

Activity and reproductive patterns of lizards in the Chaco of Argentina

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We studied the activity and breeding pattern of dominant lizard species in the Arid Chaco, the southernmost subregion of the Chaco ecoregion (Chancaní Reserve, Córdoba province, Argentina). Lizards were captured with pitfall traps over a 4-year period. In total, 1449 individuals belonging to 11 of the 12 lizard species recorded in the area were trapped. Of these, we selected six species for a detailed analysis: *Teius teyou* and *Stenocercus doellojuradoi* accounted for 63% of the captures, *Tropidurus etheridgei*, *Liolaemus chacoensis* and *Homonota fasciata* accounted for 32%, and 5% comprised *Leiosaurus paronae* and the remaining five species. All the studied species were active during the warm-rainy season (September to March). Monthly lizard captures were highly correlated with monthly mean temperature and rainfall. No captures occurred during the remaining months of the year. All reproductive tactics known for the Chaco lizards were observed in Chancaní, including single clutch in a short breeding season in summer or autumn, as well as an extended breeding season with multiple clutches. *Stenocercus doellojuradoi* and *L. paronae* showed a singular reproductive timing, suggesting the occurrence of egg retention. Compared with sub-tropical Chaco sites, the Arid Chaco only differs in the lack of winter activity, resulting from the lower temperature and rainfall regime of our study site.

Keywords: Arid Chaco; life history traits; reptiles; early adult disappearance

Introduction

One of the central questions in reptile ecology is the understanding of the adaptive significance of specific life-history traits (Vitt 1992; Du et al. 2005). More specifically, the adaptive value and the factors that determine activity and reproductive patterns in reptiles have been widely discussed (Tinkle et al. 1970; Fitch 1980; Shine 2005). Most studies have focused on comparing species (or species assemblages) between tropical and temperate regions (Fitch 1982; James and Shine 1988; Vitt 1990), and on comparing single species traits along climatic gradients (Vitt and Breitenbach 1993; Mesquita and Colli 2003; Garda et al. 2012).

Temperature and rainfall seasonality are major factors affecting the phenology and life history of lizards (Adolph and Porter 1993; Colli et al. 1997; Sears 2005). In addition, lineage, foraging mode, body size and body shape are also known factors that affect life-history characteristics among squamate reptiles (Tinkle et al. 1970;

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Vitt 1981, 1986, 1990, 1992; Colli et al. 1997; Wiederhecker et al. 2002; Mesquita and Colli 2010).

Lizards exhibit a diversity of patterns in terms of activity and reproductive timing: in tropical, non-seasonal areas where neither temperature nor rainfall is limiting at any time of the year, lizards may be active and reproduce continuously throughout the year. In tropical areas where rainfall is seasonal, lizards may restrict activity and particularly reproduction to the wet or dry season, probably depending on the phylogenetic origin of each species (James and Shine 1985; Mesquita and Colli 2010) and abiotic factors related to nesting microenvironments (Wiederhecker et al. 2002; Brown and Shine 2006). In temperate areas, low temperatures may become an additional factor limiting lizard activity and reproductive timing (Adolph and Porter 1993).

In South America, the Chaco ecoregion is the largest dry forest and the continent's second biggest forest biome after Amazonia, encompassing about 1.2 million km². It occupies territories in Argentina, Paraguay, Bolivia and a small portion of Brazil (Olson et al. 2001; The Nature Conservancy et al. 2005). The dominant Chaco vegetation is characterised by open dry woodlands dominated by *Schinopsis* (Anacardiaceae) in the north and *Aspidosperma* (Apocynaceae) in the south. Other common vegetation types are dry or seasonally flooded savannas, salt flats, halophytic scrubs and swamps (Bucher 1982; The Nature Conservancy et al. 2005).

An outstanding characteristic of the Chaco is its vast latitudinal range, extending from tropical (18°S) to temperate latitudes (~32°S) (Olson et al. 2001; The Nature Conservancy et al. 2005). Even when there are no important topographical barriers along the Chaco, its latitudinal extension generates a diversity of climates, ranging from tropical humid climates in the north to hot semi-arid climates in the south. Differences in climate and soils in turn define four distinct sub-regions known as Humid Chaco, Semiarid Chaco, Sierra Chaco and Arid Chaco (The Nature Conservancy et al. 2005) (Figure 1). Despite this environmental heterogeneity, some lizard species are widely distributed across the entire ecoregion, making the Chaco a suitable region for studying variations in ecological traits.

