

CHANGES IN FEMALE REPRODUCTION AND BODY CONDITION IN AN ENDEMIC LIZARD, *PHYMATURUS SPECTABILIS*, FOLLOWING THE PUYEHUE VOLCANIC ASHFALL EVENT

JORGELINA M. BORETTO^{1,3}, FACUNDO CABEZAS-CARTES¹, ERIKA L. KUBISCH¹, BARRY SINERVO², AND NORA R. IBARGÜENGOYTÍA¹

¹INIBIOMA (CONICET – Universidad Nacional del Comahue). Bariloche, Río Negro, Argentina

²Department of Ecology and Evolutionary Biology, Earth and Marine Sciences Building, University of California, Santa Cruz, California 95064, USA

³Corresponding author, e-mail: borettojm@comahue-conicet.gob.ar

Abstract.—Puyehue is a largely basaltic stratovolcano located in the southern volcanic zone of the Andes, with an irregular inter-occurrence intervals of eruption that affects the ecology of the native communities. The latest Puyehue eruption occurred in June 2011 and dispersed about 100 M tons of pyroclastic materials to the Patagonia steppe of Argentina, due to the West–East predominant winds, affecting an area of over 7.5 M ha. Herein we report the changes in the reproductive cycle of females and body condition of adult males, females, juveniles, and newborns of *Phymaturus spectabilis*, a lizard with a vulnerable conservation status, following volcanic ash accumulation in Argentinian Patagonian steppe. This microendemic species inhabits specific volcanic rocky outcrops, in cold and arid environments of Ingeniero Jacobacci, Río Negro, Argentina. We used the body condition index, an useful method for quantifying the energy reserves of animals, and we studied this index and the female reproductive cycle during the first (years 2011–2012) and the second (years 2012–2013) activity season post-eruption, and discussed the results in relation to the body condition and the reproductive cycle studied before eruption (years 2006–2011). We found that only 12% of adult females were reproductive during the first activity season, which indicates that most *P. spectabilis*, skipped reproduction the year of eruption. In contrast, during the second activity season 83% of adult females were reproductive. However clutch size was changed to one to three offspring, instead of the typical two offspring reported for *P. spectabilis* before the Puyehue eruption, which is also characteristic of the *Phymaturus* genus. In addition, body condition of offspring born during the second activity season was significantly lower than offspring born before the eruption. We found that body condition of juveniles and adult males was significantly lower during the first activity season than before eruption and significantly higher during the second year. The lack of improvement in the body condition of non-reproductive females during the first years might explain the skip in the reproduction given that a good body condition is crucial for reproduction. These results suggest that the ash fall caused changes in the reproduction and the body condition of a population of a lizard, *P. spectabilis*, during the first activity season. However, the population showed rapid recovery during the second activity season post-eruption, indicating heretofore unobserved plasticity in litter size.

Key Words.—abdominal palpation; conservation; Patagonia; Puyehue-Cordón Caulle

INTRODUCTION

Puyehue volcano in the southern volcanic zone of the Andes (33–46° South Latitude) is a largely basaltic stratovolcano that is mainly a product of basaltic eruptions that occurred during the late glacial time Pliocene-Pleistocene (Gerlach et al. 1988; Rapella et al. 1988; Singer et al. 2008). Historical data in the Puyehue-Cordón Caulle system indicates that eruptive activity is highly irregular (years 1893, 1905, 1921–1922, 1922, 1929, 1934, 1960, and 2011; Barrientos 1994; Singer et al. 2008; Complejo Volcánico Puyehue-Cordón Caulle 2012. Available from <http://www.sernageomin.cl/archivos/Volcanes/2012091304582290FichaVnPuyehueCord%C3%B3nCaulle.pdf> [Accessed 27 February 2013]), offering scarce opportunities to study this natural catastrophic disturbance on ecological native communities. The last eruption of Puyehue–Cordón Caulle complex started on 4 June 2011, and dispersed about 100 M tons of pyroclastic materials onto the Patagonia steppe of Argentina due to the West-East predominant winds (Gaitán et al. 2011). Approximately 65 tons of materials have been deposited per ha from San Carlos de Bariloche in the west to Ingeniero Jacobacci and Pilcaniyeu in the east (Río Negro,

Argentina; Gaitán et al. 2011; Ghermandi and González 2012).

This volcanic eruption of Puyehue–Cordón Caulle complex had a direct and manifest consequence on the biota, resulting in immediate and massive habitat loss. In Río Negro province, more than 3,300 ha were affected by the deposition and accumulation of volcanic ashes (Gaitán et al. 2011), causing an immediate impact on vegetation (Grosfeld and Puntieri 2011; Ghermandi and Gonzalez 2012), insects (Buteler et al. 2011; Huerta 2011; Martínez et al. 2012; Fernández-Arhex et al. 2013); availability of forage (Siffredi et al. 2011), and health of sheep, goat, and bovines (Robles 2011). The volcanic volatile elements and ashes of Puyehue eruption presents high concentrations of components with high insecticide potential (SiO₂ and Al₂O₃; Bubach et al. 2012; Buteler et al. 2011; Caneiro et al. 2011; Fernández-Arhex et al. 2013). After the Puyehue eruption, Honeybee (*Apis mellifera*) mortality exceeded the normal proportion in the affected areas of Río Negro and Neuquén (Huerta 2011) due to the abrasion on nectar bearing structures and the effects on plant-pollinator relationships (Martínez et al. 2012). In areas where rains fell at the same time as the ash deposition (e.g., in Pilcaniyeu), ashes were found attached to the plant biomass

