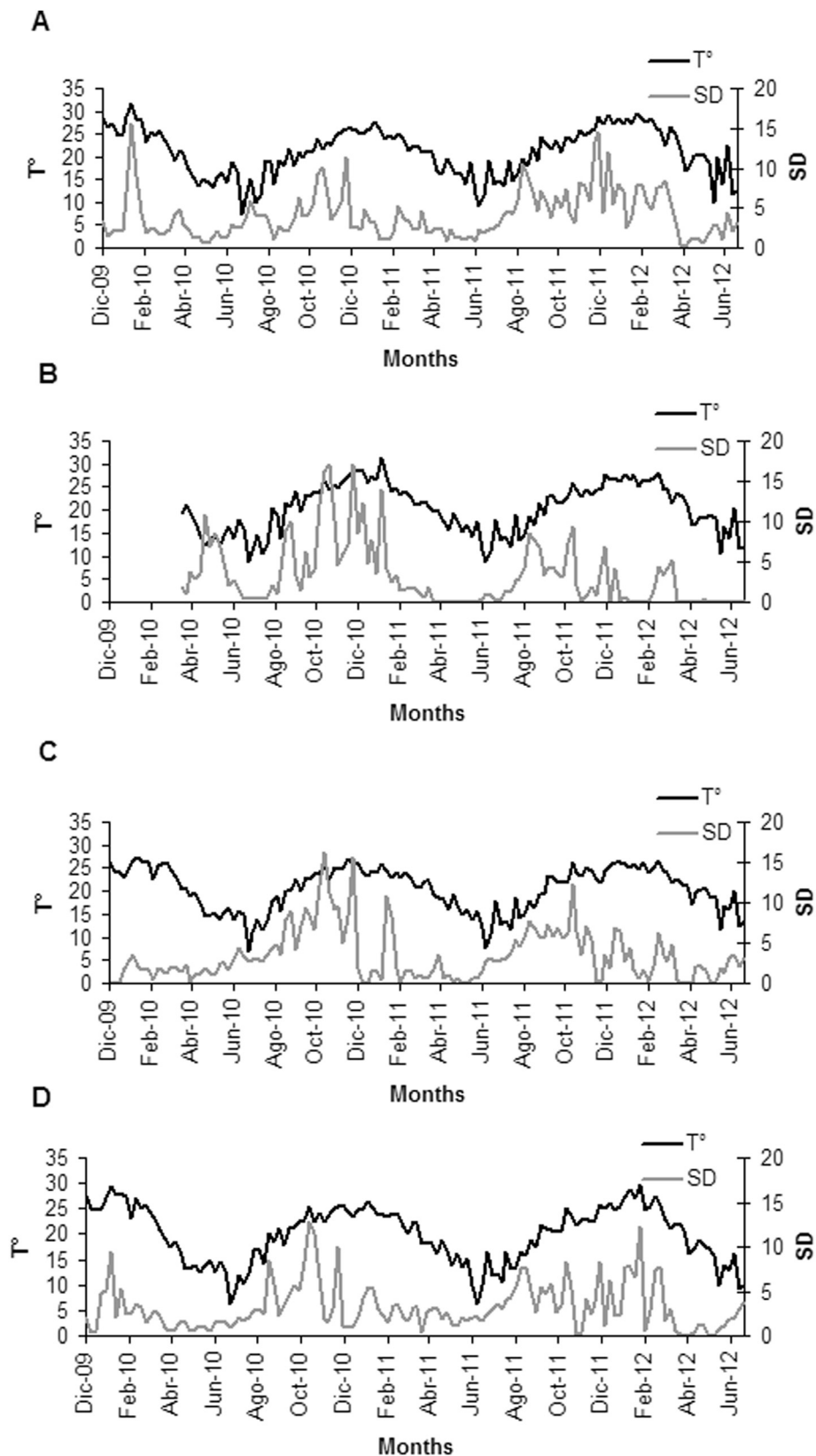


Fig. 2. Weekly mean ground-level temperatures (C°) and saturation deficits (mm Hg) registered during the study period. A) Avia Terai; B) Los Pirpintos; C) Ceibalito; D) Pozo Hondo. T°: temperature; SD: saturation deficit.

graphic Province. Furthermore, the dynamics of the non-parasitic phase of *R. (B.) microplus* described in localities from Brazil and Uruguay, which also are included in the meridional margins of *R. (B.) microplus*' distribution in America (Nari et al., 1979; Cardozo et al., 1984; Evans,

1992), are characterized by the same biological traits described in point I-V of this paragraph.

