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Persistent nesting by *Anthophora* Latreille, 1803 (Hymenoptera: Apidae) bees in ash adjacent to an active volcano

Hilary E. Erenler[1], Michael C. Orr[2], Michael P. Gillman[3],
Bethan R. B. Parkes[4], Hazel Rymer[4] and Jean-Michel Maes[5]

[1]Landscape and Biodiversity Research Group, The University of
Northampton, School of Science and Technology,
Northampton NN2 6JD, U.K.; e-mail: hilary.erenler@northampton.ac.uk
(corresponding author)
[2]Utah State University, Biology Department, Logan, Utah 84322, U.S.A.
[3]Evolution and Ecology Research Group, School of Life Sciences,
University of Lincoln, Brayford Pool, Lincoln LN6 7TS, U.K.
[4]The Open University, Department of Environment, Earth and Ecosystems,
Walton Hall, Milton Keynes MK7 6AA, U.K.
[5]Museo Entomológico de León, A.P. 527, León, Nicaragua

Abstract. Ground-nesting bees use a variety of substrates in which to establish cells and complete their reproductive cycles. Here we document the highly aberrant occurrence of a solitary bee species, *Anthophora squammulosa* Dours, 1870 (Hymenoptera: Apidae: Anthophorini), nesting within meters of an active volcanic crater in Nicaragua, Central America. The nest location is exposed to continuous, strongly acidic gas emissions (>2.7 ppm of SO_2), and sporadic vent clearing episodes that blanket the surrounding area with ash and tephra. An assessment of floral resources available within the expected homing distance of the species was cross-referenced with pollen carried by females returning to their nests. At this site, *A. squammulosa* appears to forage almost exclusively on a single plant, *Melanthera nivea* (L.) Small, 1903 (Asteraceae), that is adapted to volcanic acidic rain, despite being widely accepted as a generalist bee in the remainder of its range. Notwithstanding the extreme nature of the site, and the co-occurrence of specialist natural enemies and predators, the possibility exists that the site is selected for its beneficial attributes, such as the loose, well-drained substrate and the absence of vegetation. The converse is that the site is sub-optimal with the population constrained by habitat patchiness and limited dispersal options.

Key Words. Extremophile, *Anthophora squammulosa*, Nicaragua, sulfur dioxide, SO_2, Apoidea, volcano.

Introduction

Extremophiles, defined as organisms that inhabit physiologically-taxing environments, generate much interest as they provide an opportunity to study and characterize responses and adaptations to environmental perturbation (NOAA 2015). Sites of volcanic activity, with their associated disruptive events, epitomize extreme habitats. Volcanoes are present on every continent and erupt periodically over timeframes of decades, centuries or millennia (Smithsonian Institution 2015). The activity associated with volcanoes varies in intensity and duration and can lead to potentially catastrophic events. These include lava flows and the generation of lahars, as well as the expulsion of ash, tephra (solid volcanic particles) and noxious gases (USGS 2015). In turn, these can result in the destruction and creation of habitat and an alteration in air quality (del Moral & Grishin 1999).

Taxa-specific responses to eruptions are known from a limited number of well-studied volcanic episodes. Such studies often focus on site re-colonization and/or the recovery of earlier populations (Yamane et al. 1992, Edwards & Thornton 2001, Dalsgaard et al. 2007). Unfortunately, interpretation of biotic responses to volcanic activity is hampered by a lack of pre-eruption data (Elizalde 2014). Frequently it is only after a major eruptive event that attempts are made to quantify the direct impact that volcanic activity has had on organisms or the ecosystem services they support (Wille & Fuentes 1975, Grimm et al. 1985, USGS 1997, Martínez et al. 2012).