and this could further reduce the availability of forage by 90 to 100% (Siffredi et al. 2011). On the other hand, in areas where it did not rain (e.g., Jacobacci), the availability of forage was reduced 30 to 50% (Siffredi et al. 2011). Some areas of San Carlos de Bariloche, Pilcaniyeu and Ingeniero Jacobacci, have experienced almost daily ash fall 12 mo after the initial eruption (Complejo Volcánico Puyehue-Cordón Caulle. 2012. Available from <http://www.sernageomin.cl/archivosVolcanes/2012091304582290FichaVnPuyehueCord%C3%B3nCaulle.pdf> [Accessed 27 February 2013]).

The recent eruption of Puyehue-Cordón Caulle Volcanic Complex has provided a unique opportunity to study how the deposition of volcanic ash affects the biology of endemic lizards. Cabezas-Cartes et al. (2013) showed that the presence of volcanic ashes in the substrate must have affected the locomotor performance of the lizard *Phymaturus spectabilis* in the field, and hence, the interactions of these lizards with their environment. In particular, behaviors involving long runs (1.05 m), such as feeding and social behaviors, were affected (Cabezas-Cartes et al. 2013).

Prior to the volcanic eruption, the lizard *P. spectabilis* had been studied during its activity seasons from 2006 to 2011. Females showed an annual-biennial reproductive cycle while males showed an annual and seasonal male reproductive cycle (Boretto et al. 2014). Males are ready to mate during the spring months, and gestation occurs from mid spring until late summer, when each female gives birth to two offspring (Boretto et al. 2014). Herein we documented the changes in the reproductive cycle of *P. spectabilis* during the first and the second activity seasons after the eruption of Puyehue-Cordón Caulle Volcanic Complex occurred in June 2011. Changes in body condition of newborns, juveniles, and adult males and females of *P. spectabilis* are also reported.

MATERIALS AND METHODS

Capture site.—We carried out field work in a volcanic rocky plateau 25 km south of Ingeniero Jacobacci, Río Negro, Argentina (41°S and 69°W, 983–1064 m elevation), where there are several microendemic species of the genus *Phymaturus*. *Phymaturus spectabilis* is found in only a few outcrops in the area (Lobo and Quinteros 2005; Pincheira et al. 2008). This place is included in the Geomorphologic Region of Endorheic Depressions, in the arid district of the Monte Austral (Godagnone and Bran 2009). The dominant landscape is characterized by barren steppe and dissected rolling plains interspersed with rocky outcrops and vegetation of shrub-steppe grassy appearance (Cabrera 1971; Godagnone and Bran 2009). There is low herbaceous coverage, composed of sparse cushion bushes (*Stipa papposa*, *S. speciosa*, *S. humilis*, *Poa ligularis*, and *Bromus catharticus*) and subshrubs (*Senecio filaginoides*, *Nassauvia glomerulosa*, and *Grindelia chiloensis*) with bare soil percentages above 50% (Cabrera 1971). After the Puyehue eruption, soil and vegetation were entirely covered by large amounts of volcanic material (Figs. 1). We observed that wind action has reduced the amount of ash in the rock promontories, but ash accumulations

persisted on rock promontories protected from the west winds (Fig. 1E).

Field trips and specimens used.—We went to the field during the first (November 2011–February 2012; mid spring-midsummer) and second activity seasons (December 2012–January 2013) after the eruption of Puyehue-Cordón Caulle Volcanic Complex that occurred 4 June 2011. During these field trips, we captured 243 lizards of *P. spectabilis* by slipknot, in granite rock outcrops from 0900 to 1900. We weighed (body mass, 100-g spring scale \pm 0.5 g; Pesola AG, Baar, Switzerland), measured (snout vent-length [SVL], digital gauge, \pm 0.02 mm, Lee Tools®, China), determined sex (by the presence of precloacal pores in males), classified by abdominal palpation (see further explanation below), marked (toe-clipping), and released each lizard to the capture site based on the data registered with a GPS at the moment of capture (3-m resolution). In addition, we used a data set of specimens collected during the activity season before volcanic eruption (spring 2010–late summer 2011; n = 171; Boretto et al. 2014) to compare the body condition of the population (newborns, juveniles, adult males and females) and changes in the reproductive cycle of females before and after ashes accumulation.

After measurements and palpation, we released all lizards except those adult females with external signs of advanced gravidity that we transported to the laboratory (one female captured during summer 2012 and 13 females captured during summer 2013). We maintained gravid females in the laboratory until parturition to determine if date of parturition, clutch size, or body condition (body mass and SVL) of progeny born in captivity changed as a consequence of ashes accumulation, compared to data obtained in summer 2011 before the eruption. We maintained all females under the same conditions with food and water *ad libitum* in an individual open-top glass terrarium (35 \times 20 \times 20 cm) with a sandy substrate and a rock from the field site as shelter, UV lamp (Sylvania-Reptistar®, Germany) and an infrared lamp (150W; General Electric®, Hungary) on one side to provide a gradient of temperatures. Air temperature in the room ranged from 18.8–23.1° C. We registered the dates of parturition, clutch size, body mass, and SVL of each newborn. When all females gave birth, we transported each one with their newborns for release at the original capture site of the mother.