IP and LL are the biological parameters which are instrumental in determining the TNPP. The relationship between IP and temperature



**Table 1**

Mean values of temperature in °C (T°) and saturation deficit in mm Hg (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. AT: Avia Terai; LP: Los Pirintos; CE: Ceibalito; PH: Pozo Hondo. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	T°AT	T°LP	T°CE	T°PH	SD AT	SD LP	SD CE	SD PH
Series 1	22 Dec 2009 (SU)	24.7 <sup>a</sup>	*	23.2 <sup>a</sup>	26.8 <sup>b</sup>	2.8 <sup>b</sup>	*	1.5 <sup>c</sup>	3.7 <sup>a</sup>
Series 2	23 Feb 2010 (SU)	17.3 <sup>a</sup>	*	17.5 <sup>a</sup>	16.6 <sup>a</sup>	2.5 <sup>a</sup>	*	2.0 <sup>ab</sup>	1.6 <sup>b</sup>
Series 3	10 Mar 2010 (SU)	16.7 <sup>a</sup>	*	16.8 <sup>a</sup>	16.1 <sup>a</sup>	2.5 <sup>a</sup>	*	2.1 <sup>a</sup>	1.3 <sup>b</sup>
Series 4	24 Mar 2010 (SU)	16.4 <sup>a</sup>	*	16.1 <sup>a</sup>	14.8 <sup>a</sup>	3.1 <sup>a</sup>	*	2.5 <sup>a</sup>	1.5 <sup>b</sup>
Series 5	27 Apr 2010 (AU)	14.5 <sup>a</sup>	14.0 <sup>a</sup>	14.5 <sup>a</sup>	14.1 <sup>a</sup>	1.8 <sup>ab</sup>	4.0 <sup>c</sup>	2.3 <sup>b</sup>	1.2 <sup>a</sup>
Series 6	12 May 2010 (AU)	13.9 <sup>a</sup>	13.5 <sup>a</sup>	13.6 <sup>a</sup>	12.3 <sup>a</sup>	2.3 <sup>a</sup>	3.4 <sup>d</sup>	2.5 <sup>a</sup>	6.3 <sup>b</sup>
Series 7	16 Nov 2010 (SP)	25.3 <sup>ab</sup>	27.1 <sup>a</sup>	24.9 <sup>b</sup>	24.6 <sup>b</sup>	4.2 <sup>ab</sup>	7.8 <sup>c</sup>	5.5 <sup>b</sup>	3.6 <sup>a</sup>
Series 8	26 Nov 2010 (SP)	25.5 <sup>ab</sup>	27.1 <sup>a</sup>	24.9 <sup>b</sup>	24.1 <sup>b</sup>	3.7 <sup>ab</sup>	7.4 <sup>c</sup>	5.1 <sup>b</sup>	3.1 <sup>a</sup>
Series 9	9 Feb 2011 (SU)	18.4 <sup>a</sup>	17.8 <sup>a</sup>	17.4 <sup>a</sup>	17.1 <sup>a</sup>	2.3 <sup>a</sup>	0.8 <sup>b</sup>	1.9 <sup>a</sup>	2.3 <sup>a</sup>
Series10	4 Mar 2011 (SU)	17.7 <sup>a</sup>	17.0 <sup>a</sup>	16.8 <sup>a</sup>	16.2 <sup>a</sup>	2.4 <sup>a</sup>	0.6 <sup>b</sup>	1.8 <sup>a</sup>	2.3 <sup>a</sup>
Series 11	9 Apr 2011 (AU)	17.5 <sup>a</sup>	15.6 <sup>b</sup>	15.4 <sup>b</sup>	16.2 <sup>b</sup>	3.6 <sup>a</sup>	1.0 <sup>b</sup>	1.5 <sup>b</sup>	1.9 <sup>b</sup>
Series 12	12 May 2011 (AU)	15.0 <sup>a</sup>	14.4 <sup>a</sup>	14.1 <sup>a</sup>	13.4 <sup>a</sup>	1.9 <sup>a</sup>	0.4 <sup>b</sup>	1.8 <sup>a</sup>	2.1 <sup>a</sup>
