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ORIGINAL ARTICLE

Cumulative effects of volcanic ash on the food preferences of 2 Orthopteran species

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Abstract Inert dusts are an early form of insecticide which is still in use. One of the most common inert dusts is volcanic ash. In order to study the reaction of rangeland grasshoppers, *Dichroplus vittigerum* (Acrididae) and a katydid, *Burgilis mendosensis* (Phaneropteridae), to the presence of volcanic ash in their food sources and how this reaction changed as a function of time, we conducted paired preference tests between clean leaves of their preferred host plant and leaves exposed to volcanic ash of different grain size. The behavioral response was measured as the rating on the Thurstonian preference scale of leaves with ash in relation to clean leaves. The results showed that the avoidance of volcanic ash increased as a function of time in both species. Both species studied are occasionally exposed to volcanic activity, and come from an area in which a volcanic eruption had recently occurred. As their populations did not decrease after the ash fall, we propose that some behavioral responses such as avoidance of places with ash, works as tolerance mechanism to inert dusts exposure.

Key words *Burgilis mendosensis*; *Dichroplus vittigerum*; inert dust; preference test; thurstone scale

Introduction

The use of inert dust or wood ash is perhaps the oldest form of insecticide used by man (Brown & Bin Hussein, 1981). These natural insecticides of low mammalian toxicity like diatomaceous earth (which are made of fossilized skeletons of diatoms) or volcanic ash are allowed in the nonchemical control of stored products pests. These non-toxic insecticides can also be used against a wide range of insect species (Subramanyam & Roesli, 2000; Campolo *et al.*, 2014; Sabbour & Abd El-Aziz, 2015).

Volcanic ash could cause negative effects on some insects; its mortality by volcanic ash may be due to different phenomena such as: poisoning by ingestion, desiccation, chemical reactions at the level of insect cuticle and/or direct mechanical action (Buteler *et al.*, 2011; Fernández-Arhex *et al.*, 2013; Masciocchi *et al.*, 2013).

On June 4, 2011, a major volcanic eruption of the Puyehue volcano occurred in Chile in the “Cordón–Caulle” volcanic complex. This phenomenon changed the environmental conditions of the surrounding area affecting over 75 000 km^2 in Argentine Patagonia (Gaitan *et al.*, 2011). As in the 1980 eruption of Mt. St. Helens, the event provided a large-scale natural experiment for the study of inert dust exposure of insect populations, including some considered pests. Laboratory experiments with volcanic ash suggested that the causes of insect mortality in 1980 (Brown & Bin Hussain, 1981) were replicated by the volcanic ash of Puyehue in 2011; for example, physical entrapment, abrasion of the protective epicuticular waxes, and rapid desiccation aided by the physical

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sorptive qualities of the ash. Ingestion and inhalation of ash particles might not have been the only cause of the death of some insects (Brown & Bin Hussain, 1981); for example, Shanks and Chase (1981) demonstrated, in laboratory experiments, that weevils walking constantly in ash from eruption of mount St. Helen inhibited feeding which caused their death.

Habits, lifestyle and ecological conditions of a great number of insect species could be altered by volcanic ash, but the impact might not be the same for all insects (Marske *et al.*, 2007). The ash could cause massive destruction of the vegetation that insects use for food or habitat (Wille & Fuentes, 1975; Buteler *et al.*, 2011). Therefore, the vulnerability of insects and the possible impacts of ash are strongly influenced by environmental conditions. In low humidity and strong wind conditions, ash has greater negative effects on insect survival or fitness (Ebelling, 1961; Fields & Korunic, 2000; Stadler *et al.*, 2010; Fernandez-Arhex *et al.*, 2013, 2014). Is worth noting that low humidity and strong wind are features of the study area of this work.