Available studies on the biology and activity patterns of lizards in the Chaco ecoregion includes a few studies made in the Semiarid Chaco (Salta province, northern Argentina; Cruz 1994a, 1994b, 1996, 1997, 1998; Cruz and Ramirez Pinilla 1996; Cruz et al. 1998, 1999; Fitzgerald et al. 1999), in the Sierra Chaco (Córdoba province, central Argentina; Aun and Martori 1994; Martori and Aun 1994; Martori et al. 2002) and recently in the Humid Chaco (Corrientes, northeastern Argentina; Ortiz et al. 2014). A lack of studies on reproductive biology of lizards from northern Chaco (in Paraguay and Bolivia) makes it difficult to analyse regional patterns, or to make comparisons with other regions. However, available studies in the Argentinean Chaco allow the influence of climatic factors on activity and reproductive patterns of lizards along a climatic gradient to be studied.

Of particular interest is to determine whether or not Chaco lizard species are able to occur under a wide range of temperature and rainfall conditions, and – if so – how they are adapted to climatic restrictions. Here, we report the results of a 4-year study conducted in the southernmost part of the Arid Chaco subregion, where both annual temperature and rainfall are at the lowest values within the Chaco ecoregion, with the aim of determining the activity and reproductive patterns of six dominant Chaco

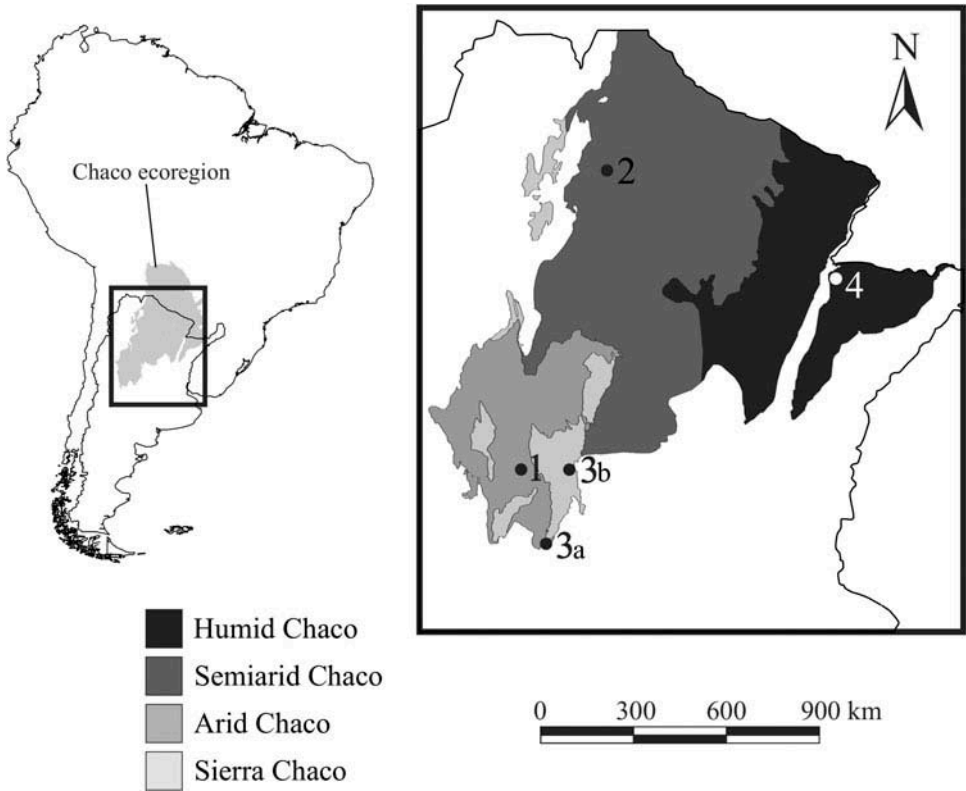


Figure 1. Map showing the Chaco ecoregion limits and its subdivisions in Argentina. Numbers refer to study sites with available reproductive studies made in the Argentine Chaco: (1) Arid Chaco (this study); (2) Semi-arid Chaco (Fitzgerald et al. 1993, 1999; Cruz 1994a, 1994b, 1997; Cruz and Ramirez Pinilla 1996; Cruz et al. 1999); (3) Sierra Chaco: (a) Martori et al. (2002), (b) Aun and Martori (1994); and (4) Humid Chaco (Ortiz et al. 2014).

lizard species. Specifically, we aimed to: (1) describe the activity and reproductive patterns of a lizard assemblage in the Arid Chaco (southern end of the Chaco ecoregion); (2) provide new basic data on the biology of *Stenocercus doellojuradoi* and *Leiosaurus paronae*, two almost-unknown Chaco endemic lizard species; and (3) compare our results in the Arid Chaco with published studies on lizards of the Semi-arid, Sierra and Humid Chaco in Argentina.

Material and methods

Study area

Our study was conducted in the Arid Chaco ecoregion (southernmost portion of the Chaco) (Olson et al. 2001), in the Chancaní Provincial Reserve (30.37°S, 65.43°W; 4960 ha) and neighbouring areas (Figure 1). Local climate corresponds to the BSh type (Hot Semi-arid) in the Köppen–Geiger classification system (Peel et al. 2007). The area is characterised by a typical monsoon pattern with contrasting seasons:

warm–rainy (October–March) and cold–dry (April–September). The average annual rainfall is 426 mm. The mean annual temperature is 18°C, with an absolute maximum of about 45°C in the summer. Below-zero temperatures and frosts are frequent in winter.