Environmental variables.—We obtained the total daily precipitation (mm) and the maximum, minimum, and mean daily temperature (° C) from January 1999 to March 2013 from the meteorological station of the National Meteorological Service, Argentinean Air Force, located in Maquinchao 70 km from Ingeniero Jacobacci. We recorded the operative temperature (T_c) on the ground every 10 min from late spring (December) 2010 to late spring (December) 2013 using data loggers (Hobo Pendant Temperature Data Logger) with PVC thermal models that simulate the thermal properties of a lizard, placed in similar conditions and exposed to solar radiation throughout the



FIGURE 1. Photographs taken in Ingeniero Jacobacci before (A and C) and after (B, D, E, and F) the ash fall produced by the eruption of Puyehue-Cordón Caulle complex. We illustrate (B) the ash fall blocking the sun and covering the environment, five months after eruption; (D) the land and vegetation affected by ash accumulation; (E) the action of wind reduced the amount of ash in the rock promontories, but ash accumulations persisted on rock promontories protected from the west winds (arrow) 17 months after eruption; (F) an individual *Phymaturus spectabilis* with ashes in its nose.

day. We designed the models using simultaneous comparisons of the body temperatures of live *P. spectabilis* to that of copper and PVC models of different sizes and colors. We used catheter probes TES TP-K01 simultaneously to register the temperatures of both the models and the lizards. We made the calibration experiments during consecutive hours and the best-fit model was a flat-gray PVC cylinder with dimensions of 90×20 mm (Spearman Rank Order Correlation body temperature vs. model, $r_s = 0.957$, $n = 51$, $P < 0.001$; Joel Gutiérrez, unpubl. data). We deployed the thermal models at different potential micro-environments used by lizards when they are in activity, such as sun or shadow. Considering the daily temperature recorded by the models, we estimated the potential activity hours of lizards considered as the hours that the lizards are outside of their shelters, performing behaviors related to basking, foraging, reproduction, and/or dispersal (Ibargüengoytía 2005). We assumed that the minimum temperature of activity is 20.0°

C because it is known to be the threshold temperature when *Phymaturus* starts activity in the field (Ibargüengoytía 2005) and the maximum temperature of activity in the field as the mean preferred body temperature (33.7° C; Joel Gutiérrez, unpubl. data). Following Sinervo et al. (2010), when the thermal availability of the habitat based on the operative temperatures exceeded the preferred body temperature, we assumed that individuals would be forced to retreat to colder crevices, which subsequently limits foraging and mating encounters. Consequently, we estimated the number of activity hours as the number of hours per day that at least one of the models showed temperatures between 20.0° C and 33.7° C.

Reproductive condition.—We performed abdominal palpation on 243 lizards captured from mid spring to late summer 2011–2012 and 2012–2013 to determine reproductive condition in males and females. We palpated each specimen involving gently rolling sections of the

TABLE 1. Climate data (Maximum and Minimum Temperature [° C], Total Precipitation [mm], and hours of activity [h]), reproductive data (percentage of vitellogenic and gravid females and clutch size), body mass (g), and body condition index of lizards *Phymaturus spectabilis* before Puyehue-Cordón Caulle eruption and during the first year and second year post-eruption. Mean and standard errors, or median, are indicated.

	<u>Before eruption</u> (Jun 1999-May 2011)	<u>First year post-eruption</u> (Jun 2011-May 2012)	<u>Second year post-eruption</u> (Jun 2012-Mar 2013)
<u>Climatic data and hours of activity</u>			
Maximum Temperature	16.47 ± 7.28	17.05 ± 8.14	16.98 ± 7.76
Minimum Temperature	2.75 ± 5.20	2.24 ± 6.35	2.65 ± 6.13
Total Precipitation	0.51 ± 0.79	0.34 ± 1.69	0.30 ± 1.56
Hours of Activity	12.00 (summer)	4.30 (summer) 3.00 (spring)	0.00 (spring)
<u>Reproductive data</u>			
Vitellogenic and gravid females	59%* (n = 36)	12% (n = 3)	87% (n = 33)
Clutch size	2* (n _{gravid females} = 14)	---	1 to 3 (n _{gravid females} = 13)
<u>Body mass (Body Condition Index)</u>			
Newborns	4.60 (0.125 ± 0.029)	---	4.55 (0.002 ± 0.021)
Juveniles	13.00 (-0.079 ± 0.023)	12.25 (-0.009 ± 0.024)	17.00 (0.054 ± 0.015)
Adult non-reproductive females	25.00 (-0.035 ± 0.027)	22.25 (-0.002 ± 0.031)	25.25 (0.097 ± 0.028)
Early gravid females	32.00 (-0.011 ± 0.023)	---	28.00 (-0.044 ± 0.018)
Advanced gravid females	31.75 (-0.067 ± 0.108)	---	34.50 (0.158 ± 0.021)
Males	26.00 (-0.009 ± 0.012)	23.25 (-0.046 ± 0.024)	25.00 (0.033 ± 0.009)

*data from Boretto et al. (2014).

lizard's abdomen between thumb and fingers to feel the size and shape of structures within the ventral section of the body, following Sinervo and Licht (1991). According to abdominal palpation and body size (SVL), we classified females following the criteria tested through morphological and histological analyses of the gonads used in Boretto et al. (2014) as juveniles, adult vitellogenic females, gravid, and non-reproductive adult females. We followed the criteria described in Boretto et al. (2014) to classify males as juveniles or adults using abdominal palpation, SVL, and the presence/absence of combat marks.

