



Volcanic ash from Puyehue-Cordón Caulle eruptions affects running performance and body condition of *Phymaturus* lizards in Patagonia, Argentina

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The Puyehue-Cordón Caulle eruption of 4 June 2011 dispersed about 100 million tonnes of pyroclastic materials resulting in ash accumulations of 30 cm depth on the Patagonian steppe, an area occupied by several lizard species. Herein we analysed, by experimental trials, the effects of ash and slope on running performance of two endemic and vulnerable species, *Phymaturus excelsus* and *Phymaturus sinervoi*, restricted to volcanic rock outcrops in Patagonia. We also determined the effect of ash fall on body condition by comparing the same populations before and after the volcanic eruption. Locomotion of *P. excelsus*, adapted to rocky and steep outcrops, was more affected in a negative way by ash. In contrast, *P. sinervoi*, which lives in mixed habitats with flat rocks and sandy substrates, ran more slowly on the inclined surface but was unaffected by ash, suggesting the two species are well adapted to the habitats they occupy. In spite of impacts of ash deposition on locomotion and potentially the feeding, reproduction and dispersal activity of *P. excelsus*, lizards captured 18 months after ash deposition showed improved body condition. Our study site for *P. sinervoi* received less ash deposition and hence body condition was similar before and after ash fall. We hypothesize that negative effects of ash on lizards were counteracted by competitive release; ash deposition caused an acute and significant increase in mortality of herbivorous competitors such as hares and sheep that feed upon the same flowers and fruits included in the *Phymaturus* diet. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, 118, 842–851.

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INTRODUCTION

Locomotor abilities of organisms not only directly affect fitness but can also indicate the state of

several underlying physiological and ecological processes such as metabolic balance, prey capture, food competition, territory defence, predator avoidance and mate choice (Irschick *et al.*, 2008; Vanhooydonck *et al.*, 2015). During locomotion, lizards have to adjust to variation in substrate parameters such as

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firmness, density, texture and a variety of obstacles and slopes that facilitate or impose constraints on locomotion (Huey & Hertz, 1982; Vanhooydonck *et al.*, 2015). Lizards often show specialized morphologies adapted to the substrates they most commonly use (Losos & Sinervo, 1989; Vanhooydonck *et al.*, 2015).

Nevertheless, extreme environmental changes can disrupt normal development or exceed the range of phenotypic plasticity on short time scales and at longer time scales they can affect an organism's life history (Badyaev, 2005). The Patagonian steppe has experienced volcanic eruptions of various magnitudes since the Miocene, 23.3 Mya (Giacosa & Heredia, 2004; Giacosa *et al.*, 2005), and this volcanic activity has continued during the Quaternary. Specifically, the Puyehue-Cordón Caulle volcanic complex is a stratovolcano with a 2.5-km-diameter summit caldera that has been active during the last 10 000 years with several explosive pulses (Lara, Naranjo & Moreno, 2004). The most recent eruptions were registered in 1893, 1914, 1919, 1921–1922 and 1960 (Singer *et al.*, 2008). Given this volcanic regime, it is reasonable to expect adaptations to ash by the organisms that live nearby. Despite the ecological and selective importance of volcanic disturbances, there are few studies of the consequences to ecosystems, probably because the opportunities to study them are relatively infrequent (Dalsgaard *et al.*, 2007; Novoa-Melson, 2013).

The Puyehue-Cordón Caulle volcanic complex (2236 m a.s.l., 40°02'S, 70°14'W) erupted on 4 June 2011 (GOES, 2011), after a quiescent period of 51 years (Singer *et al.*, 2008), and deposited 100 million tonnes of white, powdery ash covering 7.5 million ha in Patagonia, Argentina (Gaitán *et al.*, 2011). The ash also fell onto the austral forest along the Argentina–Chile border drifting throughout the steppe east to the Atlantic coast (Gaitán *et al.*, 2011; Novoa-Melson, 2013). In deserts, as in the north-west Patagonian steppe, dry ash persisted, imposing a diversity of disturbances on the dynamics of the ecosystem, affecting plants and animals including insects, domesticated livestock and reptiles (Buteler *et al.*, 2011; Grosfeld & Puntieri, 2011; Huerta, 2011; Ghermandi & Gonzalez, 2012; Martinez *et al.*, 2012; Fernández-Arhex *et al.*, 2013; Boretto *et al.*, 2014a; Cabezas-Cartes, Kubisch & Ibargüengoytía, 2014; Morales *et al.*, 2014).