Series 13	16 Jun 2011 (AU)	15.4 <sup>a</sup>	15.5 <sup>a</sup>	14.4 <sup>a</sup>	12.3 <sup>b</sup>	4.2 <sup>a</sup>	2.6 <sup>c</sup>	4.1 <sup>ab</sup>	3.2 <sup>bc</sup>
Series 14	18 Aug 2011 (WI)	20.9 <sup>a</sup>	20.6 <sup>a</sup>	20.4 <sup>a</sup>	18.5 <sup>b</sup>	6.2 <sup>ab</sup>	5.2 <sup>bc</sup>	6.5 <sup>a</sup>	5.1 <sup>c</sup>
Series 15	15 Sep 2011 (WI)	23.4 <sup>a</sup>	23.6 <sup>a</sup>	22.8 <sup>a</sup>	21.4 <sup>b</sup>	6.2 <sup>a</sup>	3.4 <sup>b</sup>	5.7 <sup>a</sup>	3.7 <sup>b</sup>
Series 16	13 Oct 2011 (SP)	25.1 <sup>a</sup>	23.5 <sup>a</sup>	23.9 <sup>a</sup>	23.2 <sup>a</sup>	7.6 <sup>a</sup>	3.2 <sup>b</sup>	5.0 <sup>c</sup>	4.0 <sup>bc</sup>
Series 17	10 Nov 2011 (SP)	26.3 <sup>a</sup>	24.3 <sup>b</sup>	24.5 <sup>b</sup>	23.7 <sup>b</sup>	8.0 <sup>a</sup>	2.3 <sup>b</sup>	3.5 <sup>c</sup>	3.2 <sup>c</sup>
Series 18	14 Dec 2011 (SP)	27.8 <sup>a</sup>	26.8 <sup>a</sup>	25.2 <sup>b</sup>	25.3 <sup>b</sup>	7.8 <sup>a</sup>	1.7 <sup>b</sup>	2.9 <sup>c</sup>	4.3 <sup>d</sup>
Series 19	4 Jan 2012 (SU)	27.4 <sup>a</sup>	24.7 <sup>b</sup>	24.1 <sup>b</sup>	26.9 <sup>a</sup>	6.8 <sup>a</sup>	1.4 <sup>b</sup>	2.6 <sup>c</sup>	6.0 <sup>a</sup>
Series 20	9 Feb 2012 (SU)	25.5 <sup>a</sup>	20.1 <sup>b</sup>	21.2 <sup>b</sup>	22.6 <sup>b</sup>	5.4 <sup>a</sup>	1.0 <sup>b</sup>	1.6 <sup>b</sup>	3.1 <sup>c</sup>
Series 21	6 Mar 2012 (SU)	19.5 <sup>a</sup>	18.9 <sup>a</sup>	18.6 <sup>a</sup>	16.9 <sup>b</sup>	3.2 <sup>a</sup>	0.9 <sup>b</sup>	2.2 <sup>c</sup>	2.2 <sup>c</sup>
Series 22	12 Apr 2012 (AU)	17.5 <sup>a</sup>	16.7 <sup>a</sup>	17.1 <sup>a</sup>	16.3 <sup>a</sup>	1.9 <sup>a</sup>	0.4 <sup>b</sup>	2.1 <sup>a</sup>	0.6 <sup>b</sup>
Series 23	11 May 2012 (AU)	16.5 <sup>a</sup>	15.1 <sup>b</sup>	15.9 <sup>ab</sup>	13.5 <sup>c</sup>	2.7 <sup>ac</sup>	0.2 <sup>b</sup>	2.2 <sup>cd</sup>	1.7 <sup>d</sup>
Series 24	14 Jul 2012 (WI)	19.2 <sup>a</sup>	17.9 <sup>ab</sup>	17.6 <sup>b</sup>	14.3 <sup>c</sup>	4.8 <sup>a</sup>	1.9 <sup>b</sup>	4.9 <sup>a</sup>	3.8 <sup>c</sup>

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

\* Temperature and saturation deficit were not recorded by logistic reasons.