We address the question of effects of volcanic activity on biota through our studies of a species of bee in the genus *Anthophora* Latreille, 1803 (Hymenoptera: Apidae: Anthophorini) that nests in volcanic ash a few meters from the open crater of a persistently active volcano in Nicaragua, Central America. In particular we consider the location of nesting, the conditions prevalent at the site, the pollen collected by the species and the competitors and natural enemies of the species at the nest site. We conclude by evaluating the costs and benefits of living in an apparently extreme environment. This study helps meet the shortfall in pre-eruptive data and contributes to our knowledge about the conditions organisms can tolerate. It also has implications for understanding how pollinators might cope in the face of increased natural or anthropogenic disturbances.

The focal species for our study is the solitary bee *Anthophora squammulosa* Dours, 1870. Our records represent a new country record and the most southerly confirmed occurrence of the species and the subgenus *Heliophila* Klug, 1807 in the New World to date (Orr et al. 2014). To our knowledge this work also documents the most extreme volcanic site at which bees have been found nesting and foraging over multiple generations.

Study site. Located in Nicaragua (11°59’04’’N, 86°10’05’’W, maximum elevation of 592 m), Masaya is a basaltic shield volcano complex that forms part of the Central American Volcanic Arc (Stoiber & Carr 1973). The complex sits within a ~6-km × 11.5-km caldera formed as a result of several large (1–10 km^3), basaltic, plinian eruptions that occurred between 2250 and 6500 BP (Rymer et al. 1998), with the caldera walls serving to delimit the extent of Masaya National Park (Parque Nacional Volcán Masaya – PNVM) (MARENA 2012).

Ash and tephra are periodically ejected from the active crater, Santiago, as a result of vent clearing activity, following temporary blockages and the build-up of gases. The most recent event occurred from 30 April 2012 to 17 May 2012, when ash was ejected to a height of 1000 m. The ash blanketed the summit carpark to a depth of 2 mm and was reported to a distance of 3 km to the southeast of the crater. Closer to the vent, super-heated rocks ejected by the blast ignited areas of dry vegetation. In total an estimated 736 m^3 of ejecta was expelled from the crater during the episode (INETER 2012).

In addition to occasional, but intense, vent clearing episodes, Santiago crater is also the source of considerable background degassing caused by the convective overturn of magma (Rymer et al. 1998) and has been reported as one of the world’s strongest sources of sulfur dioxide (SO_2) (Delmelle et al. 2001:Fig. 1). In March 2012, prior to the most recent vent clearance, the estimated output of SO_2 from Santiago reached 1002 tons per day (INETER 2012). Typically, gas emerges from the vent structure and is carried out towards the Pacific as a result of almost continuous northeasterly trade winds during the dry season (November to April) (Rymer et al. 1998, Delmelle et al. 2002). The chemical constituents of the gas plume are highly acidic, creating a clearly defined ‘kill zone’ under which vegetation is either entirely suppressed or partly damaged, depending on proximity to the source (Johnson & Parnell 1986).

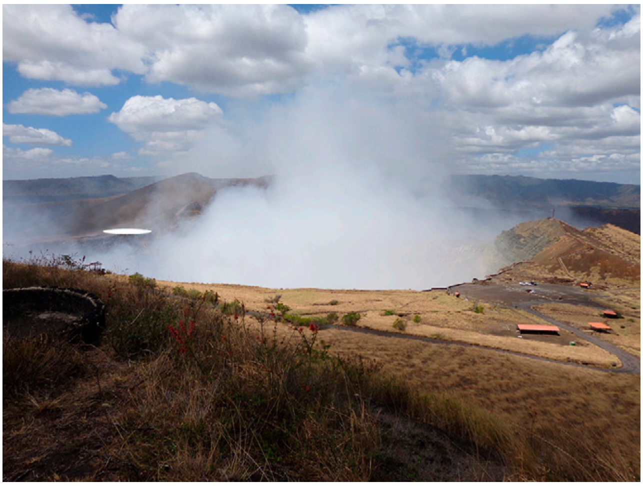

Figure 1. Santiago crater, Masaya volcano, Nicaragua. Location of main nest area shown as white oval. (Image: Ed Talbot 2015).