In particular, several microendemic lizards restricted to isolated plateaus in the Patagonian steppe, the saxicolous genus *Phymaturus*, have endured the impact of the volcanic eruptions and subsequent ash accumulation at least once every 40 years since the Miocene (Schulte, 2013). The abrupt, severe and unpredictable nature of volcanic

eruptions changes the environment drastically by depositing layers of ash consisting of a range of grain sizes, turning the substrate into a granular and sliding surface, which not only can reduce foot traction and cause slippage (Vanhooydonck *et al.*, 2015) but also can affect the physiology of plants and insects which are the most important components of the diet of *Phymaturus* (Boretto & Ibargüengoytía, 2009). Recent studies showed that the volcanic eruption affected three important components of fitness of *Phymaturus spectabilis*, Lobo and Quinteros, 2005, (Fig. 1): running performance (Cabezas-Cartes *et al.*, 2014), body condition and reproduction (Boretto *et al.*, 2014a). Volcanic ash on the substrate negatively affected the locomotor performance of *P. spectabilis* (Cabezas-Cartes *et al.*, 2014). Similarly, Boretto *et al.* (2014a, b) registered a significant decrease in the body condition and a dearth of reproduction by *P. spectabilis* during the activity season that followed the eruption.

To test the hypothesis that ash deposition has affected the vital activities of lizards, we studied the effect of ash on lizard performance by conducting laboratory trials of running speed on ash and standard (cork) substrates of two *Phymaturus* lizards, *P. excelsus* Lobo & Quinteros, 2005 and *P. sinerovi* Sclaro, Méndez-de la Cruz & Ibargüengoytía, 2012 located in zones that received different amounts of ash (Figs 1, 2). We predicted the ash to diminish running performance during sprints (short runs usually used by lizards when frightened) and long runs, especially when tested on inclines because of slipping and sliding on the granular surfaces. In addition, considering the reduction of lizard food supplies by ash (Ghermandi & Gonzalez, 2012; Fernández-Arhex *et al.*, 2013), we analysed whether ash reduced body condition of lizards, comparing the body condition of both species before and after the eruption at the same locations.

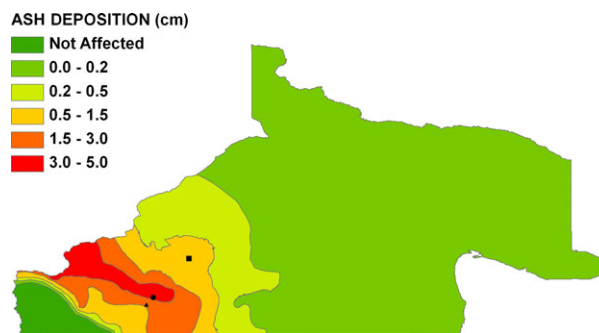


Figure 1. Ash deposition (cm), showing differences among localities of the species studied herein (square: *P. sinerovi* locality, triangle: *P. excelsus* locality) and the locality of *P. spectabilis* (circle) studied by Cabezas-Cartes *et al.* (2014).



Figure 2. Photographs of the species and the study sites showing the main landscape elements and ash deposition in the southern–central steppe of Rio Negro Province, Argentina. Abi-Saad farm (A, C) where *Phymaturus sinervoi* occurs and Ojo de Agua (B, D) where *P. excelsus* occurs.

MATERIAL AND METHODS

STUDIED SPECIES AND ENVIRONMENT

Phymaturus excelsus inhabit outcrops around the town of Ingeniero Jacobacci in varying degrees of isolation among the volcanic plateaus (see Scolari & Ibarguengoytia, 2007; Scolari & Ibarguengoytia, 2008). The population sampled in the present study inhabits the rocky top of a high plateau near Ojo de Agua (69°51'W, 41°32'S). The habitat has a moderately steep slope and the majority of the habitat consists of rocky substrate (Fig. 2). *Phymaturus sinervoi* inhabits sites 87 km north-east from the locality of *P. excelsus* (69°17'W, 40°53'S). Unlike the habitat of *P. excelsus*, *P. sinervoi* lives in an isolated biotope of the tableland with plains and plateaus surrounded by a sandy steppe with shrubs typical of the Patagonian Ecoregion (Morello *et al.*, 2012; Scolari *et al.*, 2012; Fig. 2).