**Table 2**

Proportions of egg cluster hatching of *Rhipicephalus (Boophilus) microplus*. AT: Avia Terai, LP: Los Pirintos, CE: Ceibalito, PH: Pozo Hondo. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	AT	LP	CE	PH
Series 1	22 Dec 2009 (SU)	1	1	1	1
Series 2	23 Feb 2010 (SU)	1	1	1	0.85
Series 3	10 Mar 2010 (SU)	0.95	0.90	0.95	0.95
Series 4	24 Mar 2010 (SU)	0.95	0.90	0.26	0.95
Series 5	27 Apr 2010 (AU)	0	0	0	0
Series 6	12 May 2010 (AU)	0	0	0	0
Series 7	16 Nov 2010 (SP)	0.15	*	0.44	0.68
Series 8	26 Nov 2010 (SP)	0.60	*	0.60	0.60
Series 9	9 Feb 2011 (SU)	1	1	0.95	1
Series 10	4 Mar 2011 (SU)	0.95	1	1	1
Series 11	9 Apr 2011 (AU)	1	0.90	0.21	0
Series 12	12 May 2011 (AU)	0	0	0	0
Series 13	16 Jun 2011 (AU)	0	0	0	0
Series 14	18 Aug 2011 (WI)	0	0	0	0
Series 15	15 Sep 2011 (WI)	0.80	0.55	0	0
Series 16	13 Oct 2011 (SP)	0.80	0.80	0.18	0.14
Series 17	10 Nov 2011 (SP)	0.75	0.60	0.60	0.44
Series 18	14 Dec 2011 (SP)	0.26	*	0.80	0.30
Series 19	4 Jan 2012 (SU)	*	0.70	0.85	0.70
Series 20	9 Feb 2012 (SU)	0.90	1	0.40	0.13
Series 21	6 Mar 2012 (SU)	0.55	1	1	1
Series 22	12 Apr 2012 (AU)	0.30	0.81	0.53	0
Series 23	11 May 2012 (AU)	0	0	0	0
Series 24	14 Jul 2012 (WI)	0	0	0	0

\* Eggs clusters were flooded.

was, expectedly, negative. The higher the temperature, the shorter the IP. The same direction in the relationship between these two parameters was already described for *R. (B.) microplus* in other ecological areas of the Southern Cone of America in northern Argentina, southeast Brazil, southeast Paraguay and Uruguay (Cardozo et al., 1984; Ivancovich et al., 1984; Evans, 1992; Brizuela et al., 1996; Nava et al., 2013; Canevari et al., 2017), and also for the closely related species *R. (B.) australis* (formerly named as *R. (B.) microplus* in