To the southwest of Santiago crater, and directly beneath the gas plume, the strongest effects of the continual degassing are visible, with the area devoid of all vegetation. Surprisingly, it is here that *A. squammulosa* nest gregariously (Figs. 1, 2). The substrate in the nest area consists of successive layers of ash interspersed with basaltic tephra and typically has a hardened impervious surface crust to a depth of 2 mm. This is believed to have formed in a manner similar to that observed at Irazú volcano in Costa Rica, where rainfall and subsequent precipitation of soluble salts by evaporation turned fine-grained soft loose ash into a cement-like surface (USGS 2009). The nest area extends to about 40 m southwest of the vent, at which point exposed lava is visible and the ash/tephra nesting substrate ceases. In total, the available nest area covers approximately 2800 m^2, all of which is highly exposed and therefore subject to strong winds, high temperatures and seasonal downpours. The annual mean temperature at Masaya is 28°C, with annual mean rainfall 1500 mm (McSweeney et al. 2012, MARENA 2012).

Study species: Anthophora squammulosa *Dours.* The *Anthophora* (*Heliophila*) are exceptionally fast fliers, recognizable by the characteristic high-pitched whine of their wings during flight. In the New World, the species are largely generalists and visit multiple plant families, although they exhibit a preference for Asteraceae (Brooks 1988). *Anthophora squammulosa* is typical in these respects; however, its range is unusual for the group (Orr et al. 2014). Formerly the senior synonym of *Anthophora curta* Provancher, 1895, their total range appeared to be from Washington southward into Honduras and as far east as Texas in the U.S.A. Now split from *A. curta*, the true range of *A. squammulosa* is known to begin near Central Mexico and extend southwards to Nicaragua, making it the southernmost species of the subgenus in the New World. In discerning its true distribution, threats to its habitat were also uncovered; almost its entire range is projected to be in 'critical or endangered' state over the next 30 years, primarily due to habitat destruction, according to the World Wildlife Fund (Orr et al. 2014). Its status may prove to be at greater risk than first thought if it nests in other similarly precarious volcanic environments.

Prior to this study, virtually nothing was known of the biology of *A. squammulosa*, and it appeared relatively unremarkable except for its range. With this study, however, it becomes clear that its nesting biology is highly aberrant for the group.

Ground nesting appears to be prevalent in the *Anthophora* (*Heliophila*), and several species have previously been observed nesting in aggregations (Torchio & Youssef 1968, Torchio 1971). Aggregated, or clustered, nesting is relatively common among bees as a whole, with several hypotheses proposed for this (Roubik 1992). Nest site suitability is seen as a major driving factor for this behavior, as many bees have stringent requirements for substrate type, sun exposure, slope, and other variables (Michener et al. 1958, Potts & Willmer 1998, Xie et al. 2013; but see Roulston & Goodall 2011). This may prove especially important in more tropical locations, such as Nicaragua, as bees are noted to avoid nesting at sites where extensive root systems of fast-growing plants might invade underground nest tunnels and cavities. In such cases, bees have been noted to preferentially select areas with sparse or little vegetation (Sakagami & Michener 1962, Roubik 1992).

Material and Methods

Observations of nesting females were made during five visits in three distinct seasonal periods from 2013 to 2015: early dry season (1–30 December 2013), mid-dry season (3–16 February 2013; 24 February–14 March 2014; 23 February–6 March 2015) and wet season (11–25 July 2013). All observations were made between 09:00 and 16:00 hours on days without precipitation. Nest architecture was explored in February–March 2015 and is covered separately in a forthcoming review of the nesting biology of the *Anthophora* (*Heliophila*).

Assessment of Nest Site Area. The area surrounding the active crater and into the nearby seasonally dry forest has been explored extensively by HEE and MPG on eleven separate field trips across different seasons from 2008–2015. These visits have helped confirm that, apart from two isolated *A. squammulosa* locations with a few nests, the present study site is the only large, repeatedly occupied location.