Statistical analysis.—We used the statistical software Sigma Stat 3.5[®] (Systat Software Inc., Chicago, Illinois, USA), SPSS 17.0[®] (Chicago, Illinois, USA), and Sigma Plot 10.0[®] (Systat Software Inc., Chicago, Illinois, USA). All data met the assumptions for parametric analysis unless otherwise stated. When the data did not meet the assumptions of normality and homogeneity of variance required for parametric tests, we used non-parametric test. We analyzed the data using linear regression analyses, Spearman Rank Order Correlation, *t*-tests (unpaired and paired), one-way Analysis of Variance (ANOVA), Kruskal-Wallis one-way Analysis of Variance on Ranks, Mann Whitney Rank Sum, and Wilcoxon Signed Rank Test and Dunn's Method. For the analysis of changes in body condition of lizards before and after Puyehue eruption, we used the body condition index (BCI) of each individual as an estimator of the energy stores or fat reserves. We calculated the BCI of each lizard as the residual score of the Linear Regression of ln-transformed body mass against ln-transformed SVL (Waye and Mason 2008). Lizards that weigh more than predicted for their length have a positive residual (BCI) and were considered to being relatively good condition. We divided the data set

into groups: newborns and juveniles; non-reproductive adult females; reproductive females; adult males. We used a one-way ANOVA, with year as the factor, to compare BCI before and after Puyehue eruption. We then used the Tukey test to find the sources of variation.

We tested assumptions of normality and homogeneity of variance using the one-sample Kolmogorov-Smirnov test and the Levene test, respectively (Sokal and Rohlf 1969). Analyses were considered statistically significant when $P < 0.05$. Means are given ± 1 SE.

RESULTS

Climatic changes.—The maximum daily temperatures during the first (June 2011-June 2012; $t = -1.72$, $df = 340$, $P = 0.087$) and second years after eruption (June 2012-March 2013; $t = 0.010$; $df = 275$, $P = 0.991$) were not different from historical data collected before the eruption (June 1999-June 2011). Nevertheless, the minimum daily temperatures were significantly lower during the first ($t = 2.19$, $df = 355$, $P < 0.029$) and the second year ($t = 2.96$, $df = 281$, $P < 0.003$) after eruption. The comparison of the daily temperatures after eruption showed that maximum daily temperatures were higher during the first than during the second year ($W = -4551.00$, $n = 292$, $P < 0.044$), but there were no significant differences in the minimum daily temperatures between the first and the second years post-eruption ($t = 1.12$, $df = 277$, $P = 0.265$; Figs. 2; Table 1).

We found that the daily total precipitation during the first and the second year after the Puyehue eruption were significantly lower than before the volcanic event (June 1999-May 2011 versus June 2011-May 2012 mean daily total precipitation, $W = -23802.00$; $n = 366$, $P < 0.001$; June 1999-February 2011 versus June 2012-February 2013 mean daily total precipitation, $W = -12388.00$, $n = 270$, $P < 0.001$). Daily total

