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Movement decisions in natural catastrophes: how a flying scavenger deals with a volcanic eruption

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Understanding how organisms react to natural catastrophes is of special interest for ecologists and managers because they may drive changes in species distributions and abundance and indeed cause extinctions. Particularly, explosive volcanic eruptions promote major changes in the environment forcing organisms to make decisions, first allowing them survive and then, to obtain the best balance between the costs and benefits derived from such changes. Our objective was to study the movement decisions of a large scavenger bird, the Andean condor (*Vultur gryphus*), facing a volcanic eruption that injected millions of tons of abrasive ash into the atmosphere causing pronounced changes in the environments where these birds reside. By using a large dataset of GPS-based locations obtained before, during, and after the eruption, we explored how the ash fall and subsequent changes in livestock mortality patterns affected the movement behavior of the studied species. Interestingly, we found that the birds: 1) did not show significant changes in their home ranges, 2) reacted to the ash plume only a very short distances from it, and 3) did not change their foraging habitat preferences in accordance with the patterns of livestock mortality caused by the eruption. Our work discusses the various trade-offs that free-ranging animals perceive under conditions of natural catastrophe and how movement decisions may eventually alter fitness-related traits.

Key words: **Andean condor, movement behavior, Southern Volcanic Zone, volcanic ash, *Vultur gryphus*.**

INTRODUCTION

Catastrophic events are large spatially extended, infrequent, and unpredictable phenomena traditionally though to create ecological crunches for animal populations. In particular, catastrophes triggered by climatic and geological forces such as storms, severe floods, and volcanic eruptions are seen as drivers of important behavioral and physiological changes because they promote sudden and unexpected alterations in the physical environment, the chemical composition of soil and air, and resource availability (Hughes 1994; Boyle et al. 2010; Ropert-Coudert et al. 2014). However, many studies show that the effects of catastrophes are often short lived, with populations rapidly recovering their numerical and functional properties (Jones et al. 2001; Dalsgaard et al. 2007; Tryjanowski et al. 2009). Because natural catastrophes are expected to increase in magnitude and frequency due to climate change (Easterling et al. 2000), it is important to better understand how animals make decisions in such scenarios and how such decisions may determine the fate of individuals.

Animals faced with disturbance events may decide to remain in the affected areas or to emigrate. What they decide probably depends on the balance between costs and benefits that they perceive. The decision of staying can be made when costs related to the disturbance do not outweigh the loss of familiar areas where animals obtain valuable resources. For instance, some species could have pre-existing adaptations that allow them to buffer the consequences of a catastrophe and prevent the loss of reproductive and feeding sites (e.g., Hayward

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et al. 1982). Likewise, the decision of staying can be associated with the perception of catastrophe-induced profits. It has been shown that events that temporally disturb the normal dynamics of ecological processes often act as resource-releasing phenomena, importantly enhancing the survival and reproduction rates among consumers (Ostfeld and Keesing 2000). The decision to emigrate (at least temporally) is expected to occur when environmental disorders exceed certain critical thresholds and put the animal health and survival at risk (e.g., Streby et al. 2015). In any case, animals dealing with catastrophic events seem to be subject to important trade-offs, with certain species-specific traits (e.g., life-history strategy, trophic level) being probably the ultimate factors determining each type of response.

Interestingly, for some species such as scavengers the balance between costs and benefits may change throughout a catastrophe. In the initial phase, these species like many others are exposed to unfamiliar and threatening environmental conditions that may cause devastating effects on individuals and the whole population (Finkelstein et al. 2010). Over time, a common feature of nearly every natural catastrophe is an increase in mortality rates, with its concomitant rise in the availability of animal carcasses. If scavengers are capable of moving into such areas, they might take advantage of abundant and spatially clumped food resources, possibly compensating the inherent negative burden of such scenarios. However, those pulses of food superabundance typically are followed by a depletion of the resource below normal levels, which is predicted to reverse the initially favoring conditions for consumers (Ostfeld and Keesing 2000). It is therefore reasonable to think that search patterns of scavenger species fluctuate through time and that they are consistent with the changes induced by the catastrophe.