The density of nests was assessed on three occasions: February 2013, July 2013, and February 2015. A transect of approximately 120 m running parallel to the southwest crater, and passing through the main nest area, was established using GPS coordinates. A 1-m × 1-m quadrat was placed every four meters and the number of nest entrances present within it was counted. In the February 2013 sample, timed observations of 15 min duration were also made every sixth quadrat ($n = 5$), during which time the presence of other species in the quadrats to a height of 30 cm was noted. The slope of the main nest area was measured with a Leica Na2000 level using standard surveying techniques.

Quantifying SO_2 Concentration at the Site. The concentration of SO_2 was assessed using two complementary techniques. First, sulfation plates were deployed at three distances from the crater edge (Fig. 2). The plates were prepared following the protocols of Huey (1968), whereby approximately 10 ml of lead dioxide paste was placed in a 50-mm petri dish and dried overnight at 60°C. This was covered with a lid and sealed with parafilm to prevent contamination during storage and transportation. In the field the plates were attached with duct tape to objects such as lava outcrops, a wooden shelter and exposed branches of deciduous trees (depending on location), and their exposure time was noted. On collection, the plates were transported to the

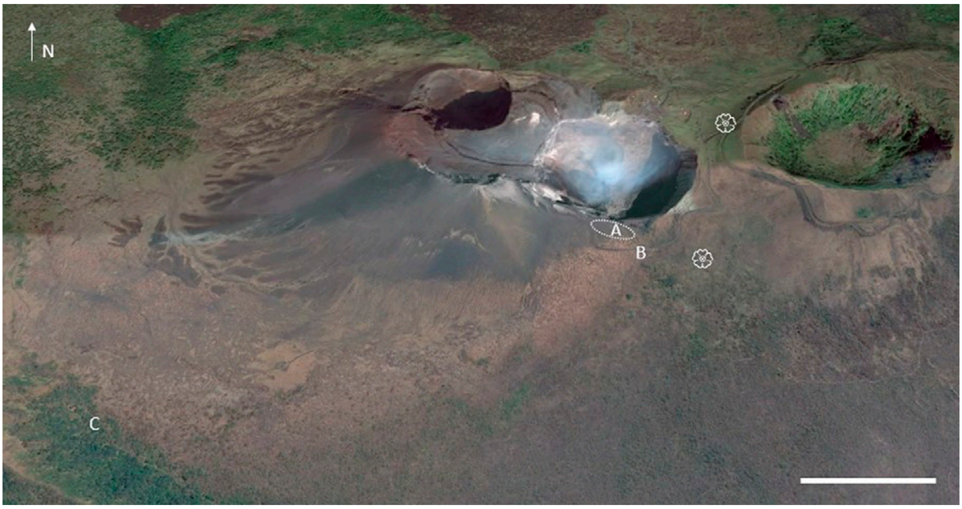

Figure 2. Aerial view of Santiago crater (center) and location of main nest site for *Anthophora squammulosa* (dotted oval). Gas monitoring sites: A Nest location, B Guard hut, C Los Chokoyos trail. Nearest flower resources (*Melanthera nivea*) are marked with a white flower. Scale bar = 500 m. Google Earth, Imagery date 29 March 2014 (Digital Globe 2015).

Open University laboratory (Milton Keynes, U.K.) for analysis. The contents of the plates were extracted in a sodium carbonate solution and analyzed using ion-chromatography (IC 3000).

The use of these plates, whereby SO_2 reacts to form lead sulfate, is an acknowledged method for recording sulfur deposition from volcanic degassing (Delmelle et al. 2001). Although not designed specifically for this purpose, they also return values for other volcanic anions such as fluoride and chloride, indicating (in the case of the latter) capture of volcanic HCl (Delmelle et al. 2001). Blank-corrected results for sulfate, chloride and fluoride (mg l^{-1}) were converted to dry deposition rates of SO_2, HCl and HF (mg m^{-2} day^{-1}) based on the area of the plate and the total exposure time. Field controls were deployed upwind of the plume and in the nearby town of Masaya and travel and laboratory blanks were used. The controls and blanks contained low concentrations of chloride and fluoride, but sulfate was below the limit of detection (less than 1 mg/l).