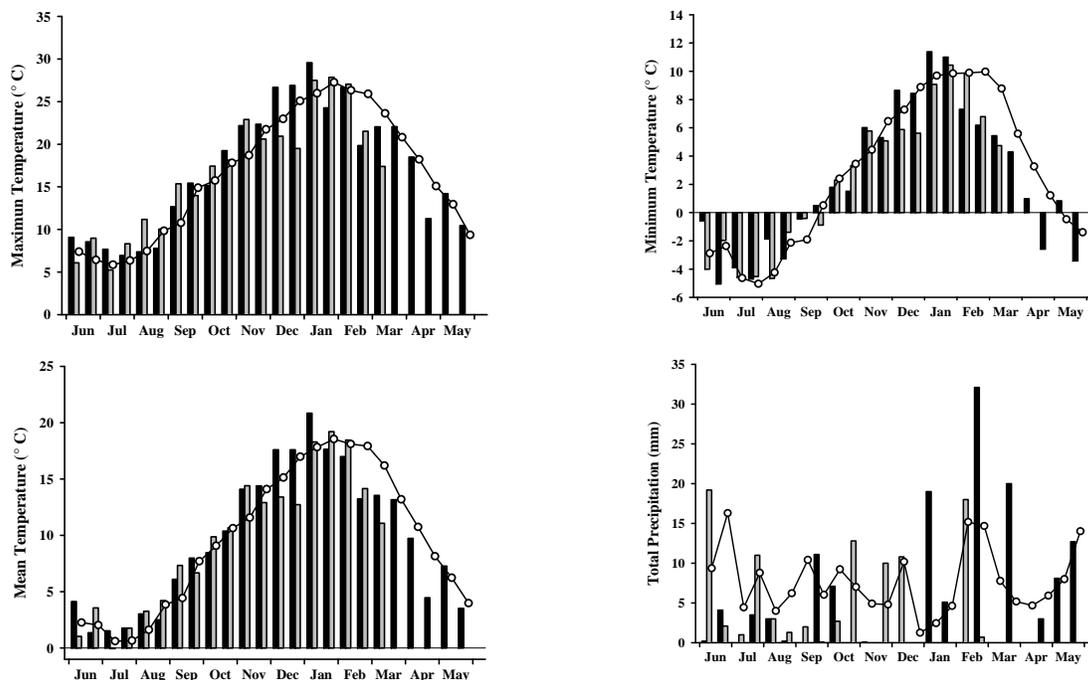


FIGURE 2. Climatic conditions from the nearest meteorological station to the study site (Maquinchao, 70 km northeast of Ingeniero Jacobacci) before eruption of Puyehue-Cordón Caulle complex (from January 1999 to May 2011; solid line), during the first activity season post-eruption (June 2011 to May 2012; black bars) and during the second activity season post-eruption (June 2012 to March 2013; gray bars). Biweekly means of maximum (A), minimum (B), and mean (C) temperatures ($^{\circ}\text{C}$), and biweekly means of total mean precipitation (D) are presented.

precipitation during the first year was not significantly different from those from the second year post-eruption ($W = -113.00$, $N = 270$, $P = 0.620$; Fig. 2D; Table 1).

Potential hours for lizards activity.—During the summer period (12 December to 8 February) that corresponds to the period of gestation in females *P. spectabilis*, lizards had significantly fewer hours of activity during the first activity season post-eruption (5.03 ± 0.43) than before eruption (9.36 ± 0.68 ; $U = 857.50$, $n = 118$; $P < 0.001$; Table 1). The hours of activity during the spring period (1 October to 12 December) that corresponds to the

period of time when females normally exhibit the peak of vitellogenesis and ovulation (Boretto et al., unpubl. data) did not show differences between the first (3.8 ± 0.61) and the second year post-eruption (3.10 ± 0.56 ; $U = 1037.50$, $n = 146$; $P = 0.223$; Table 1).

Changes in the female reproductive cycle.—We found that from the total sample of adult females captured during the first activity season after Puyehue eruption (spring 2011–summer 2012; $n = 25$) that only one female presented prominent follicles in the ovary in mid spring, one female presented one embryo in uterus by abdominal palpation in

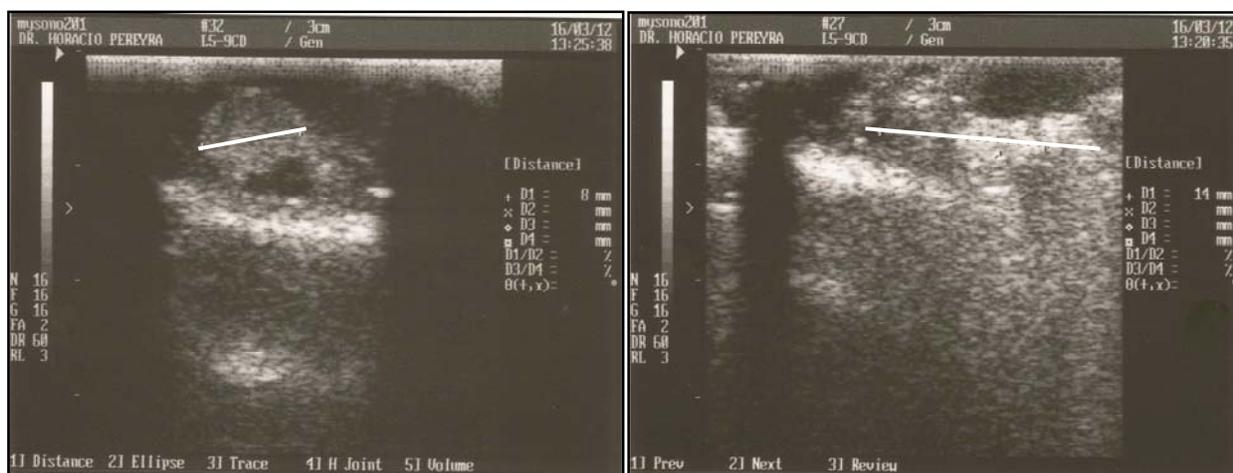


FIGURE 3. Ultrasound monitoring of female *Phymaturus spectabilis*. A vitellogenic female with a follicle of 8 mm (left), and a gravid female with an early developed embryo of 14 mm long (right) are shown.

late spring, and we captured one female gravid in midsummer (1 February 2012), which was confirmed by echography (Fig. 3; Table 1). We transported this single gravid female captured in midsummer to the laboratory and maintained her in captivity until early autumn (28 March 2011), but parturition did not occur.

During the spring of the second activity season after Puyehue eruption, we captured and palpated 24 adult females. Twenty were reproductive females and four were non-reproductive females (Table 1). In early summer, we transported 13 adult females captured with external signs of advanced gravidity to the laboratory and maintained them in captivity until parturition. All females gave birth in midsummer, from the third week of February until the first week of March. Ten gravid females gave birth to two offspring each, whereas two females gave birth to three offspring each, and one female gave birth to only one offspring (Table 1). The offspring born in captivity appeared in good body condition ($SVL_{\text{range}} = 44.4\text{--}50.6$ mm; $\text{body mass}_{\text{range}} = 3.4\text{--}5.6$ g; $BCI_{\text{range}} = 0.21\text{--}0.23$; Table 1), except for one that died during the parturition from the female that gave birth to three offspring.