The results of survival experiments are fairly consistent in that volcanic ash, like other inert dusts, causes a decrease in the survival of animals forced to stay in an ash-containing environment. It is possible that insects might not be passive players when exposed to an aggressive agent; they might develop avoidance strategies to decrease the damage produced by ash/inert dusts (Fernández-Arhex *et al.*, 2014). Phytophagous insects have evolved mechanisms to avoid exposure to these environmental factors, such as recovering water losses through juicy food intake, and acquired habits to hide and protect themselves (Viejo Montesinos, 1996). Fernández-Arhex *et al.* (2013) suggested that grasshoppers living in a dry environment were able to obtain enough humidity from fresh leaves to compensate for the negative environmental effects caused by the combination of low humidity, strong winds and ash. Therefore, it is also important to perform preference tests to observe if the insect can discriminate between positive and negative stimuli (infer things that animals can perceive as harmful).

The aim of this study was to evaluate, for the first time, the possible impacts of volcanic ash on the food sources of the grasshopper *Dichroplus vittigerum* (Blanchard, 1851) (Acrididae) and a katydid, *Burgilis mendosensis* (Rehn, 1913) (Phaneropteridae). *D. vittigerum* has a distribution comprising the meadows presents in northern Patagonian (moist, low-lying place with lush vegetation due to subterranean water; Cigliano & Otte, 2003). Carbonell *et al.* (2006) found that this species caused damages on crops and pastures in Chile. *Burgilis* is a South American endemic Phaneropterine katydid. Both are phytophagous insects which damage plant tissues of different host species mainly in pastures and crops and can be occasional insect pests in northern Patagonia.

Several species of rangeland grasshoppers (Acrididoidea) and katydids (Tettigonioidea) are pests of plants (Ibrahim, 1983; Latchininsky *et al.*, 2007). These insects play an important role in nutrient and energy cycling, and often compete with livestock and wildlife for grazing (Fielding & Brusven, 1995). In northern Patagonia, South America, the grasshopper *Dichroplus vittigerum*, and the katydid *Burgilis mendosensis* (Phaneropteridae) are polyphagous chewers on grasses and dicotyledons. They affect natural grasslands that are the main food source for extensive livestock (Wysiecki & Sánchez, 1992).

Materials and methods

For experiments, were collected in the field the last nymphal stages of *D. vittigerum* in Colonia Suiza, Bariloche, Río Negro (S 41º04′ 23.77″, W 71º32′ 14.41″) and *Burgilis mendosensis* in Fernandez Oro, Río Negro (S 35º56′ 56.25″, W 67th 54′ 30.78″) Argentina. Individuals were transported and kept in the laboratory under semicontrolled conditions (20.43 ± 0.01 °C, 39.57% ± 0.09% RH) to raise them to adulthood. Once in adulthood, they were placed in cages during 24 h without food. After that, individuals of *D. vittigerum* (0.25 ± 0.008 g) and *Burgilis mendosensis* (0.19 ± 0.01 g) were used to perform paired preference test. Preference tests were conducted under laboratory conditions with controlled temperature and humidity to determine food preferences and the effect of volcanic ash. Insects used were not previously exposed to ash in the field. They were collected (last nymphal stage before moving on to adult) in areas without volcanic ash.

Paired tests which are the most informative setup for extracting quantitative results from discrete choice data, were used to evaluate food preferences (Bruzzone & Corley, 2011). Paired choice tests coupled with the Thurstone–Mosteller model allow also to quantify and model time variation in preferences (Böckenholt, 2002). For this purpose, we offered 2 (1 for each treatment) fresh dandelion (*Taraxacum officinale* F. H. Wigg; Asterales: Asteraceae) leaves to grasshoppers and we offered 2 miner's lettuce plants (1 for each treatment) (*Claytonia perfoliata*) to katydids (Fernandez-Arhex *et al.*, 2013; Fernandez-Arhex *et al.*, 2014). The leaves were, or were not, sprinkled with 0.5 g of volcanic ash of 3 different particle sizes. Consequently, 4 treatments were performed: clean leaves (CL), leaves with fine ash (<500 μm, FL), leaves with thick ash (>500 μm, TL), and leaves with medium ash (= 500 μm, ML). In total there were 6 paired test combinations and 60 insects were used (CL vs. FL, CL vs. TL, CL vs. ML, FL vs. TL, FL vs. ML, and TL vs. ML) with 10 replicates each. Volcanic ash was sieved and classified into 3 categories according to the size of the particles: fine ash, thick ash and medium ash. The particle size was determined by the Attemberg international system for classifying soils, which states that if the particle is greater than 0.5 mm is classified as coarse sand while if less is classified as fine sand. Subsequently, the sub-samples (both soil and ash) were unified and 2-mm sieve was used to obtain an adequate sample for measuring pH and electrical conductivity. Then again was sieved with a mesh of 0.5 mm for a smaller sample size distribution that would measure the concentration of organic matter by the method of Walkley & Black (Sparks *et al.*, 1996).