Australia (Harley, 1966; Sutherst et al., 1988). In this point, however, it is important to take into consideration that the linear relationship between the IP and temperature only occurred above a threshold temperature value since eggs did not hatch when the monthly mean temperature was below 20 °C (see Results section). The LL has been determined by the mean temperature and saturation deficit. The higher the T and SD, the shorter the LL (see Results section). This can be exemplified by the comparison among the series of February 2010, 2011 and 2012 (series 2, 9 and 20). The LL in series 20 was shorter than in series 2 and 9 (see Table 4), and the T and SD to which were exposed ticks of series 20 were higher than T and SD to which were exposed the ticks corresponding to series 2 and 9 (see Table 1). Dissimilarities in T and SD also explain the differences among localities in LL. However, these significant differences are not unidirectional, and the general pattern is characterized by the shortest LL for those larvae that hatched in summer and the longest LL for the larvae that hatched in autumn. This negative relationship between LL and temperature has been previously described for *R. (B.) microplus* in different American countries, including Argentina (Ivancovich, 1975; Cardozo et al., 1984; Brizuela et al., 1996; Davey et al., 1994; Canevari et al., 2017). Considering as a whole the results obtained by Nava et al. (2013), Canevari et al. (2017) and during this study, it is possible to conclude that in dry and sub-humid areas of the Chaco Biogeographic Province in northern Argentina, regardless of the type of vegetation (e.g. pastures of *P. maximum* and *Chloris gayana*, thorny and semi-deciduous forests), the temperature is the principal factor explaining the cessation of the life cycle of *R. (B.) microplus* in the coldest period of the year, while LL is mainly shortened by the summer's high temperatures. Particularly in the area of study comprised in this work, at similar conditions of temperature, a higher saturation deficit could also negatively affect the LL in pastures of *P. maximum*.

Determining the TNPP for each tick cohort is mandatory to know the dynamics of a *R. (B.) microplus* population in a given area under certain ecological conditions (in this case, pastures of *P. maximum* in northern Argentina), and consequently, to design strategic methods of tick control. The longer TNPPs correspond to those series formed by females exposed in *P. maximum* grasses from mid-summer to early

**Table 3**

Incubation period (days) of eggs of *Rhipicephalus (Boophilus) microplus*. AT: Avia Terai, LP: Los Pirpintos, CE: Ceibalito, PH: Pozo Hondo. Differences were tested with the non-parametric Kruskal-Wallis test. Values correspond to the mean followed by the range in parenthesis. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	AT	LP	CE	PH
Series 1	22 Dec 2009 (SU)	20	20	20	20
Series 2	23 Feb 2010 (SU)	28	28	28	28
Series 3	10 Mar 2010 (SU)	35	35	35	35
Series 4	24 Mar 2010 (SU)	54.2 (48–90) <sup>a</sup>	88.4 (62–90) <sup>b</sup>	64.2 (36–92) <sup>a</sup>	66.15 (48–78) <sup>a</sup>
Series 5	27 Apr 2010 (AU)	–	–	–	–
Series 6	12 May 2010 (AU)	–	–	–	–
Series 7	16 Nov 2010 (SP)	36 (24–39) <sup>a</sup>	–	36.5 (24–39) <sup>a</sup>	37.5 (24–39) <sup>a</sup>
Series 8	26 Nov 2010 (SP)	37 (33–39) <sup>a</sup>	–	36.2 (34–38) <sup>a</sup>	36 (34–38) <sup>a</sup>
Series 9	9 Feb 2011 (SU)	32.4 (28–35) <sup>a</sup>	34 (28–35) <sup>a</sup>	32.6 (28–35) <sup>a</sup>	35 (28–36) <sup>a</sup>
Series 10	4 Mar 2011 (SU)	38.2 (38–42) <sup>a</sup>	39.6 (38–42) <sup>a</sup>	38.8 (38–42) <sup>a</sup>	38.2 (38–42) <sup>a</sup>
Series 11	9 Apr 2011 (AU)	66.7 (64–73) <sup>a</sup>	91 <sup>b</sup>	73.0 (64–76) <sup>a</sup>	–
Series 12	12 May 2011 (AU)	–	–	–	–
Series 13	16 Jun 2011 (AU)	–	–	–	–
Series 14	18 Aug 2011 (WI)	–	–	–	–
Series 15	15 Sep 2011 (WI)	50.8 (45–54) <sup>a</sup>	48.6 (45–64) <sup>a</sup>	–	–
Series 16	13 Oct 2011 (SP)	43.5 (40–49) <sup>a</sup>	41.5 (34–49) <sup>a</sup>	41.5 (34–49) <sup>a</sup>	43.5 (40–49) <sup>a</sup>
Series 17	10 Nov 2011 (SP)	31.0 (24–45) <sup>a</sup>	27.5 (20–32) <sup>a</sup>	29.0 (20–32) <sup>a</sup>	27–5 (20–32) <sup>a</sup>
Series 18	14 Dec 2011 (SP)	26.4 (24–40) <sup>a</sup>	–	29.3 (24–40) <sup>a</sup>	24.8 (24–40) <sup>a</sup>
Series 19	4 Jan 2012 (SU)	–	33.5 (26–49) <sup>a</sup>	34.6 (26–34) <sup>a</sup>	34 <sup>a</sup>
Series 20	9 Feb 2012 (SU)	23.8 (18–34) <sup>a</sup>	23.8 (18–34) <sup>a</sup>	31.5 (18–49) <sup>a</sup>	23.8 (18–34) <sup>a</sup>
Series 21	6 Mar 2012 (SU)	30.1 (30–31) <sup>a</sup>	20.6 (15–31) <sup>a</sup>	30.9 (30–31) <sup>a</sup>	36 (30–46) <sup>a</sup>
Series 22	12 Apr 2012 (AU)	64	75	75	–
Series 23	11 May 2012 (AU)	–	–	–	–
Series 24	14 Jul 2012 (WI)	–	–	–	–