The dominant vegetation in Chancaní Provincial Reserve is dry semi-deciduous woodland. The canopy is discontinuous (15 m high), dominated by *Aspidosperma quebracho-blanco* (Apocynaceae) and *Prosopis flexuosa* (Fabaceae). The shrub stratum (4 m high) is thorny, dense and almost continuous, dominated by *Larrea divaricata* (Zygophyllaceae), and *Mimozyanthus carinatus* and *Acacia furcatispina* (Fabaceae) (Carranza et al. 1992).

Lizard sampling

We used capture data from two studies conducted between 2004 and 2008 (11,792 trap days⁻¹). In the first study (from January 2004 to March 2005 and from December 2005 to March 2006; 3192 trap days⁻¹), lizards were captured using eight pitfall trap arrays combined with funnel traps, distributed in two sites inside the Chancaní Provincial Reserve. Fences were 10 m long and 0.5 m in height, connected to four 45-L buckets, in a Y-shaped arrangement.

During the second study (from October 2006 to March 2007, and from October 2007 to February 2008; 8600 trap days⁻¹) lizards were captured using 100 drift-fence pitfall traps distributed in four sites with 25 traps each: two inside Chancaní Provincial Reserve (same sites as the first study), and two in neighbouring areas. Each fence was 2 m long and 0.50 m high, and was connected to a unique central 18-L, 30-cm-diameter plastic bucket, assembled in a Y-shaped arrangement.

The minimum distance between traps was 30 m in both studies. We consider that differences in trap design did not affect our conclusions, since we did not compare lizard abundances between studies. At each study, all traps were active at the same time. Because of the different lengths of months, we expressed monthly captures in lizards per trap day⁻¹. Non-systematic searches were made in the area during the non-sampling periods as a complementary technique.

All lizard specimens captured were identified, measured (snout–vent length, SVL), toe-clipped to avoid double counting and palpated to recognise females carrying oviductal eggs (gravid females). Individuals identified as recaptures were excluded from analyses. In addition, individuals were classified into adult or sub-adult (juveniles and neonates) age classes, according to the shortest SVL recorded for reproductive individuals (females or males) available in the literature, as follows: *Homonota fasciata* (female; Phyllodactylidae): 35.0 mm (Aun and Martori 1994); *Liolaemus chacoensis* (male; Liolaemidae): 37.0 mm (Cruz and Ramirez Pinilla 1996); *Teius teyou* (female; Teiidae): 76.1 mm (Cruz et al. 1999); *Tropidurus etheridgei* (female; Tropiduridae): 49.9 mm (Cruz 1997); *Tupinambis rufescens* (female; Teiidae): 330.0 mm (Fitzgerald et al. 1993), *Vanzosaura rubricauda* (female; Gymnophthalmidae): 31.4 mm (Cruz 1994b); and *Mabuya dorsivittata* (male; Scincidae): 31.0 mm (Aun et al. 2011). Due to the lack of studies on reproduction of the two Chaco endemic *S. doellojuradoi* (Tropiduridae) and *L. paronae* (Leiosauridae), we set an arbitrary value as the minimum value for adults, based on the bimodal distribution of size frequencies (SVL, mm). Thus, the SVL category with the smallest value between modal classes (*S. doellojuradoi*: 45.0 mm; *L. paronae*:

55.0 mm) was considered the minimum SVL for adults. We were not able to separate age classes for *Liolaemus* sp. (Liolaemidae) and *Cnemidophorus serranus* (Teiidae) due to the low number of captured individuals. For each species, individuals showing a navel crack were assigned to the neonate category. Therefore, recruitment date was defined as those months when neonates were present. The resulting data set allowed us to infer annual activity, hatchling data, number of clutches per season, reproductive timing and (in some cases) time to reach maturity of the most abundant lizard species of the assemblage.

Data analysis

For the purposes of this study, we excluded *C. serranus*, *Liolaemus* sp., *Vanzosaura rubricauda*, *Tupinambis rufescens* and *Mabuya dorsivittata* from the analysis because of the low number of individuals captured. The association between monthly captures of lizards (all species pooled) and climate [e.g. mean monthly temperature (°C) and mean monthly rainfall (mm)] was assessed through a Spearman rank test. Climatic data of the same period of lizard sampling was provided by Servicio Meteorológico Nacional of Argentina (<http://www.smn.gov.ar>), and corresponded to a weather station located in Villa Dolores city, 86 km far and at similar elevation to our study area.

Adult activity of each species was analysed separately by comparing the number of captured adults (lizards per trap day⁻¹) among months through a Kruskal–Wallis test. Post-hoc multiple comparisons (Tukey and Kramer) were made using the package PMCMR (Pohlert 2014). All analyses were performed in R 2.15.1 (R Core Team 2013) with an alpha level of 0.05.