Each individual was introduced into a plastic container (36 cm × 28.5 cm × 16 cm). The offered stimuli were placed at the end corners of the container. We observed each individual in its respective container at the same time daily (10:00 am). The individual choice was considered as the response variable, specifically when the insect was either resting or eating on the branch or leaf offered. Elections and movements made by the insect were monitored for 1 week. Leaves were renewed daily to preserve freshness, except for katydid species were the plant was renewed every 2 d.

The data were analyzed using a Bayesian approach which proposes a series of explanatory models choosing one of them with a model selection procedure. By using the deviance information criterion (DIC), we aimed at finding the best balancing fit and complexity model from a set of plausible candidate models.

In order to measure the effect of volcanic ash on Orthoptera species feeding preferences, we used several variations of Thurstone's case V model of comparative judgments (Thurstone, 1927; Bradley & Terry, 1952) which is the most common way to generate a preference scale from a series of paired comparisons (Böckenholt, 2006). This linear scale is called *Thurstone scale* and expresses the degree of attractiveness/preference for one of the options from the experimental subjects. High values indicate preference, and minor/negative values indicate rejection. Since this scale is an "interval scale," in which the interval between any 2 scale values has meaning, but the numerical value of any single score is arbitrary (Stevens, 1946), we had to choose an arbitrary origin of coordinates for these scales (zero preference). The plants without ash were fixed arbitrarily as zero in the Thurstone scale. Positive values for the ash treatment means that the insects were attracted to the ash, and negative means repulsion.

Several models based on Thurstone's case V were proposed to evaluate the host plant preferences depending on the experimental setup.

Two models were proposed to explain the data of grasshoppers:

1. Simplest model (CVMG, Thurstone's case V simple preference model). The preference was considered constant, with no changes through time.
2. Time effect model (CVTG, the preferences of host plant changed linearly as a function of time, with the positive slope meaning increase in preference through time, and the negative slope an increasing repulsion).

A total of 4 models were proposed to explain the data of katydids:

1. Simplest model (CVML, similar to 1)
2. Time effect model (CVTL, similar to 2)
3. Place effect model (CVPL, because the plant was reused, in this model the preference is affected by the motivation of the insect to change the plant, given that it already is on 1 plant). In this case an autoregressive parameter was added to account for the effect of the previous election
4. Time and Place effect (CVTPL, a combination of the 2 previous models).

We selected the model with the lowest value of deviance information criterion (DIC) (Gelman, 2003).

Since we did not have *a priori* information for the studied variables, we used as an uninformative *a priori* distribution for all the parameters, a normal distribution with mean 0 and deviance 10 and a normal likelihood to measure the function fit. To calculate the *a posteriori* distribution of the parameters for each model we performed 2 million iterations, from which we discarded the first million as a burn-in. From the remainder we chose 1 in 100 to avoid autocorrelation. Geweke plots were used to test convergence (Geweke, 1992) and perform visual inspection of variable traces. Analyses were performed by the PyMC library for Bayesian estimation (Patil *et al.*, 2010) for the Python programming language.