The analysis of the reproductive stages of recaptured adult females showed the skipping of reproduction during the first year post-eruption. This was based on three gravid females that we captured during the activity season before eruption that were non-reproductive during the first activity season post-eruption (Fig. 4). In addition, five non-reproductive females we captured during the first activity season were gravid during the second activity season after the volcanic eruption (Fig. 4).

Changes in body condition index of lizards.—We found that newborns born in captivity during the second activity season after Puyehue eruption had lower BCI than offspring born before eruption ($t = 3.51$, $df = 46$, $P < 0.001$; Table 1). In addition, juveniles exhibited significant differences in BCI among the years ($F_{2,145} = 9.16$, $P < 0.001$); specifically, the juveniles captured during the first year post-eruption exhibited significantly lower BCI than juveniles captured before eruption ($P < 0.047$), and juveniles captured during the second year after eruption exhibited significantly higher BCI than before eruption ($P < 0.001$; Table 1).

Body condition of adult non-reproductive females captured both before and after eruption did not exhibit significant differences ($F_{2,50} = 3.10$, $P = 0.054$). Gravid females captured at the beginning of gestation in late spring of the second year after eruption did not exhibit significant differences in BCI than gravid females captured in late spring of the activity season before eruption ($t = 1.13$, $df = 38$, $P = 0.138$). However gravid females with advanced stages of gestation captured during the second year post-eruption (mid-summer 2013) showed higher BCI than those gravid females captured before eruption (mid-summer 2011, $t = -2.32$, $df = 21$, $P < 0.001$; Table 1).

Adult males captured during the first year after eruption exhibited significantly lower BCI than males captured during the second activity season post-eruption ($F = 7.44$, $P < 0.001$; Tukey, $P < 0.001$), but there were no differences between adult males captured the first activity season post-eruption and before eruption ($P = 0.206$), nor were there differences between males captured the second activity season post-eruption against before eruption ($P =$

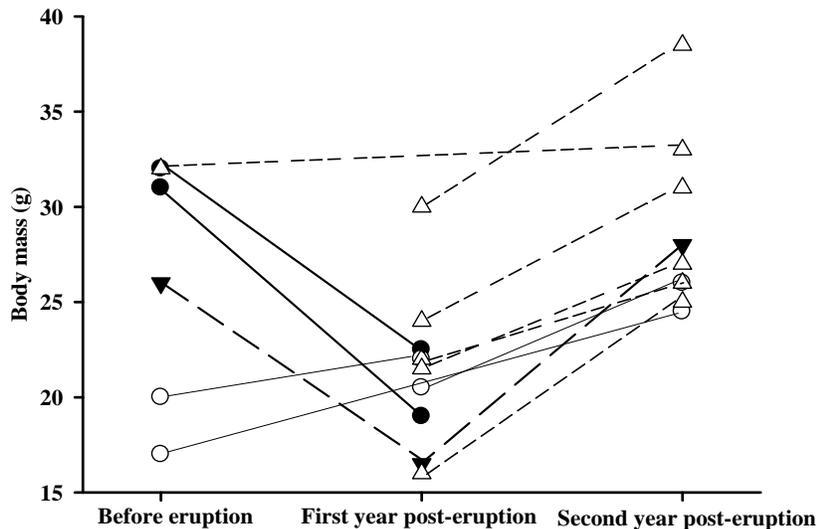


FIGURE 4. Body mass and reproductive stages of recaptured adult females of *Phymaturus spectabilis*, showing the skipping of reproduction during the first activity season after Puyehue-Cordón Caulle eruption. Females captured gravid before eruption and subsequently captured non-gravid during the first activity season post-eruption (black circles); females captured non-gravid in each activity season (white circles); females captured gravid before eruption, non-gravid during the first activity season, and gravid during the second activity season post-eruption (black triangles); females captured non-gravid twice (white triangles), are presented.

0.058).

Juvenile lizards recaptured the first ($t = -1.44$, $df = 8$, $P = 0.187$) or the second activity season post-eruption ($t = -1.68$, $df = 6$, $P = 0.143$) did not show significant changes in their body condition than before the Puyehue eruption. Similarly, juveniles captured during the first activity season post-eruption and recaptured in the second year did not exhibit significant differences in their body condition ($U = 75.00$, $P = 0.064$).

Recaptured adult males and non-gravid females *P. spectabilis* did not exhibit significant differences in body condition before and after the first year post-eruption ($t = -1.04$, $df = 10$, $P = 0.323$), or between the first and the second activity season post-eruption ($U = 83.00$, $n = 11$, $P = 0.149$). However, adult lizards captured during the activity season before eruption and recaptured during the second activity season post-eruption, exhibited a significant increment in their BCI ($t = -4.88$, $df = 10$, $P < 0.001$).