Results

We captured 1449 individuals belonging to 11 of the 12 lizard species recorded in the area (Pelegri et al. 2006) (Figure 2). *Teius teyou* and *Stenocercus doellojuradoi* accounted for 63% of total captures, and were the dominant species. *Tropidurus etheridgei*, *Liolaemus chacoensis* and *Homonota fasciata* were moderately abundant (32% of total captures), whereas the remaining species (*Leiosaurus paronae*, *Vanzosaura rubricauda*, *Mabuya dorsivittata*, *Tupinambis rufescens*, *Cnemidophorus serranus* and *Liolaemus* sp.) were rare (5% of total captures) (Figure 3). All of the lizard species were active from September to March. Only a few individuals of *T. etheridgei* were observed (but not captured) on some exceptionally warm days in the winter. Monthly lizard captures were highly correlated with monthly mean temperature (Spearman Rho = 0.845, $P < 0.001$) and mean monthly rainfall (Spearman Rho = 0.793, $P = 0.002$) (Figure 4). The number of species captured was two in September, seven in October, 10 in November, eight in December, seven in January, nine in February and 10 in March, decreasing to zero from April to August (Figures 3 and 4). The activity and presence of gravid females and neonates, and juveniles showed important differences among species, which are described in the following paragraphs (see Figure 4).

Teius teyou: Adults were active from October to February. The number of captures was similar from October to January, declining in February and being drastically reduced in March. Only a few large adults were trapped in October and November, suggesting a very low adult survival between seasons. Gravid females

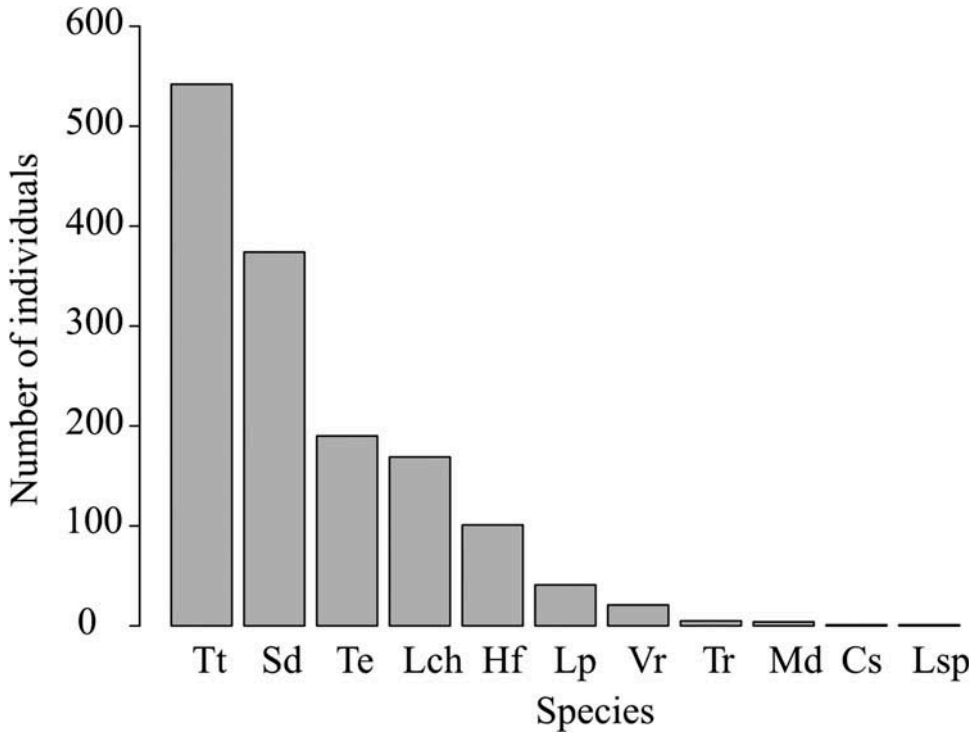


Figure 2. Number of lizards captured during the study. Abbreviations: Tt: *Teius teyou*, Sd: *Stenocercus doellojuradoi*, Te: *Tropidurus etheridgei*, Lch: *Liolaemus chacoensis*, Hf: *Homonota fasciata*, Lp: *Leiosaurus paronae*, Vr: *Vanzosaura rubricauda*, Tr: *Tupinambis rufescens*, Md: *Mabuya dorsivittata*, Cs: *Cnemidophorus serranus*, Lsp: *Liolaemus* sp.