The dominant landscape of the Patagonian Ecoregion, inhabited by both species, is characterized by a shrubby barren steppe, with open ground, gravel and effusive rocks, low herbaceous coverage, with coverage of bare soil exceeding 50% (Cabrera, 1971). The outcrops of Patagonia are characterized by a diverse, regionally varied flora (Speziale & Ezcurra, 2012). The predominant plant families are the Poaceae and Asteraceae adapted to the arid and harshly cold

environments present since the last glacial period; some of the plant species found on the southern walls of outcrops are considered relicts of a palaeoflora (Speziale & Ezcurra, 2012). Other important plant families present on the outcrops are the Solanaceae, Fabaceae and Boraginaceae. All families include important species of the diet of *Phymaturus*.

After the Puyehue eruption, soil, rocks and vegetation were entirely covered by large amounts of volcanic material (Fig. 2C, D). The depth of the ash layer varies in the two study sites, being deeper in the *P. excelsus* locality (Fig. 1). The presence of ash on the rocks changed their roughness making them more slippery for lizard locomotion. Also, ash covered the leaves of bushes from which *Phymaturus* feed, and reach rock crevices where lizards were hibernating. Two years after the eruption, we observed that wind action had reduced the amount of ash in the rock promontories, but ash accumulations persisted on rocks protected from the prevailing westerly winds (Cabezas-Cartes *et al.*, 2014).

The ecological and life-history traits of *P. excelsus* and *P. sinervoi* remain largely unknown, but preliminary observations reveal the lizards have a predominantly herbivorous diet and they are viviparous. Natural sympatric predators are the lizards *Leiosaurus belli* and *Pristidactylus nigroigulus*, the

colubrid snakes *Philodryas patagoniensis* and *Philodryas trilineata*, and the viperid *Rhinocerophis ammodytoides*, all of which are common in the study areas (Scolaro & Iburgüengoytia, 2007). Other predators are raptors and mammals including foxes and ferrets that are also abundant in the area (Cabezas-Cartes, 2013).

LIZARD CAPTURES

The individuals of *P. excelsus* ($N = 37$) and *P. sinervo* ($N = 19$) were captured by hand or noose in the Patagonian steppe in the vicinity of Ingeniero Jacobacci, Río Negro Province, Argentina (Table 1), on 12 and 13 December 2010 before the eruption of the Puyehue-Cordón Caulle Volcanic Complex. The same populations were sampled again on 6 and 7 December 2012, 18 months after the event: we captured *P. excelsus* ($N = 63$) and *P. sinervo* ($N = 29$).

The individuals captured in 2012 were used for locomotor performance trials and to compare body condition with the sample obtained in 2010 before the eruption. Each individual was geo-referenced (GPS Garmin Map 60C Sx) at capture to allow us to return each individual to the capture site after the experiments.

SEX, SEXUAL MATURITY AND MORPHOLOGY

After the experiments, we recorded body mass (using a 100-g Pesola spring scale ± 0.5 g) and snout-vent length (SVL) using a Vernier calliper (± 0.02 mm). Sex was determined by the presence of pre-cloacal pores in males and adulthood was determined according to the minimum adult sizes previously observed in the *patagonicus* group of the genus *Phymaturus* (80 mm for males and females; Iburgüengoytia, 2004;

Boretto & Iburgüengoytia, 2009; Boretto *et al.*, 2014b) and corroborated by abdominal palpation, criteria that were tested by Boretto *et al.* (2014b).

BODY CONDITION

For the analyses of body condition we used the scaled mass index (M_i) of each individual as an estimator of the energy store or fat reserves. The scaled mass index of condition (M_i) was calculated as:

$$M_i = M_i \times [\text{SVL}_0/\text{SVL}_i]b^{\text{SMA}},$$

where M_i and SVL_i are the mass and SVL of the individual, SVL_0 is the arithmetic mean SVL of the population, and b^{SMA} is the standardized major axis slope from the regression of \ln mass on \ln SVL for the population (Peig & Green 2009, 2010). The b^{SMA} exponent was calculated using the package 'lmodel2' (Legendre, 2015) in R (R Core Team, 2015).