Results and discussion

The analysis of the proposed models showed that both grasshoppers and katydids have a tendency to avoid plants with volcanic ash as time exposed to it increased (Figs. 1A and B). The model selected for grasshoppers

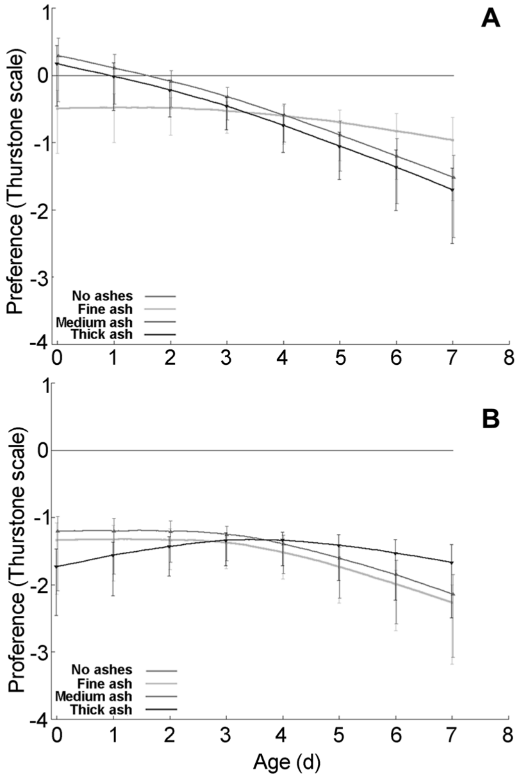

Fig. 1 Preference as a function of time for the Katydid (A) and Grasshoppers (B). The continuous line at $y = 0$ is the assumed preference value of the clean leaves (since this value is used as a reference, it does not have an estimation error). Light, medium and dark gray values corresponded to fine, medium and thick ash respectively. Error bars corresponded to 95% credibility intervals for the estimated variables, and the line connecting the points, the median of the estimated preference values after the Montecarlo Simulations. Although the models are linear, the lines are curved because they are the average of several simulations.

Table 1 Values of DIC (Deviance Information Criterion) for the models proposed to measure the effect of volcanic ash on feeding preferences of *Dichroplus vittigerum*.

No.	Model	DIC
1	CVMG	235.81
2	**CVTG**	**221.23**

Note: Selected model in bold.

Table 2 Values of DIC (Deviance Information Criterion) for the models proposed to measure the effect of volcanic ash on feeding preferences of *Burgilis mendosensis*.

No.	Model	DIC
1	CVML	304.70
2	CVTL	298.72
3	CVPL	293.77
4	**CVTL**	**292.68**

Note: Selected model indicated by bold.

Table 3 Estimated values of the variables of the selected models. Mean and standard deviation of the montecarlo simulations are reported here.

Variable	Mean	Standard deviation
Katydid		
Fine ash origin	-0.2112	0.4112
Fine ash slope	-0.0571	0.1192
Medium ash origin	0.5761	0.4240
Medium ash slope	-0.2488	0.1228
Thick ash origin	0.4603	0.4146
Thick ash slope	-0.2583	0.1187
Home effect	0.4429	0.1533
Grasshoppers		
Fine ash origin	-0.6927	0.5589
Fine ash slope	-0.1259	0.1483
Medium ash origin	-0.5977	0.5487
Medium ash slope	-0.1181	0.1474
Thick ash origin	-1.0722	0.5635
Thick ash slope	0.0110	0.1470

with a minimum DIC value CVTG corresponded to the time effect, which explained that the aversive effects of volcanic ash, increased as a function of time (Table 1; model 2). On the other hand, the model selected for katydids was CVTPL (Time and Place effect), which explained the preferences for food plant change as a combination of time and place effect (Table 2; model 4). The last model shows that while the insect preferred to remain on the plant previously chosen, it also increased rejection of the ash with time. In this experiment, the katydids preferred to feed on leaves without volcanic ash (Fig. 1A), but in the first few days the leaves with coarser dust grains (ML and TL) were slightly preferred over the clean leaves. However, with time, the leaves with ash began to be increasingly rejected, until finally they were the least preferred. Leaves with fine ash were always rejected in relation to the clean leaves. The slope in preference for the 3 grain sizes was always negative, meaning that the aversive effect of all ash increased with time (Table 3).

Grasshoppers showed a different pattern, always rejecting leaves with ash if clean leaves were offered as an alternative (Fig. 1B). However, the pattern of preference between ash grain size was not constant; the least preferred at the beginning were the TL, but in the course of the days, the relation reversed as the FL and ML showed a slightly negative slope whereas the Thurstone score of the TL remained almost constant (with a small positive slope,Table 3).