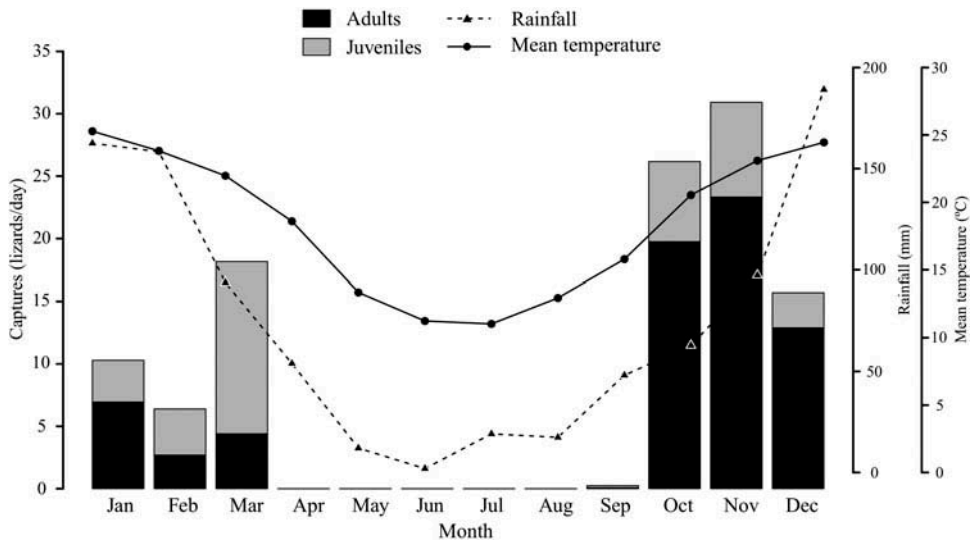


Figure 3. Annual activity of adult (black bars) and juvenile (grey bars) lizards in the southernmost portion of the Chaco. Monthly mean values for rainfall (dashed lines) and temperature (solid lines) are shown.