We calculated the M_i of each lizard for adult males, non-pregnant adult females and juveniles; pregnant females were excluded from the analyses. We determined the statistical significance of the difference in mean M_i scores of each category before and after the eruption using a *t*-test.

LOCOMOTION PERFORMANCE TRIALS

Running trials were carried out with the lizards captured in December 2012. Immediately after capture, lizards were brought to the laboratory in individual cloth bags to minimize stress. The locomotor performance trials were carried out within 48 h of capture between 10:00 and 20:00 h, when lizards are normally active in their natural environment. Lizards were not fed during the experiments.

Table 1. Latitude, longitude and altitude (m a.s.l.) of the study sites, snout-vent length (SVL, mm) and body mass (g) of *Phymaturus excelsus* and *P. sinervo* captured in December 2010 (pre-eruption) and December 2012 (post-eruption)

| Coordinates and (altitude) of the study sites | Sex and reproductive condition | <i>N</i> | | SVL (mm) | | Body mass (g) | |
|---|--------------------------------|----------|------|------------------|------------------|------------------|------------------|
| | | 2010 | 2012 | 2010 | 2012 | 2010 | 2012 |
| <i>Phymaturus excelsus</i> | | | | | | | |
| 41.32°S, 69.41°W (1217 m a.s.l.) | Adult males | 17 | 22 | 87.58 \pm 0.78 | 88.08 \pm 0.71 | 24.26 \pm 0.48 | 27.0 \pm 0.57 |
| | Adult females | 13 | 33 | 88.75 \pm 1.27 | 92.09 \pm 0.60 | 24.11 \pm 0.90 | 30.91 \pm 0.61 |
| | Juveniles | 7 | 8 | 68.62 \pm 5.74 | 64.83 \pm 2.16 | 10.51 \pm 1.18 | 11.31 \pm 1.26 |
| <i>Phymaturus sinervo</i> | | | | | | | |
| 40.53°S, 69.17°W (997 m a.s.l.) | Adult males | 10 | 16 | 88.41 \pm 0.86 | 89.66 \pm 1.02 | 28.30 \pm 1.07 | 29.71 \pm 1.11 |
| | Adult females | 6 | 6 | 87.83 \pm 2.54 | 91.84 \pm 3.12 | 26.83 \pm 1.49 | 31.40 \pm 3.09 |
| | Juveniles | 3 | 7 | 65.33 \pm 7.02 | 67.64 \pm 2.45 | 10.33 \pm 2.91 | 11.71 \pm 1.51 |

Means \pm SE and sample sizes (*N*) are indicated.

The trials were carried out following the same methodology used by Cabezas-Cartes *et al.* (2014) at ambient temperatures (18.3–23 °C; Table 2), which were within the range of field active temperatures of *P. excelsus* (12–44.4 °C, our unpubl. data) and *P. sinervo* (17.1–33.5 °C, our unpubl. data). Before each run, the body temperature (T_b) of each lizard was measured using a catheter probe (TES TP-K01, 1.62 mm diameter) introduced *c.* 1 cm inside the cloacae connected to a TES 1303 thermometer (TES Electrical Electronic, ± 0.03 °C). Running trials were done on a racetrack 0.07 m wide and 1.05 m long (between the first and the last photocell), leading to a shelter. Photocells, positioned at 0.15-m intervals along the track and connected to a computer, sensed lizard motion and thereby speed over each 0.15-m section. During analysis, each run was broken into a sprint-run component (SR; first 0.15-m section), and secondly a long-run component (LR; 0.15–1.20 m), indicative of locomotor capacity of the lizard to perform activities such as foraging, territorial defence and courtship. Each lizard ran three consecutive times in each treatment combination and we did not find any effect of fatigue as we did not find differences among the first, second or third runs performed by each lizard (repeated-measures ANOVA, $P > 0.05$ in all treatments for trial effect). Thus, only the maximum run speed of the three runs performed for either SRs or LRs (V_{\max}) by each lizard was used in analyses.

EXPERIMENTAL DESIGN

Each specimen ran under four treatments in a randomized sequence, produced by a full factorial combi-

nation of track surface (cork or ash) and slope (incline or level). The angle of incline used for the treatment was 10°, which is the angle of repose of the very fine volcanic material. We used cork because it provides excellent traction without being abrasive (in contrast to sand paper) and is considered to induce optimal performance in most species (see Vanhooydonck *et al.*, 2015). To simulate the accumulation of volcanic ash in the field we covered the floor of the racetrack with a 0.5-cm layer of volcanic ash taken from the lizards' environment. Lizards always rested for at least 4 h between each of the four successive treatments.