As with inert dusts, there is an inverse correlation between particle size and toxicity of volcanic ash (Chiu, 1939a,b; Stadler *et al.*, 2010), but there is no clear relationship between preference and grain size in this study. While katydids immediately rejected FL, its slope in preference was much lower than the other grains, meaning that perhaps the response of this species was saturated from the beginning. Grasshoppers, on the other hand, didn't show a clear difference in grain size effect. Although fine ash is the most harmful, the grasshoppers found to be sensitive to all 3 types of grain. While the katydids were found to be more sensitive to fine ash but the effect of the other grain sizes occurred cumulatively.

In our work, no grasshopper or katydids died during the experiment. So, for these species, volcanic ash is not toxic (at least for 6 d) to the digestive system. But on the other hand, it is known that constant inhalation and exposure to volcanic ash induces mortality in adult grasshoppers (Fernández-Arhex *et al.*, 2013), explaining that the avoidance to ash increased with time.

This work demonstrates that the Orthoptera could have the ability to perceive and discriminate damage. The results showed that both grasshoppers and katydids avoided the ash, and also showed that the aversive effect of ash increased as a function of time. Grasshoppers also, with time, began to discriminate between clean and contaminated food sources that *a priori* were not perceived as different, either by learning or by another behavioral mechanism, such as a perception by cumulative damage. This behavior helps to reduce mechanical damage in their mouthparts and gastrointestinal tract caused by inert dust.

This study is important because, as volcanic eruptions are a sort of large-scale "Natural Experiment" for the study of inert dusts, the observed behavior shows how, an initially susceptible insect, could become tolerant or even resistant. Volcanic eruptions are a common phenomenon in the Patagonian Region which affects wide areas each time they occur. For example, the 2011 volcanic eruption in the "Cordón–Caulle" volcanic complex in Chile, produced a volcanic ash fall that covered 7.5 million ha in Argentine Patagonia (Gaitan *et al.*, 2011). There have been 22 major volcanic eruptions since 1800 in the Andean Southern Volcanic Zone (Global Volcanism Program 2015). Most of the Patagonian Region is comprised of arid and semiarid areas where humidity is low, so ash remains for over a year before being "fixed" to the soil, and the effects persist in the worst conditions (i.e., low humidity) for more than a generation. Animals inhabiting a region where volcanic eruptions are a recurrent phenomenon are also periodically affected by ash, so there is a possibility that a naturally-selected mechanism of avoidance of the effects of inert dusts might be present in pest insects native of these areas.

Conclusion

Several studies have demonstrated that susceptibility of insects to ash produced a decrease in population level (Akre, 1980; Akre *et al.*, 1981; Shanks & Chase, 1981; Masciocchi *et al.*, 2013), and that the life-expectancy of insects forced to ash exposure was reduced both in exotic (Buteler *et al.*, 2011), and native species (Fernández-Arhex *et al.*, 2013, 2015). On the other hand, when laboratory preference tests were performed on native phytophagous insects by offering to choose between hosts or habitats covered with volcanic ash the results were mixed: Pietrantuono *et al.* (2014) found no effect of the ash in the host preference test of a shield bug (*Sinopla perpunctata*), but in Pietrantuono *et al.* (unpublished data), leafminers avoided volcanic ash as a pupation site. Contrary to the case of exotic pests such as *Vespula* spp. (Masciocchi, 2013), in the case of katydids and grasshoppers, their populations persisted during the dustfall, and in the immediate years following the eruption (Fernández-Arhex, unpublished data), suggesting the presence of some mechanism that helps these insects to be resistant or at least tolerant to a large-scale application of inert dusts. Given that if forced to live in a place full of volcanic dust their life expectancy was shortened as any other insect tested, the behavior observed in this study is a possible viable mechanism to explain that populations persisted or even increased after the volcanic eruption. This kind of behavior in insects reduces the effectiveness of inert dusts as an insecticide.

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Disclosure

The authors declare that they have no conflict of interest to declare.

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