DISCUSSION

Volcanism is a natural phenomenon in the Patagonian Region, and, especially during the Tertiary and Quaternary periods, it has deposited large amounts of pyroclastic materials (Rapella et al., 1988; Singer et al., 2008), giving rise to volcanic and basaltic environments that *Phymaturus* lizards inhabit. The type locality of several species of Liolaemids is near a volcano in the Andean Mountains (Ceï 1986, 1993; Pincheira-Donoso et al. 2008; Morando et al. 2013, among others), a region with an important historical volcanic activity. Phylogeographic evidence suggests that these lizards have evolved in the presence of this natural disturbance (Singer et al. 2008), which might have produced localized extinctions followed by immigration from unaffected areas (Díaz-Gómez 2009). The present study documents how catastrophic changes in the environment, as a consequence of the deposition of large amounts of volcanic ashes of the eruption of Puyehue-Cordón Caulle complex starting on 4 June 2011, affected the female reproductive cycle and changed the clutch size and the body condition of newborn, juvenile, and adult male and female *Phymaturus spectabilis*. The detrimental effects of ashes observed herein on reproduction and body conditions of *P. spectabilis* agrees with performance results of Cabezas-Cartes et al. (2013), which highlights that ashes affected the locomotion of lizards, perhaps increasing risk of predation by birds or mammals.

Studies performed before the recent volcanic event (2006–2010 years) showed that females of *P. spectabilis* reproduce annually or biennially and exhibit a fixed clutch size of two offspring (Boretto et al. 2014). A similar female reproductive cycle and a low clutch size have been reported in other *Phymaturus* that inhabit the Patagonian steppe of Argentina (*P. tenebrosus*, Ibargüengoytía 2004; *P. zapalensis*, Boretto and Ibargüengoytía 2009). The cold and desert environments of the Patagonia Argentina where *Phymaturus* inhabit, together with hormonal and physiological restrictions inherent to ovoviviparity (Callard et al. 1992; Custodia-Lora and Callard 2002), prevent females from completing vitellogenesis, becoming gravid,

and storing fat within one activity season (Ibargüengoytía 2004; Ibargüengoytía et al. 2008; Boretto and Ibargüengoytía 2009). It has been proposed that flexibility in frequency of reproduction is a coping mechanism to unpredictable climates or when the length and thermal quality of the activity season are variable (Boretto and Ibargüengoytía 2006; 2009). When the activity seasons are relatively cool and/or short and postpartum feeding opportunities are limited, females devote the following season to growth and store reserves (e.g., capital breeding) for future reproductive bouts, but under benign conditions, reproduction can resume within one year (Saint Girons 1985; Cree 1994; Ibargüengoytía and Cussac 1996; Boretto and Ibargüengoytía 2009). The result found in the present study adds support to these observations, given that females of *P. spectabilis* clearly skipped reproduction during one year, as a mechanism to cope with detrimental environmental changes caused by Puyehue eruption. During the activity seasons before the eruption (2006 to 2011 years), 59% of adult females were vitellogenic or gravid each year (Boretto et al. 2014), whereas only 12% of females were reproductive during the first activity season after ash fall. Additionally, gravid females captured in summer 2011 with external signs of advanced gravidity gave birth during mid-February 2011, while the only one gravid female captured in summer 2012 (confirmed by echography and kept in a laboratory in the same conditions until mid-April) did not give birth. The delay in date of births would be deleterious for newborns because late births reduce the time to feed and store reserves for the brumation period (Wilson and Cree 2003).

The skipping of a year of reproduction in *P. spectabilis* females, the lower body condition of juveniles and adult males, and the lack of improvement in the body condition of non-reproductive females during the first activity season after eruption may be a consequence of a combination of different factors. Ash accumulation in the field has detrimental effects on vegetation (Grosfeld and Puntieri 2011; Ghermandi and González 2012) and insects (Buteler et al. 2011; Huerta 2011; Martínez et al. 2012; Fernández-Arhex et al. 2013). We also documented climatic changes on precipitation and temperature after Puyehue eruption. Precipitation significantly decreased after eruption and the drought period extended even to the second activity season post-eruption of lizard *P. spectabilis*. The great amounts of ashes in the field, and the lower precipitation that limited the ash incorporation into the soil, has caused a great impact on vegetation, reducing the presence of plant species in gaps and the recruitment of annual and matrix dominant species (Ghermandi and González 2012). In addition, a radical and immediate insecticidal effect of ashes has been reported on the insect community, for insect host plants, and pollination (Buteler et al. 2011; Huerta 2011; Martínez et al. 2012; Fernández-Arhex et al. 2013). It is expected that the negative impact of ashes observed on vegetation and insects will hence affect the ecology of herbivorous and/or insectivorous lizard populations. While the genus *Phymaturus* has been considered strictly herbivores (Ceï 1986, 1993), new records showed that *Phymaturus* include insects in the diet, such as *P. zapalensis* (Boretto and Ibargüengoytía, 2009), *P. excelsus*

and *P. spectabilis* (Cabezas-Cartes and Scolaro, pers. comm.). The detrimental effects of ashes on insect community (Buteler et al. 2011; Huerta 2011; Martínez et al. 2012; Fernández-Arhex et al. 2013) and vegetation (Grosfeld and Puntieri 2011; Ghermandi and Gonzalez 2012), as well as the reduced availability of forage (Siffredi et al. 2011) will likely affect the normal feeding of lizards. This could alter the body conditions of individuals and, as a consequence, the reproductive cycles of females *P. spectabilis*, because variation in food availability and nutritional content is reflected in changes in the growth rates and scarcity of calcium, important for the vitellogenesis, with attendant effects on reproduction (Lagarde et al. 2003). In addition, while we did not find significant changes in the maximum daily temperatures, we found that the minimum temperatures were lower during the first and the second activity season after eruption. These results are consistent with comparisons of the number of activity hours of lizards because we found that lizards had more hours of activity before eruption than after eruption. This drop in activity time was likely due to the impact of ash in the atmosphere, lowering incident solar radiation for these *Phymaturus* lizards that bask to maintain activity body temperatures.