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

**Table 4**

Larval longevity (days) of *Rhipicephalus (Boophilus) microplus*. AT: Avia Terai, LP: Los Pirpintos, CE: Ceibalito, PH: Pozo Hondo. Differences were tested with the non-parametric Kruskal-Wallis test. Values correspond to the mean followed by the range in parenthesis. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	AT	LP	CE	PH
Series 1	22 Dec 2009 (SU)	50.7 (15–106) <sup>c</sup>	15 <sup>a</sup>	97.4 (70–119) <sup>d</sup>	23.8 (13–26) <sup>b</sup>
Series 2	23 Feb 2010 (SU)	145.8 (132–155) <sup>b</sup>	131 <sup>a</sup>	131 <sup>a</sup>	131 <sup>a</sup>
Series 3	10 Mar 2010 (SU)	126.1 (111–135) <sup>c</sup>	111 <sup>b</sup>	111 <sup>b</sup>	95.2 (70–97) <sup>a</sup>
Series 4	24 Mar 2010 (SU)	77.5 (41–83) <sup>c</sup>	42.5 (41–70) <sup>a</sup>	57.5 (40–68) <sup>b</sup>	54.6 (14–70) <sup>ab</sup>
Series 5	27 Apr 2010 (AU)	–	–	–	–
Series 6	12 May 2010 (AU)	–	–	–	–
Series 7	16 Nov 2010 (SP)	35.3 (28–39) <sup>a</sup>	–	30.7 (28–39) <sup>a</sup>	35.5 (28–51) <sup>a</sup>
Series 8	26 Nov 2010 (SP)	35.3 (28–39) <sup>a</sup>	–	34.6 (28–39) <sup>a</sup>	52 (40–76) <sup>b</sup>
Series 9	9 Feb 2011 (SU)	118.3 (107–141) <sup>a</sup>	116 (92–141) <sup>a</sup>	142.2 (120–155) <sup>b</sup>	120.4 (119–141) <sup>a</sup>
Series 10	4 Mar 2011 (SU)	110.3 (64–113) <sup>ab</sup>	99.4 (64–113) <sup>a</sup>	114.4 (114–119) <sup>b</sup>	100 (77–112) <sup>ab</sup>
Series 11	9 Apr 2011 (AU)	74.6 (63–113) <sup>c</sup>	50.1 (36–51) <sup>b</sup>	31 <sup>a</sup>	–
Series 12	12 May 2011 (AU)	–	–	–	–
Series 13	16 Jun 2011 (AU)	–	–	–	–
Series 14	18 Aug 2011 (WI)	–	–	–	–
Series 15	15 Sep 2011 (WI)	20.8 (15–34) <sup>a</sup>	33.2 (15–40) <sup>b</sup>	–	–
Series 16	13 Oct 2011 (SP)	20.0 (15–34) <sup>a</sup>	20.4 (15–34) <sup>a</sup>	36 <sup>b</sup>	36 <sup>b</sup>
Series 17	10 Nov 2011 (SP)	11.4 (6–21) <sup>a</sup>	20 <sup>b</sup>	32.8 (11–48) <sup>c</sup>	33.5 (11–26) <sup>c</sup>
Series 18	14 Dec 2011 (SP)	15 <sup>a</sup>	–	48 <sup>a</sup>	15 <sup>a</sup>
Series 19	4 Jan 2012 (SU)	–	49.8 (36–63) <sup>b</sup>	51.2 (13–75) <sup>b</sup>	12 <sup>a</sup>
Series 20	9 Feb 2012 (SU)	23.8 (21–39) <sup>a</sup>	69.7 (54–92) <sup>c</sup>	54.5 (12–77) <sup>b</sup>	54 <sup>b</sup>
Series 21	6 Mar 2012 (SU)	80.9 (27–107) <sup>ab</sup>	77 (39–93) <sup>a</sup>	95.5 (50–113) <sup>b</sup>	82.2 (64–113) <sup>ab</sup>
Series 22	12 Apr 2012 (AU)	30 <sup>a</sup>	67.5 (43–73) <sup>b</sup>	34 (32–48) <sup>a</sup>	–
Series 23	11 May 2012 (AU)	–	–	–	–
Series 24	14 Jul 2012 (WI)	–	–	–	–