The second method of quantifying the gas loading at the nest location was to use SO_2 diffusion tubes (Gradko Environmental). These were attached to lava outcrops located within ten meters of the nest area and at control sites, where they were exposed for ten days to obtain the concentration of $SO_{2.}$ Accuracy of readings was assessed by exposing tube pairs at two sites as per the methods of Delmelle et al. (2002). The mean relative deviation between tubes in pairs was 0.4%. After collection, the tubes were returned to the Gradko Environmental laboratory (Winchester, Hampshire, U.K.) for analysis using ion chromatography. Controls and blanks contained < 0.005 µgS.

Assessing Available Floral Resources. To assess the complete floral 'menu' available to the bees, flower resources within a radius of 725 m from the centre of the main nest area were assessed (1.65 km^2 including both near and far sides of the active crater) during two days in February 2013 and a day in February and a day in March in 2015.

Based on observations by two of the authors (HEE and MPG), this timing combined a high prevalence of different flower resources and optimal levels of bee nesting activity.

The radius of 725 m was chosen as it represents the approximate homing distance for 50% of females based on the parameters described in Greenleaf et al. (2007)—i.e., $\log_{10}$ (typical homing distance, km) = -1.643 + 3.242 $\log_{10} X$, where X = female intertegular span (mm). The mean intertegular span (2.9 ± 0.11 mm) was calculated from ten females measured in February 2013.

Samples of all plant species presenting open flowers were collected to create pollen reference slides. The slides were prepared by swabbing dehiscing anthers using fuchsin gel on the point of a size 0 Continental insect pin. The gel was placed on a microscope slide, gently heated and then sealed with a cover slip.

Assessing the Composition of Transported Pollen-Loads. To assess the identity of pollen carried by female bees, ten individuals returning to their nests were caught using a hand net and placed in individual plastic vials in both February 2013 and March 2015. Voucher specimens were prepared using ethyl acetate with pollen removed by swabbing the scopa on both legs of each bee using fuchsin gel (Kearns & Inouye 1993). Microscope slides were prepared using the same methods as for floral resources. Pollen grains per slide were counted and determined using the prepared reference slides. Specimens and slides are held at the University of Northampton, U.K.

RESULTS

Nest Site Location and Density of Nests. There is only one area within the 5400 ha of Masaya National Park where *A. squammulosa* nests gregariously. Although nest holes have been observed in two additional areas (both within 600 m of the crater edge), these appear as isolated groupings, with a maximum of two or three nest entrances within an area of 20 m^2. The sites where these occasional nest entrances occur differ from the main site for a number of reasons: firstly, they are not directly under the gas plume; secondly, although an ash substrate is present, one site has been partly colonized by weedy vegetation, whilst the other is in a depression and therefore susceptible to inundation and surface flooding (HEE, personal observation). In contrast, the main nesting site is bare of vegetation, continually exposed to gases from the active crater in the dry season when the bees are on the wing, and is located on a slope of 8.4% facing in a south to southwesterly direction.

The density of nests in the 60 1-m × 1-m quadrats ranged between 1–14 nests in February 2013 (mean 4.5 ± 2.98 per quadrat) and 1–18 nests in February 2015 (mean 5.6 ± 3.42 per quadrat) with a total of 136 and 169 nests observed, respectively. No nests were observed in the wet season (July 2013).