Here, we examine individual movement responses of a large flying scavenger, the Andean condor (*Vultur gryphus*), to an explosive volcanic eruption in NW Patagonia that largely affected condors' home ranges (Supplementary Figures S1 and S2). The eruption of the Puyehue–Cordón-Caulle Volcanic Complex (from here on Puyehue volcano) ejected about 1500 million m³ of volcanic ash to the atmosphere (Gaitán et al. 2011) causing unhealthy environmental conditions and producing massive livestock mortality (Robles 2011; Flueck 2013). In this context, we first hypothesized that the volcanic eruption was perceived as a threat by condors which led them to trigger movement responses aimed at preventing potential damaging effects. Particularly, we predicted that they avoided the overexposure to volcanic ash by: 1) reducing the size of their home range; 2) experiencing spatial drifts of home ranges, and 3) moving away from the daily ash dispersal trajectories. Then, we hypothesized that condors' foraging patterns were modified by the spatiotemporal changes in abundance of food caused by the ash fall. Accordingly, we predicted that condors foraged preferentially in the most affected areas when livestock mortality occurred, but they avoided those areas after food depletion. We tested these hypotheses by studying the movement behavior of adult individuals wearing GPS tags before, during, and for 1 year after the eruption.

MATERIALS AND METHODS

Study area and volcanic eruption

The study was carried out in north-western Patagonia, Argentina, and Chile. The area includes the Andes Mountains (West) and the Patagonian steppe (East) separated by a transitional area (ecotone) between them (Supplementary Figure S2). The weather is characterized by a mean annual precipitation that declines from ca.

4000 mm in the western part to ca. 500 mm in the eastern part and is largely concentrated during autumn and winter (March to August). The dominant winds blow from the West with the higher intensities being recorded during the spring (September to December) (Paruelo et al. 1998).

The region belongs to the Southern Volcanic Zone (33°S–46°S, 72°W) which includes at least 60 historically and potentially active volcanoes and numerous minor eruptive centers (Tilling 2009). Taken together, these volcanoes have shown a highly variable eruptive behavior with low activity and long repose times (up to decades) which alternated with high-activity phases and frequent eruptions in only few years. In particular, the Puyehue–Cordón Caulle Volcanic Complex (2236 m a.s.l., 40°35′S–72°6′W) has erupted at least 7 times in the last 2 centuries showing a fairly regular pattern (Dzierma and Wehrmann 2010).

The latest eruption of the Puyehue volcano began on 04 June 2011, with volcanic activity lasting approximately 8 months but gradually losing intensity. The initial explosive phase produced eruption columns that reached up to 12 km in height to then stabilize between 2 and 3 km. More than 950 million tons of ash were ejected to the atmosphere during the 3 months following the eruption (Gaitán et al. 2011). Much of this material drifted downwind to the east, scattered on 24 million ha of Patagonia and deposited in layers varying in thickness and particle size (Gaitán et al. 2011) (Supplementary Figure S2). Despite being chemically inert, ash was mainly constituted of silica making it highly abrasive which caused moderate to severe damages on people's health, water provision systems, and both terrestrial and air traffic (Caneiro et al. 2011). Volcanic ash from the Puyehue volcano also caused blindness among livestock, and the consumption of ash-covered grasses resulted in digestive problems and tooth wear, altogether leading local farms to suffer major losses of animals (mainly sheep) (Robles 2011; Flueck 2013). Livestock mortality was concentrated during the first 3 months after the eruption and generally increased with ash-deposits thickness, with some farms losing up to 25% of total production. Furthermore, many animals were evacuated from the affected areas 3 months after the eruption and returned between 6 and 8 months later.

Study species and movement data

The Andean condor is a large flying bird inhabiting the Andes Mountains, from Venezuela to the south of Argentina and Chile (del Hoyo 1994). This bird is a long-lived obligate scavenger that feeds mainly on carcasses of medium-to-large-sized mammals (Lambertucci et al. 2009). They forage and roost in groups, but they breed solitarily (del Hoyo 1994; Lambertucci 2010). Egg incubation generally occurs during the austral spring, with hatching taking place at early summer. Condors raise only 1 chick every 2 or 3 years, which commonly spends the following 4 or 6 months in the nest to then progressively leave the breeding area (Lambertucci and Mastrantuoni 2008). The studied population is among the largest one for the species distribution range with about 300 individuals (Lambertucci 2010). They rely almost exclusively on exotic species as food source, particularly livestock which since their introduction to the region has mostly replaced native ungulate species (Lambertucci et al. 2009). Livestock densities currently reach up to 95 livestock units per km² (1 livestock unit is equivalent to 1 adult sheep; SENASA—National Animal Health Service, unpublished data). In the study area, the GPS-tagged condors fly over a large area (up to 800 km in latitude and 300 km in longitude) moving from the breeding areas mainly located in the Andes to foraging grounds on the steppe (Lambertucci et al. 2014).