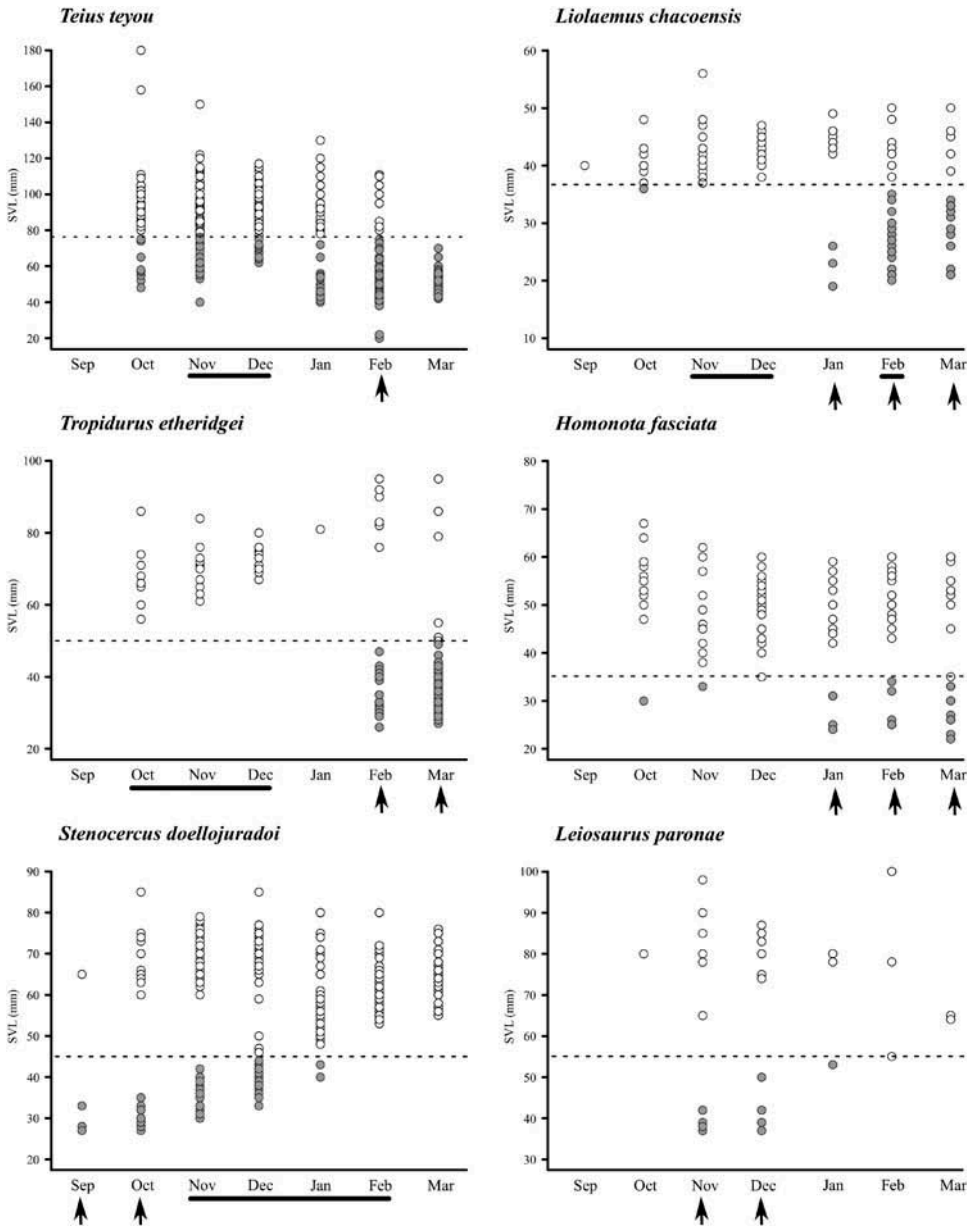


Figure 4. Monthly size distribution of adults (open circles) and juveniles (grey circles) of the lizard species of the Arid Chaco with the highest number of captures. Dotted lines indicate minimum size of adults for each species. Black lines under months indicate presence of gravid females. Arrows indicate months with presence of neonates. SVL: snout-vent length.

were detected in November and December. The smallest gravid female captured was 78.0 mm in SVL. Juveniles were present from October to March, with neonates being trapped in February.

Liolaemus chacoensis: Adults were captured from September to March, with a low number of captures in September and higher numbers in the remaining months. Gravid females were captured in November, December and February. The smallest reproductive female was 45.0 mm SVL. Juveniles and neonates were captured from January to March, suggesting that they reach adult size early in the following breeding season.

Tropidurus etheridgei: Adults were captured from October to March, with the biggest individuals being trapped in February and March. Gravid females were found from October to December. The smallest gravid female was 70.0 mm in SVL. Neonates were captured in late summer (February and March). Juveniles were captured only in February and March. From then on, they showed a slight increasing trend in size until the end of the breeding season. Juveniles reached adult size by the start of the following breeding season.

Homonota fasciata: Adults were trapped from October to March. It was not possible to check females for the presence of eggs. The smallest individual recorded (22.0 mm in SVL) was captured in March. A few juveniles were detected in September and October, and a much higher number appeared from January to March, peaking in March. The observed pattern is compatible with the presence of two laying periods in the same breeding season.

Stenocercus doellojuradoi: Adults were active from September (smallest number) to March. Adult females with palpable eggs were found in late spring and mid-summer (November to February). The smallest gravid female was 51 mm in SVL. Neonates were observed in spring (September and October). Juveniles of larger size were captured in the consecutive months, reaching adult size in February.

Leiosaurus paronae: Adults were captured from October to March. No gravid females were recorded. Hatchlings were captured in November and December, with a few, large-sized individuals in February. Juveniles may reach adult size from January onwards in the same breeding season.

Early adult disappearance was observed in two species: *T. teyou* and *L. chacoensis*. *Teius teyou* captures decreased rapidly in February and were reduced by 92% in March (Kruskal–Wallis test, chi-squared = 102.0239, df = 6, $P \ll 0.0001$; Tukey–Kramer, $P < 0.05$). *Liolaemus chacoensis* captures also fell from February to March (Kruskal–Wallis test, chi-squared = 22.6795, df = 6, $P \ll 0.0001$; Tukey–Kramer, $P < 0.05$). In both cases, the observed declines started shortly after the hatchling period of each species (Table 1).

Discussion

Reproductive cycles

Our results confirm the highly seasonal breeding pattern of Chaco lizards, regardless of whether sites are located in the temperate or subtropical latitudinal zones. The comparison of the breeding patterns observed in the temperate Arid Chaco (this study) with those recorded in the subtropical Semi-Arid Chaco (Cruz 1994a, 1994b, 1997, 1998; Cruz and Ramirez Pinilla 1996; Cruz et al. 1999) shows that the only significant difference is the continual activity of juveniles and adults of small-sized species in the Semi-Arid Chaco, whereas the activity of adults of large species remains restricted to the warm–wet season in both sites. Fitzgerald

Table 1. Number of adult (A) and juvenile (J) lizards per species captured monthly between 2004 and 2008 in Chancami Reserve, Córdoba, Argentina.

Species	Sep		Oct		Nov		Dec		Jan		Feb		Mar		Total
	A	J	A	J	A	J	A	J	A	J	A	J	A	J	
<i>Teius teyou</i>	0	0	39	12	138	37	88	15	38	29	10	94	0	52	552
<i>Stenocercus doellojuradoi</i>	1	5	12	18	51	38	56	24	49	2	73	0	48	0	377
<i>Tropidurus etheridgei</i>	0	0	8	0	12	0	12	0	1	0	6	30	7	100	176
<i>Liolaemus chacoensis</i>	1	0	14	2	31	0	24	0	8	3	9	26	5	20	143
<i>Homomota fasciata</i>	0	0	13	1	14	1	25	0	10	4	17	6	9	10	110
<i>Leiosaurus paronae</i>	0	0	1	0	6	6	10	6	3	1	4	0	2	0	39
<i>Vanzosaura rubricauda</i>	0	0	1	2	2	1	4	1	0	0	1	2	1	1	16
<i>Mabuya dorsivittata</i>	0	0	0	0	1	0	0	0	1	0	4	0	2	0	8
<i>Tupinambis rufescens</i>	0	0	0	0	1	0	0	1	0	0	0	1	0	1	4