STATISTICAL ANALYSIS

We used *t*-test comparisons to analyse differences between body condition of individuals before (2010) and 18 months after (2012) the Puyehue-Cordón Caulle eruption. When the assumptions of normality and homogeneity of variance were not fulfilled, we used Mann–Whitney rank sum tests. The effects of morphology, body mass, SVL and body temperature on *P. excelsus* and *P. sinervo* speed was tested using simple regression analyses.

The effect of substrate and slope on speed was determined using speed as the residuals obtained from regression of body temperature against V_{\max} . Residuals were used to avoid thermal dependence on speed, considering that the regressions of body temperature against V_{\max} resulted in significant slopes in both species ($P < 0.05$). The main effects and interactions of the locomotor performance treatments were analysed using a two-way repeated-measures

Table 2. Maximum run speeds (V_{\max}) and body temperatures of *P. excelsus* and *P. sinervo* for sprint runs and long runs under the four treatments

| Treatment | Body temperature (°C) Mean \pm SE (range) | Sprint runs (ms ⁻¹) | | Long runs (ms ⁻¹) | |
|----------------------------|--|---------------------------------|-----------|-------------------------------|-----------|
| | | Mean \pm SE | Range | Mean \pm SE | Range |
| <i>Phymaturus excelsus</i> | | | | | |
| On the level | | | | | |
| Cork | 21.33 \pm 0.18 (19.6–25.3) | 1.05 \pm 0.07 | 0.35–3.66 | 0.78 \pm 0.03 | 0.46–1.37 |
| Ash | 22.38 \pm 0.12 (20.7–23.7) | 0.77 \pm 0.05 | 0.25–1.65 | 0.63 \pm 0.04 | 0.25–2.07 |
| Slope | | | | | |
| Cork | 22.21 \pm 0.19 (19.6–24.8) | 0.99 \pm 0.12 | 0.26–5.17 | 0.69 \pm 0.03 | 0.31–1.18 |
| Ash | 21.88 \pm 0.13 (20.2–23.6) | 0.69 \pm 0.05 | 0.21–1.19 | 0.62 \pm 0.02 | 0.32–1.10 |
| <i>Phymaturus sinervo</i> | | | | | |
| On the level | | | | | |
| Cork | 21.02 \pm 0.13 (20.1–23.0) | 1.16 \pm 0.08 | 0.26–2.54 | 0.96 \pm 0.05 | 0.42–1.31 |
| Ash | 21.91 \pm 0.08 (21.2–23.2) | 1.10 \pm 0.05 | 0.37–1.51 | 1.15 \pm 0.05 | 0.48–1.68 |
| Slope | | | | | |
| Cork | 21.89 \pm 0.08 (21.2–22.7) | 0.98 \pm 0.05 | 0.26–1.44 | 0.94 \pm 0.05 | 0.34–1.36 |
| Ash | 21.30 \pm 0.18 (19.7–23.2) | 0.94 \pm 0.06 | 0.37–1.68 | 0.84 \pm 0.04 | 0.39–1.21 |

ANOVA (two-way RMANOVA) as we measured the speed of the same individuals under the four treatments. In a two-way RMANOVA, as the sample is exposed to each condition in turn, the measurement of the dependent variable is repeated. The simple effects of each level of the factors were analysed using all pairwise multiple comparison procedures (Bonferroni adjustment) to perform multiple comparisons between different combinations of the two levels of the two factors.

We used the statistical software Sigma Stat 3.5, SPSS 15.0 and R (R Core Team, 2015). The assumptions of normality and homogeneity of variance for parametric procedures were confirmed using Kolmogorov–Smirnov and Levene’s tests, respectively.

RESULTS

LIZARD BODY CONDITION BEFORE ERUPTION (2010) AND 18 MONTHS POST-ERUPTION (2012)

In *P. excelsus* body condition was better after the eruption in adult males (Mann–Whitney, $U = 70$, $P = 0.002$), adult females ($t_{23} = -3.437$, $P = 0.002$) and juveniles ($t_{13} = -3.804$, $P = 0.002$). The body condition of *P. sinervoii* was unchanged by ash deposition in adult males ($t_{24} = -0.042$, $P = 0.967$) adult females ($t_7 = -0.158$, $P = 0.879$) and juveniles ($t_8 = -0.318$, $P = 0.758$).