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

autumn. The maximum values of TNPP recorded in exposures of late spring and early summer (late December, January, early February) were approximately 50 to 150 days. This wide oscillation of almost 100 days is explained by short-terms differences in microclimatic conditions between the four localities. For example, in series 1, the TNPP was significantly longer in CE and AT than in PH (see Table 5), which is explained by the higher temperatures and saturation deficit in PH to which females, eggs and larvae were exposed (see Table 1). However, for the same period but in other years (series 8 and 18), these wide differences between these three localities were not observed. Finally, the shortest TNPPs were recorded in the series formed by the

females exposed in spring.

These patterns of TNPP are strongly determined by the LL, and, as it was mentioned above, the LL is negatively affected by higher temperatures. Therefore, predictively the results of this work show that the longer LL periods correspond to the series of females exposed in mid-summer and early autumn and that the shortest LL periods belong to the larvae originated from the females exposed in spring. Taking into consideration the POP and IP, it can be deduced that the larvae originated from the females exposed in spring quest on the pastures during the hottest part of the year (early and mid-summer), the larvae originated from females that were exposed in early summer were

**Table 5**

Total non-parasitic period (time (days) from exposure of the female to the date of death of the last larva) of *Rhipicephalus (Boophilus) microplus*. AT: Avia Terai, LP: Los Pirpintos, CE: Ceibalito, PH: Pozo Hondo. Differences were tested with the non-parametric Kruskal-Wallis test. Values correspond to the mean followed by the maximum value in parenthesis. SP: spring; SU: summer; AU: autumn; WI: winter.