et al. (1999) attributed the observed winter activity in the subtropical Semi-Arid Chaco to differential thermoregulatory constraints of lizards of different sizes, which hinder the activity of medium-sized and large lizards. Cruz (1997) also proposed that juvenile activity of *T. etheridgei* in the Chaco of northern Argentina could be explained by year-round prey availability. In summary, the most likely explanation for the observed differences in annual activity among the two sub-regions is the lower winter temperatures of the Arid Chaco. Low temperatures may affect both lizards' temperature regulation and prey availability. In the case of both the Semi-Arid and the Humid Chaco, mean temperature during the winter period remains above 10°C, whereas in Chancaní it decreases below 10°C from May to August (data from Servicio Meteorológico Nacional of Argentina). It is assumed that mean temperatures below 10°C indicate very limited biological activity for both plants and animals (Breckle 2002). In addition, lizard winter activity may also be influenced by dry conditions (low rainfall), at least in the Semi-Arid Chaco. The only available study on the reproductive biology of a lizard (*Tropidurus torquatus*) from the Humid Chaco (at about the same latitude as the study site in the Semi-Arid Chaco) reported year-round activity of both adults and juveniles, and two clutches per season (Ortiz et al. 2014). The Humid Chaco has higher rainfall and a shorter dry season than the other Chaco subregions. The winter mean temperature is also over 10°C (Servicio Meteorológico Nacional of Argentina).

Specific differences

Even when the six dominant species studied in the Arid Chaco restricted their activity and reproductive cycle to the warm–wet season, there were significant within-season differences that deserve closer examination. Following Fitch (1970), the observed variations can be assigned to two groups: summer breeding and autumn breeding (Figure 4):

- (1) Summer breeding: Ovulation and mating take place in spring, and egg laying and hatching in summer. Neonates appear at the end of the breeding season, and juveniles become adults early in the following season (Fitch 1970). In the Arid Chaco, *L. chacoensis*, *T. etheridgei*, *T. teyou* and *H. fasciata* are included in this group. *Liolaemus chacoensis* and *T. etheridgei* laid only one clutch per season, in contrast with the Semiarid Chaco where both species laid multiple clutches (Cruz and Ramirez Pinilla (1996).

Teius teyou shows two distinctive characteristics: first, neonates appear in late summer, but larger juveniles are captured throughout the activity season, suggesting that juveniles may take longer than one breeding season to reach adult condition. Second, adults show early disappearance in midsummer.

Homonota fasciata in Chancaní had two clutches and presence of neonates in early spring and late summer, a generalised trait among gekkonids (Vitt 1986). However, the number of clutches seems variable. In the northern Semiarid Chaco, Cruz (1994a) reported two clutches of one egg per reproductive period, whereas Aun and Martori (1994) and Martori et al. (2002) reported both one and two clutches for *H. fasciata* in two localities at about the same latitude as Chancaní (Figure 1). The

reported differences in clutch number may indicate an adaptive response to variations in year-to-year variations in climate and/or food supply (Fitch 1985).

- (2) Autumn breeding: As a response to a short summer, ovulation and mating take place during mid-late summer, and egg laying extends from the next late spring to early summer. Hatchlings appear only at the beginning of the following season and grow rapidly, reaching adult size late in the same breeding season. In the Arid Chaco, *S. doellojuradoi* is included in this group. Egg retention until the next spring is the most plausible operating mechanism proposed as an adaptation to increase hatchling survival to cold winters by delaying egg deposition (Warner and Andrews 2003), and it is a common strategy in species of high altitudes (Guillette and Casas Andreu 1980). Accordingly, the genus *Stenocercus* is of Andean origin, which later expanded to adjacent lowland areas (Torres-Carvajal 2007). *Leiosaurus paronae* may also fit in this autumn breeding pattern, although a larger sample would be needed to support this hypothesis. Based on the actual knowledge of Chaco lizard reproduction (summarised in this work), these may be the only two species exhibiting egg retention in the whole Chaco.

Our results indicate that environmental conditions in the southern end of the Chaco restrict breeding to the warm–wet season, allowing two main strategies, early breeding or delayed breeding with egg retention. Moreover, a reduction in the number of clutches appears to be the main adaptive response to the shorter summers (Fitch 1985) that characterise the southern border of the Chaco.