Presence of Predators and Associated Organisms. The most frequently observed species found in and flying over the timed observation quadrats were *Bembix multipicta* Smith, 1873 (Hymenoptera: Sphecidae) (mean 5.6 ± 4.39, $n = 28$), *Centris flavifrons* (Fabricius, 1775) (Hymenoptera: Apidae) (mean 1.6 ± 1.14, $n = 8$) and *Microbembex monodonta* (Say, 1824) (Hymenoptera: Sphecidae) (mean 1.4 ± 1.52, $n = 7$). Two species of the cleptoparasitic *Dasymutilla* Ashmead, 1899 (Hymenoptera: Mutillidae) were also observed in the quadrats: *D. araneoides* (Smith, 1862) and *D. canina* (Smith, 1855), each represented by a single individual. Females from two additional *Dasymutilla* species, *D. pulchra* (Smith, 1855) and *D. mirabilis* Manley & Pitts, 2007, were also found walking over the ash in the nest area in search of host nest entrances.

The predation of adult *A. squammulosa* individuals by the robberfly *Efferia anomala* (Bellardi, 1861) (Diptera; Asilidae) was witnessed on three occasions.

SO_2 Concentration. The sulfation plate controls suggested there were no other significant sources of sulfate, chloride or fluoride in the area after blanks had been accounted for. Similarly for the diffusion tubes, the SO_2 concentrations at the control points were below the limits of detection (0.005 µgS).

Deposition rates for SO_2 were at their highest in the nest area, and decreased with distance from the crater. The maximum SO_2 deposition at the nest site location was 6764 mg m^{-2} d^{-1} compared with 1382 mg m^{-2} d^{-1} at the guard hut, just 165 m away. The mean SO_2 deposition rate was more than six times greater at the nest area than the mean rate 1.5 km downwind (Table 1). SO_2 concentrations calculated from nine diffusion tubes in 2015 showed an average of 1.4 ± 0.63 ppm in the nest area (range 0.79–2.73 ppm), equating to 3595.13 µg S m^{-3}.

Flower Resources Available and Pollen Collected. In total 14 species from 11 plant families were in flower within 725 m of the main nest site (Table 2). The majority of pollen (>99%) carried by foraging females was from *Melanthera nivea* (L.) Small, 1903 (Asteraceae) (mean number of *M. nivea* pollen grains carried = 1070 ± 1300, range 82–3600). The remaining 0.2% represented isolated grains of *Tecoma stans* (L.) Juss. ex Kunth, 1819 (Bignoneaceae)*, Dalechampia scandens* L., 1753 (Euphorbiaceae) and an unidentified species.

Discussion

This study reveals *A. squammulosa* as one of only a few species of bee, and the first *Anthophora* (*Heliophila*), nesting in volcanic ash. An important distinction is that the previous record is for a small number of species of different genera using a vertical ash and loess-like soil facade in an exposed roadside cutting in Guatemala, some 6 km from a vent source (Batra & Schuster 1977). In contrast, our study is from ash adjacent to an active volcano and subject to both continual degassing and occasional vent clearing episodes, meaning fresh ash is regularly deposited at the nest site. Furthermore, the observation of *A. squammulosa* is a new record for the country and becomes the most southerly collection record to date for the subgenus *Heliophila* in the New World. The recent split of *A. squammulosa* from the presumed sister species *A. curta* (Orr et al. 2014) means the discovery of the species at Masaya is consistent with its known distribution from Central Mexico southwards. Additional

Table 1. Mean deposition rates for SO_2, HCL and HF (mg m^{-2} d^{-1}) using sulfation plates and mean SO_2 (ppm) using diffusion tubes.

Sulfation plates		Mean Deposition rate ± SE (range) (mg m^{-2} d^{-1})		
Location (Fig. 2)	sample size (*n*)	SO_2	HCl	HF
Nest area (A)	2	6034±1032 (5305–6764)	1055±174 (932–1178)	175±9 (169–182)
Guard hut (B)	2	1153±323 (925–1382)	139±41 (110–167)	30±7 (25–36)
Los Chokoyos trail (C)	40	898 ± 803 (30–2900)	94±79 (5–295)	24±17 (5–67)
Diffusion tubes		Mean SO_2 ± SE (range) (ppm)		
Nest area (A)	9	1.35±0.63 (0.79–2.73)		

Table 2. Plants in flower within 725 m of main nesting site in 2013 and 2015. Presence, absence, +/-.