Environmental catastrophes are predicted to have a major influence on the survival of small, isolated animal populations. For example, volcanic ash has had a significant impact on forest canopy arthropods, but this effect was limited in both intensity and duration (Marske et al. 2007). Similarly, most species of forest bird community of the Lesser Antillean island of Montserrat were substantially lower following major ash falls from the eruption of the Soufrière Hills volcano; however, it was observed that this effect was short-lived, with rapid population recovery in subsequent years (Dalsgaard et al. 2007). We found that the consequences for female reproduction and body condition of lizards *P. spectabilis* was of a limited duration, given that during the second activity season after eruption, the majority of adult females captured were reproductive and body condition of juveniles and adults males were higher than during the first activity season post-eruption. In addition, gravid females captured in mid-summer 2013 gave birth in February-March, in the same period of time as before eruption. Nevertheless, some effects persist during the second activity season, the clutch size was changed (fixed in two before eruption versus one to three after eruption), and the body condition of lizards born in captivity from gravid females captured before eruption (summer 2011) were better than offspring born in captivity from gravid females captured after eruption (summer 2013). We observed an important re-vegetation during the second activity season and the action of winds reduced the amount of ash in the rock promontories that *P. spectabilis* inhabit (pers. obs.). The ecological recuperation of the environment and the apparent improvement in feeding opportunities by re-vegetation could explain the increased percentage of reproductive females (83%) and the higher body conditions of lizard's *P. spectabilis* during the second activity season comparing with the first activity season post-eruption.

Volcanic ash produced disorders in the health of livestock aggravated according to the quantity and chemical composition of ash falls, the presence of winds, or rains (Robles 2011). Several individual *P. spectabilis*, *P. tenebrosus*, *Homonota darwini*, and *Liolaemus elongatus* were found with ashes in the nose and eyes, as well as sliding on rocks (Cabezas-Cartes et al. 2013; pers. obs.). The decreased forage (Siffredi et al. 2011) has resulted in the several cases of animal death by inanition, and ashes also caused diarrhea in bovines, colic, and death in equines, and spontaneous abortion in goats, which are typical responses to stressful climate and/or food stress (Robles 2011). While lizards of *P. spectabilis* showed a remarkable physical and reproductive recovery in the second activity season after eruption, it is necessary to track the population to continue the study of the consequences of this natural event especially considering that all *Phymaturus* of the *patagonicus* group including *P. spectabilis*, have a Vulnerable status of conservation (Abdala et al. 2012).

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JORGELINA M. BORETTO is an Assistant Investigator of CONICET, and conducts research in the Laboratory of Eco-physiology and Life History of Reptiles of the Department of Zoology at INIBIOMA (CONICET-Universidad Nacional del Comahue), San Carlos de Bariloche city, Río Negro Province, Argentina. She has a Ph.D. from Centro Regional Universitario Bariloche of Universidad Nacional del Comahue. Her research interests include the study of reproductive biology, environmental endocrinology, and conservation of lizards of the genus *Phymaturus* and others liolaemids from cold climates of Patagonia Argentina. (Photographed by Carla Piantoni)



FACUNDO CABEZAS-CARTES is a Doctoral Scholarship Fellow of Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) at Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA) in Bariloche, Argentina. He graduated with a degree in biology from the Universidad Nacional de Córdoba and is currently a Ph.D. student at the Universidad Nacional del Comahue. His research interests include ecophysiological adaptations to harsh climates, biogeography, and conservation of *Phymaturus* lizards. (Photographed by Jorgelina Boretto)



ERIKA KUBISCH is an Assistant Professor of Statistics. She has a Ph.D. in Biology from Centro Regional Universitario Bariloche of Universidad Nacional del Comahue. Her research interests include the study of ecophysiology, effects of climate change, and conservation of lizards and tortoises of Argentina. (Photographed by Jimena Fernández)



BARRY SINERVO is a Professor, Level VI, of Ecology and Evolutionary Biology, University of California, Santa Cruz. His research interests include behavioral ecology, effects of natural and sexual selection on reproduction, reptilian communities, speciation, and the effects of climate change on reptile populations. (Photographed by Erika Kubisch)



NORA R. IBARGÜENGOYTÍA is a CONICET Researcher and a Chair of the Laboratory of Ecophysiology and Life History of Reptiles of the Department of Zoology at INIBIOMA (CONICET-Universidad Nacional del Comahue), S.C. de Bariloche, Argentina. Her major interest is in the ecophysiological evolution of squamate reptiles. Her research has focused largely on reproductive biology, thermal physiology, and the effects of climate change on reptile populations. Her current projects include studies on physiological responses to cold climate, evolution of viviparity, and effects of climate change on the genus *Phymaturus*, *Liolaemus*, and *Tropidurus*. (Photographed by Carla Piantoni)