EFFECTS OF BODY MASS, SVL AND TEMPERATURE ON *P. EXCELSUS* AND *P. SINERVOI* SPEED

In both *P. excelsus* and *P. sinervoii*, the V_{\max} values of SRs and LRs were not predicted by sex, SVL or body mass ($P > 0.05$). Hence, juveniles and adults were pooled for analyses. However, T_b was correlated with the V_{\max} of LRs in the inclined treatment over cork in *P. excelsus* ($F_{1,46} = 7.728$, $P = 0.008$), and correlated with the speed of LRs on the level over cork in *P. sinervoii* ($F_{1,25} = 6.526$, $P = 0.017$). Consequently, for comparative purposes, the residuals of T_b vs. V_{\max} were used as adjusted values of speed for the following analyses.

EFFECTS OF SUBSTRATE AND SLOPE ON *P. EXCELSUS* SPEED

In SRs *P. excelsus* speed was lower over ash, but was not affected by slope, and there was no interactive effect of slope and substrate (Table 3). Specifically, lizards ran slower over ash than over cork on the level and on inclined surfaces (Table 3, Fig. 3A).

In LRs speed was negatively affected by both ash and slope. Lizards ran faster on cork on the level and inclined surfaces, and speeds on cork were

slower on inclined compared with level surfaces. However, mean speed when running over ash was not affected by slope (Table 3, Fig. 3B). Therefore, the interaction between slope and substrate was significant.

EFFECTS OF SUBSTRATE AND SLOPE ON *P. SINERVOI* SPEED

In SRs *P. sinervoii* speed was affected only by the slope (Table 3). Over cork, lizards ran faster on the level than on inclined surfaces (Table 3, Fig. 3A). In the same way, the adjusted speeds of LRs were only affected by the slope. Lizards ran faster on the level than on inclined surfaces over both cork and ash (Table 3, Fig. 3B).

DISCUSSION

Under stressful situations, an individual’s phenotypic attributes most closely related to fitness such as body condition, reproductive biology and locomotor performance are thought to be the most buffered against internal and external stressors (Waddington, 1941; Schmalhausen, 1949; Stearns & Kawecki, 1994; Badyaev, 2005). The scarcity of post-eruption precipitation in the Patagonian steppe restricted the assimilation of ash into the soil, strongly affecting the richness and the abundance of vegetation (Ghermandi & Gonzalez, 2012) used by lizards to feed and shelter. Short-term effects of ash on lizard populations could be related to changes in the abundance of insects (Buteler *et al.*, 2011; Morales *et al.*, 2014) and reduction of flowers to feed upon. This is consistent with the poor body condition and the low number of reproductive females observed the first year after eruption in *P. spectabilis* (Boretto *et al.*, 2014a). However, long-term effects of ash fall produced a decrease in the abundance of predators that feed on lizards and a decrease in the herbivorous competitors of lizards (Butcher, 1981; Arendt, Gibbons & Gray, 1999; Dalsgaard *et al.*, 2007). In the present study, we registered a better body condition 18 months after the eruption in *P. excelsus* similar to the rapid recovery evidenced by high reproductive success registered in *P. spectabilis* 2 years after the eruption (Boretto *et al.*, 2014a). We explain the improvement in body condition of these two species 18 months post-eruption as a result of the increased availability of flowers and fruits probably as a result of the high mortality of livestock (i.e. sheep and goats) produced by the abrasive effects of ash on their intestinal walls (Robles, 2011). In contrast, the lower energetic demands of lizards in comparison to mammals (McNab, 2012) might have precluded them