Family		2013	2015
Asteraceae	*Ageratum conyzoides* L., 1753	+	+
	Melanthera nivea (L.) Small, 1903	+	+
Bignoniaceae	*Tecoma stans* (L.) Juss. Ex Kunth, 1819	+	+
Campanulaceae	*Lobelia laxiflora* Kunth, 1819	+	+
Euphorbiaceae	*Dalechampia scandens* L., 1753	+	-
	Euphorbia colletioides Benth., 1846	-	+
Fabaceae	*Mimosa pudica* L., 1753	-	+
Malvaceae	*Sida ciliaris* L., 1759	-	+
	Waltheria indica L., 1753	-	+
Plantaginaceae	*Russelia sarmentosa* Jacq., 1760	+	+
Rubiaceae	*Sherardia arvensis* L., 1753	-	+
Sapindaceae	*Serjania schiedeanea* Schltdl., 1844	-	+
Solanaceae	*Solanum* sp. L., 1753	-	+
Verbenaceae	*Lantana* sp. L., 1753	+	+

collection effort in Nicaragua would be invaluable for determining its prevalence in the southernmost reaches of its range. As the Central American Volcanic Arc extends from Tacaná in Guatemala to Irazú volcano in Costa Rica, further examination of volcanic sites within the range may prove fruitful.

That said, other specimens of this species have been collected in areas too far from volcanic activity for ash to be the only substrate they use. Based on the nesting habits of another species, *Anthophora flexipes* Cresson, 1879, which nests in both sand and sandstone, it is unsurprising that *A. squammulosa* might exhibit plasticity in nesting substrate choice (Torchio & Youssf 1968). Despite this, its choice in Nicaragua is both unconventional and unexpected. It may be that further north *A. squammulosa* nests in desert pavement or similar substrates; this being the known nesting substrate of its presumed sister species, *A. curta* (Hicks 1934, Orr et al. 2014). Further studies throughout its range are necessary to test this idea.

The occurrence of the species at this location, where periodic extreme degassing events and vent clearing activity occur, makes its existence precarious. This is exacerbated by the fact that the species is only known from a range limited to ecoregions that are, or are soon to be, in critical or endangered status due to anthropogenic activities (Orr et al. 2014). The twin challenges of an extreme environment and destruction of other suitable habitats may eventually lead to southern range losses. With no other records of *A. squammulosa* known from Nicaragua, recolonization of the site following a volcanic eruption seems unlikely but not impossible. The presence of the species in its current location alongside predators and cleptoparasites such as *Dasymutilla* demonstrates that colonization occurs, and persists, in the most unlikely of habitats. It is only by documenting such sites prior to major natural disturbances that it is possible to fully utilize such locations as 'exemplary living laboratories' (Elizade 2014) for the purposes of studying recovery processes in biological communities (del Moral & Grishin 1999). Habitat suitability modeling, such as that used in Orr et al. (2014), may prove useful in locating such pre-eruption sites for future studies of this and other taxa.

There are several distinct challenges to any organism living in close proximity to a persistently active volcano. Perhaps greatest among these at Masaya is the high level of sulfur dioxide. During the most recent degassing crisis (1993–2000), passive emissions from the vent increased from 600 t d^{-1} to a peak of approximately 1850 t d^{-1} (Delmelle et al. 2001, 2002). Since then, emissions have subsided to approximately 220 t d^{-1}, (Parkes 2015). Despite a reduction in overall degassing, levels at the nest site remain extremely high when compared to the 1998 and 1999 downwind records. We found sulfur levels of 7772 mg m^{-2} d^{-1} in December 2013 (Parkes 2015), and sulfur dioxide readings of 2.72 ppm, both at the main nest site. To put this in context with human-generated SO_2 sources, in 2015 the nest site at Masaya saw a mean recording of 3595.1 ± 1667.04 µg S m^{-3} (maximum 7275.8 µg S m^{-3}), which is an order of magnitude higher than the most atmospherically SO_2 polluted area in Europe (annual average peak of 238 µg S m^3 (maximum 2441 µg S m^{-3}), downwind from a copper smelting plant (Nikolić et al. 2010).