	Date of exposition	AT	LP	CE	PH
Series 1	22 Dec 2009 (SU)	80.6 (133) <sup>b</sup>	42 <sup>a</sup>	119.4 (146) <sup>c</sup>	50.8 (53) <sup>a</sup>
Series 2	23 Feb 2010 (SU)	182.8 (190) <sup>b</sup>	166 (166) <sup>a</sup>	166(166) <sup>a</sup>	166 (166) <sup>a</sup>
Series 3	10 Mar 2010 (SU)	170.5 (177) <sup>c</sup>	153 (153) <sup>b</sup>	153 (153) <sup>b</sup>	132.9 (137) <sup>a</sup>
Series 4	24 Mar 2010 (SU)	147.1 (180) <sup>b</sup>	145 (167) <sup>a</sup>	145(167) <sup>a</sup>	134.2 (155) <sup>a</sup>
Series 5	27 Apr 2010 (AU)	–	–	–	–
Series 6	12 May 2010 (AU)	–	–	–	–
Series 7	16 Nov 2010 (SP)	83.3 (85) <sup>a</sup>	–	82.1 (85) <sup>a</sup>	85.1 (87) <sup>a</sup>
Series 8	26 Nov 2010 (SP)	82.4 (85) <sup>a</sup>	–	82.6 (84) <sup>a</sup>	100 (121) <sup>b</sup>
Series 9	9 Feb 2011 (SU)	165.3 (183) <sup>a</sup>	164 (183) <sup>a</sup>	188.6 (197) <sup>b</sup>	167 (184) <sup>a</sup>
Series 10	4 Mar 2011 (SU)	158.2 (162) <sup>a</sup>	151.4 (162) <sup>a</sup>	164 (168) <sup>a</sup>	154.5 (161) <sup>a</sup>
Series 11	9 Apr 2011 (AU)	168.5 (193) <sup>a</sup>	147.1 (149) <sup>b</sup>	106.5 (114) <sup>c</sup>	–
Series 12	12 May 2011 (AU)	–	–	–	–
Series 13	16 Jun 2011 (AU)	–	–	–	–
Series 14	18 Aug 2011 (WI)	–	–	–	–
Series 15	15 Sep 2011 (WI)	90.4 (95) <sup>a</sup>	91.2 (111) <sup>a</sup>	–	–
Series 16	13 Oct 2011 (SP)	74.2 (90) <sup>a</sup>	74.4 (90) <sup>a</sup>	84.5 (92) <sup>a</sup>	86.5 (92) <sup>a</sup>
Series 17	10 Nov 2011 (SP)	61.2 (73) <sup>a</sup>	47.5 (59) <sup>b</sup>	76.8 (87) <sup>c</sup>	63.2 (65) <sup>a</sup>
Series 18	14 Dec 2011 (SP)	55.5 (62) <sup>a</sup>	–	84.3 (95) <sup>b</sup>	46.8 (62) <sup>a</sup>
Series 19	4 Jan 2012 (SU)	–	93 (119) <sup>b</sup>	95.1 (116) <sup>b</sup>	53 (53) <sup>b</sup>
Series 20	9 Feb 2012 (SU)	59.7 (80) <sup>a</sup>	100.5 (133) <sup>b</sup>	93.1 (95) <sup>b</sup>	85.3 (97) <sup>b</sup>
Series 21	6 Mar 2012 (SU)	118.3 (145) <sup>a</sup>	116.7 (131) <sup>a</sup>	144.5 (151) <sup>b</sup>	140.2 (166) <sup>b</sup>
Series 22	12 Apr 2012 (AU)	101 (101) <sup>a</sup>	152.5 (155) <sup>b</sup>	130 (130) <sup>c</sup>	–
Series 23	11 May 2012 (AU)	–	–	–	–
Series 24	14 Jul 2012 (WI)	–	–	–	–

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

exposed to the microclimatic conditions of late summer and autumn, while the larvae that hatched from the eggs of the females exposed from mid-summer to early autumn lived under the microclimatic conditions of autumn and winter.

The use of chemical acaricides might be minimized or prevented through the implementation of pasture spelling, which serves to control the cattle tick populations by denying host to free-living larvae (Sutherst et al., 1979; Norton et al., 1983). Larvae of *R. (B.) microplus* die by starvation and desiccation after a proper period of pasture spelling. The usefulness of this method to apply it as a complement or alternative to chemical acaricides entirely depends on accurate information on the total non-parasitic period of *R. (B.) microplus* in different periods of the year. In the area analysed in this study, the spelling period of the *P. maximum* grasses that is needed to ensure total control of *R. (B.) microplus* consists of approximately 19–20 weeks if the spelling starts in late spring and early summer, but if the spelling begins in mid- and late summer or in autumn, the required period is about 27–28 weeks. These values were obtained in light of the maximum values of the total non-parasitic period recorded for each season (see Table 5). A previous ecological study on the non-parasitic phase of the life cycle of *R. (B.) microplus* performed by Canevari et al. (2017) also in areas of the Chaco Phytogeographic Province but in other pastures (i.e. *C. gayana*) has reached similar results. This fact suggests that the periods needed to control the cattle tick by pasture spelling are relatively constant along of the Chaco Phytogeographic Province in northern Argentina, irrespective of the type of megathermic grass used as a forage resource in cattle production systems.

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