Table 3. Main effects, simple effects and interactions of slope and substrate on the adjusted speed of sprint runs (SR) and long runs (LR) of *P. excelsus* and *P. sinervoi*

| Main effects | | | Simple effects | | |
|----------------------------|---------------------|----------|----------------|--|----------|
| Type of run | <i>F</i> | <i>P</i> | Treatment | Difference between mean adjusted speeds ± SE | <i>P</i> |
| <i>Phymaturus excelsus</i> | | | | | |
| Slope | | | | | |
| SR | $F_{1,38} = 0.780$ | 0.383 | Cork | 0.006 ± 0.134 | 0.966 |
| | | | Ash | 0.117 ± 0.049 | 0.023* |
| LR | $F_{1,46} = 6.213$ | 0.016* | Cork | 0.114 ± 0.029 | < 0.001* |
| | | | Ash | -0.004 ± 0.036 | 0.917 |
| Substrate | | | | | |
| SR | $F_{1,38} = 12.256$ | 0.001* | On the level | 0.238 ± 0.096 | 0.018* |
| | | | Uphill | 0.349 ± 0.125 | 0.008* |
| LR | $F_{1,46} = 30.033$ | < 0.001* | On the level | 0.180 ± 0.039 | < 0.001* |
| | | | Uphill | 0.063 ± 0.025 | 0.017* |
| Slope × Substrate | | | | | |
| SR | $F_{1,38} = 0.584$ | 0.450 | | | |
| LR | $F_{1,46} = 5.976$ | 0.018* | | | |
| <i>Phymaturus sinervoi</i> | | | | | |
| Slope | | | | | |
| SR | $F_{1,25} = 9.008$ | 0.006* | Cork | 0.222 ± 0.084 | 0.014* |
| | | | Ash | 0.125 ± 0.066 | 0.069 |
| LR | $F_{1,25} = 30.447$ | < 0.001* | Cork | 0.126 ± 0.046 | 0.011* |
| | | | Ash | 0.225 ± 0.053 | < 0.001* |
| Substrate | | | | | |
| SR | $F_{1,25} = 0.939$ | 0.342 | On the level | 0.103 ± 0.077 | 0.192 |
| | | | Uphill | 0.006 ± 0.071 | 0.939 |
| LR | $F_{1,25} = 0.874$ | 0.359 | On the level | -0.076 ± 0.044 | 0.093 |
| | | | Uphill | 0.022 ± 0.052 | 0.672 |
| Slope × Substrate | | | | | |
| SR | $F_{1,25} = 0.999$ | 0.327 | | | |
| LR | $F_{1,25} = 1.657$ | 0.210 | | | |

Statistical parameters and *P* values are indicated.

*Significant results (*P* < 0.05).

from dying as a consequence of the reduced availability of food. Whereas the lower deposition of ash in the habitat of *P. sinervoi*, and the commensurately small mortality of competitive herbivores, could explain the lack of changes in lizard body conditions at that study site (Fig. 1).

Stressful environments can influence the phenotypic variability, via increased mutation and by increment of recombination, providing a source of variation on which natural selection can act in a flexible way to changes in environmental conditions (Hoffmann & Parsons, 1997; Badyaev, 2005). The great variability of mimetic colour patterns, the flat bodies and short-limbed morphology characteristic of the genus *Phymaturus* allow them to be cryptic on volcanic outcrops and to use rock crevices on steep walls as shelters to avoid predation from raptors, snakes and mammals (Ceï, 1986; Scolaro, 2005; Goodman, 2007; Cabezas-Cartes, 2013;

Cabezas-Cartes *et al.*, 2014). The presence of the white volcanic ash could not only make lizards more noticeable to predators, but also could diminish the locomotor performance of *P. excelsus* in sprint and long runs. In contrast, *P. sinervoi* was affected by slope rather than by ash.

It has been proposed that the performance of a species on different substrates is more dependent on the dynamics of locomotion (locomotor forces, body weight and substrate resistance forces) rather than on specialization to a given habitat (Vanhooydonck *et al.*, 2015). For example, some saxicolous liolaemids and lacertids have been observed to show no effect on performance over sandy vs. rocky substrates (Tulli, Abdala & Cruz, 2012; Vanhooydonck *et al.*, 2015). However, in *P. sinervoi*, habitat specialization seems to play the main role in the differences in performance over different substrates. *P. sinervoi* speeds were not affected by the change in the texture of the