The effect of SO_2 on bees includes reduced activity levels and interruptions in foraging activity, potentially increased larval developmental time, reductions in adult longevity; decrease in pupal survival and larval feeding, and the potential to upset host-parasite relationships (Ginevan et al. 1980 and references within). Ginevan et al. (1980) found deleterious effects at levels as low as 0.28 ppm. It is unknown how *A. squammulosa* operates at Masaya, where levels peak at approximately ten times this value.

Ash is a second, distinct, environmental challenge faced by *A. squammulosa* at Masaya. Wille & Fuentes (1975) found that during two years of ash eruptions at Irazú in Costa Rica, insect populations were impacted in several ways, both externally and internally. Externally, the physically abrasive nature of ash reduced exoskeleton thickness and led to higher rates of desiccation. Internally, the ingestion of ash-contaminated pollen and nectar caused both chemical and physical damage. These authors also noted that ground nesting bees were more susceptible to the effects of ash than cavity nesters due to increased contact time with the material. *Anthophora squammulosa* females spend considerable time clearing wind-blown ash from nest entrances using brush-like appendages on their hind legs. These structures are typical for *Anthophora*, but nothing is known at present of any specific adaptations/behaviors to deal with the external and internal effects of ash. A further set of abiotic factors associated with the volcano at the Masaya site are likely to impact on the bee population. These include strong winds, which may reduce flight activity/number of flying hours, the hard substrate that characterizes the surface layer of ash following rainfall, and high ground temperatures associated with underground heating (influence of proximity to magma chamber) combined with solar heating at a site lacking vegetation.

To compound the abiotic conditions at the site, floral resources within the homing range are limited. It is known that vegetation in a 22 km^2 area directly under the volcanic plume is regularly damaged as a result of persistent degassing (Delmelle et al. 2002), but it is the area closest to the active crater (where the nests are located) that is most severely affected, being completely devoid of vegetation. Two disturbance features are responsible for this. Firstly, strong gas emissions mean few plants are able to establish due to a combination of acidification of the soil and leaf damage by volcanic acid rain (Johnson & Parnell 1986). Secondly, ash and tephra sporadically blanket the area, leading to defoliation as well as occasional fires that serve to clear the area (Dalsgaard et al. 2007; HEE, personal observation). Despite this, *A. squammulosa* appears to forage successfully (and exclusively at this site) on *Melanthera nivea*, a plant with known adaptations to volcanic acid rain (Johnson & Parnell 1986:Fig. 3). Additional pollen analyses at other sites are necessary to determine whether this

Figure 3. *Anthophora squammulosa* female on *Melanthera nivea* flower. Scale bar = 1 cm (Image: Hilary Erenler 2013).

species preferentially visits a single plant species at each site, or if this selection is unique to a volcanic environment.

In contrast to the perception of an extreme and therefore deleterious habitat, nesting in ash next to a persistently active volcano seems to offer several benefits to *A. squammulosa*. The warm open area on a relatively gentle slope with a distinct lack of vegetation and a loose substrate may provide ideal nesting conditions. Although specialist natural enemies are present, their density and activity may also be impaired by the high levels of gas. Without further knowledge, these ideas remain working hypotheses for future study. Such research will rely on comparative studies from other nesting locations. Indeed, currently we cannot exclude the possibility that the site is sub-optimal and that the population is constrained by philopatry, dispersal and habitat patchiness.

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