Constrained adult activity

An interesting characteristic of lizard activity in the Arid Chaco is the marked decrease of adult activity of *Teius teyou* and – to a lesser degree – *L. chacoensis* in late summer. The same pattern has been reported for *T. teyou* in the Semi-Arid Chaco (Cruz et al. 1999) and for *Teius ocellatus* in Brazil (Bujes 1998). Since trapping data depend on activity, we cannot differentiate between reduced activity and early mortality.

Disappearance of adult lizards early in the mid-breeding season is relatively common in arid and semi-arid regions. A number of lizard taxa that inhabit arid environments in Australia have been reported to become dormant shortly after juvenile emergence, despite favourable environmental conditions (James 1991).

Different hypotheses have been proposed to explain a non-overlapping activity between adults and hatchlings: (1) avoidance of competition among age classes (Tinkle et al. 1993); (2) avoidance of cannibalism events (Pizzatto et al. 2008); and (3) factors that affect adults and neonates differently, such as thermal constraints (as proposed by Fitzgerald et al. 1999).

Avoidance of competition: early disappearance of adults may result in an increase in juvenile survival through reduced competition with adults. An experiment of almost-complete removal of adults of *Sceloporus graciosus* resulted in significant increases in growth rates of hatchling and yearling stages during both the year of the removal and the following year (Tinkle et al. 1993).

There are no available studies analysing abundance, survivorship or body condition of younglings of *T. teyou* and *L. chacoensis* in the absence of adults of these species. However, studies on feeding ecology of *T. oculatus* – a species very similar to *T. teyou* – showed that even when the mean volume of preys eaten by adults is higher than that eaten by juveniles, adults continue eating small-sized preys (Cappellari et al. 2007), suggesting that competition between hatchlings and adults of *T. teyou* could occur if adults were present. In this scenario, juveniles would benefit from the reduced presence of adults.

Avoidance of cannibalism: Cannibalism is relatively common, as reported by Siqueira and Rocha (2008) for Tropicoduridae, Scincidae, Liolaemidae and Geckonidae lizards from Brazil. Moreover, teiid lizards are known predators of juveniles of other lizard species (Siqueira and Rocha 2008). Non-overlapping activity was reported as a mechanism to avoid cannibalism in the toad *Bufo marinus* in Australia (Pizzatto et al. 2008). Although neonate predation has not been reported for the lizard species studied here, this possibility cannot be discarded, since finding neonates in the gut contents of adult lizards would depend on the presence of neonates on the date of adult capture.

Factors affecting adult and neonates differently: Segregated activities between adults and neonates can also result from differential thermal constraints among age classes, or early adult disappearance. The fact that this characteristic appears in species belonging to very different taxonomic groups (Liolaemidae and Teiidae) suggests that phylogeny is less significant than adaptive factors. Fitzgerald et al. (1999) attributed early adult disappearance in subtropical Chaco to differential thermoregulatory constraints of lizards of different sizes, which also favoured winter activity of juvenile lizards. However, although thermoregulatory factors may be significant in winter, they do not explain the drop in captures we observed in the warmest months of the year (January–February). Acosta and Martori (1990) explained the early disappearance of adults of *T. oculatus* after the oviposition period (after Rose 1981) as a mechanism to reduce predation risk and save energy, increasing survival probability. Rose (1981) originally proposed that adult inactivity might be an adaptive strategy rather than a response to climate. The author also found that older and bigger males of *Sceloporus virgatus* reduced their activity periods to the point that they were unable to maintain their territories. Since the effectiveness of the drift-fence pitfall traps method relies on activity (McDiarmid et al. 2011), it is not possible to differentiate between reduced activity and early mortality of the adults of *T. teyou* and *L. chacoensis* in our study. However, if these lizards did become inactive shortly after reproduction, the reduction of the fat bodies due to the reproductive effort could affect winter survival, as reported for the Australian agamid *Ctenophorus fordi* (Cogger 1978).

The main conclusions of our work can be summarised as follows: (1) reproduction and activity of lizards in the Arid Chaco is highly seasonal, and mainly restricted to the spring and summer, probably due to low winter temperatures and the highly seasonal rainfall; (2) most abundant lizard species of the Argentinean Chaco show variation in reproduction timing: early breeding in the summer or delayed breeding in autumn, with a variable number of clutches; (3) egg retention is likely present in *S. doellojuradoi* and *L. paronae*, a unique condition among Chaco lizard species; (4) adult abundance of *T. teyou* and *L. chacoensis* decreased early in the summer, most

likely because of mortality after mating, which in turn may have benefited hatchlings by reducing intraspecific competition and probably cannibalism risk.

The observed differences in lizard breeding cycles are usually attributed to the species' phylogenetic background, which in fact implies a rather contradictory reasoning, since only those breeding patterns that are adaptive (or neutral) can thrive in a given environment (Fitch 1985), regardless of their phylogenetic origin. More research would be necessary to understand the specific combination of reproductive cycle, egg weight, clutch size, adult survival, and food availability and quality that allows each of the studied species to survive in the southern Chaco environment.

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Disclosure statement

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