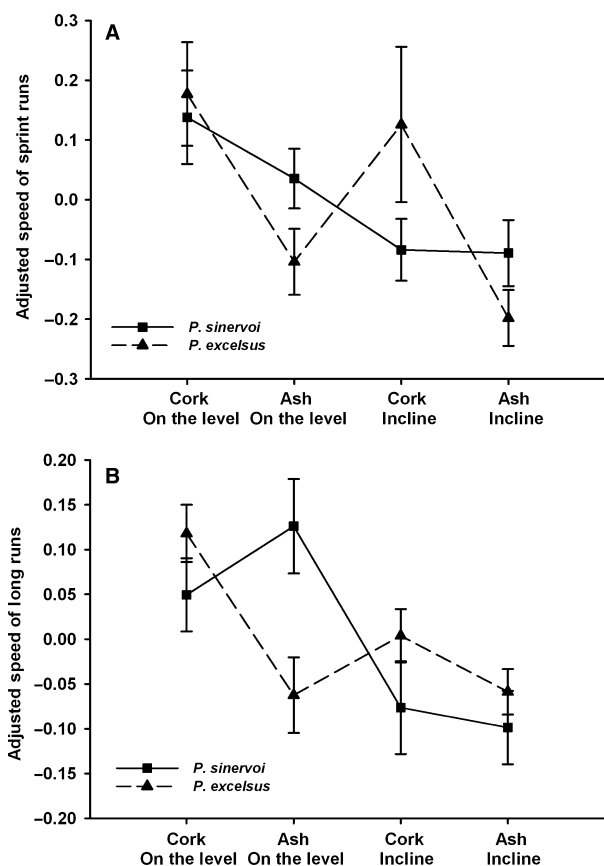


Figure 3. Adjusted speed of sprint runs (A) and long runs (B) of *Phymaturus excelsus* (triangles and dashed lines) and *P. sinervoii* (squares and solid lines) in the four treatments in a combination of track surface (cork or ash) and slope (incline or level).

substrate but the slope reduced speeds in both types of runs. These patterns suggest that they are specialized to run on the level, on both rocks and loose substrates, a result that is consistent with the habitat of *P. sinervoii*, which is characterized by flat rocky surfaces surrounded by sandy substrates.

By contrast, in *P. excelsus*, ash affected similarly short and sprint runs and the effect of the slope varied according to the locomotor activity performed. For example, in sprint runs the slope did not affect the speed while in long runs the effect of the slope depended on the type of substrate over which lizards ran, and ash and slope interacted significantly to alter performance. As a result, without ash, lizards ran faster on the level than on inclined surfaces, but over ash lizards were so affected by the loose substrate that they ran at a similar slow speed on the level and on inclined surfaces. Ash deposition differentially affected the habitats of the *Phymaturus* species (Fig. 1), and considering the effect of ash on locomotor performance some species may be more

constrained than others by ash deposition. For example, the range of *P. spectabilis* is included within the area most affected by ash deposition (Fig. 1), which combined with the micro-habitat selected by the species and the negative effect of ash on locomotor performance (Cabezas-Cartes *et al.*, 2014) have probably resulted in the most detrimental effects. However, the present results show that the impact of ash and slope depends upon an interplay among the degree of adaptation to rocky vs. sandy habitats of each species and the frequency and severity of volcanic ash falls.

Environmental catastrophes are predicted to have a major influence on the survival of small and isolated animal populations (Marske, Ivie & Hilton, 2007), such as those of *Phymaturus*. The present and former studies show that even though there is a detriment in locomotor performance, *Phymaturus* lizards seems to be adapted to these catastrophic disturbances that have occurred periodically since the origin of the genus. Most lizards of the genus *Phymaturus* showed a decreased ability to run over ash on the level and inclined surfaces, which could have affected especially *P. excelsus* and *P. spectabilis* that live among steep outcrops. Nevertheless, in other species such as *P. sinervoii*, which seems to be better adapted to run over sandy substrates and which inhabits flatter rock promontories, the sliding effects caused by ash seem to be ameliorated. Disturbances caused by volcanic eruptions have immediate and long-term effects on reptile populations. The immediate constraints caused by the accumulation of volcanic ash probably affected their vital activities such as feeding, reproduction (Boretto *et al.*, 2014a) and escape from predators (Cabezas-Cartes *et al.*, 2014). However, due to the effect of natural disturbance on the entire ecosystem, the deleterious effect on locomotion seems to be counteracted by competitive release causing greater availability of flowers and fruits, manifesting in a better body condition during the second year post-eruption. Overall, these lizard populations seem to cope well with this disturbance with a physiology adapted to food scarcity and reduction in locomotor capacities (Cabezas-Cartes *et al.*, 2014; this study) which occurred during the first activity season after eruption.

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