Condors were trapped in the surroundings of Bariloche city using cannon net traps baited with a sheep carcass. During the austral spring of 2010, we tagged 10 adult birds (6 females and 4 males) with PTT-100 50-g Solar Argos/GPS tags (Microwave Telemetry Inc.). During the spring of 2011, other 10 adult birds (5 females and 5 males) were tagged with backpack 100-g Solar GPS-GSM CTT-1070–1100 (Cellular Tracking Technologies CLL). The units were duty cycled to get the maximum numbers of possible positions (a position every 1h for the PTT-100 and one every 15min for the CTT-1070–1100). In all cases, they provided 3-dimensional position of each bird.

Data analyses

To explore possible changes in home-range patterns, individual fixed-kernel density estimators were computed (Worton 1989). Likelihood cross-validation (CV; Horne and Garton 2006) and least square CV (LSCV; Seaman and Powell 1996) methods were explored as tools to select the smoothing parameter (h). In general, the CV method generated multiple disjunctive small contours, thus we considered more appropriate to use LSCV that produced more continuous and realistic home ranges. In order to reduce potential bias caused by small sample size, home-range estimations were only performed on datasets with a minimum number of locations. This number was defined on the basis of the asymptotic value of home-range area curves computed in ABODE (beta v5, Laver 2005). We used 95% volume contours to examine home-range size variation between 3 months before (t_1) and 3 months after (t_2) the eruption. We also used the spatial–temporal analysis of moving polygons (Smulders et al. 2012) to estimate 3 different home-range behaviors: 1) home-range fidelity (areas used in both t_1 and t_2), 2) contraction drift (areas used in t_1 but not in t_2), and 3) expansion drift (areas used in t_2 but not in t_1) (see Figure 3a for a graphical representation). Thus, we were able to capture changes not only in home-range size but also in the spatial adjustments of them. The area corresponding to each behavior was expressed as a percentage of the total home-range size (i.e., $t_1 + t_2 - t_1 \cap t_2$). These analyses were repeated for the same time periods (months) of the following year (2012) when the effects of volcanic ash were significantly reduced. Differences in home-range size between periods (t_1 and t_2) were determined using Mann–Whitney tests for dependent sample, whereas descriptive statistics were computed to summarize the importance of each behavior (i.e., fidelity, contraction, and expansion of home range).

To assess the influence of the ash plume on the movement paths of condors, a biased correlated random walk model (BCRW; Turchin 1998) was fitted to the data. In a BCRW, an animal takes movement steps at regular time intervals with movement direction $\omega_{[t]}$ being a compromise between directional persistence (i.e., the natural tendency to move in the same direction as in the previous step) and a set of n biases in response to environmental cues located at directions $\varphi_{1[t]}$, $\varphi_{2[t]}$ … $\varphi_{n[t]}$. In vector terms, this directional compromise can be expressed as

$$\mathbf{v}_{[t]} = \begin{pmatrix} \cos(\omega_{[t-1]}) \\ \sin(\omega_{[t-1]}) \end{pmatrix} + \beta_1 \begin{pmatrix} \cos(\varphi_{1[t]}) \\ \sin(\varphi_{1[t]}) \end{pmatrix} + \beta_2 \begin{pmatrix} \cos(\varphi_{2[t]}) \\ \sin(\varphi_{2[t]}) \end{pmatrix} + \cdots \beta_n \begin{pmatrix} \cos(\varphi_{n[t]}) \\ \sin(\varphi_{n[t]}) \end{pmatrix}$$

where $\mathbf{v}_{[t]}$ is the expected movement direction at time t and $\omega_{[t-1]}$ is the movement direction performed by the animal in the previous step. The βs measure the strength of each cue in determining the movement direction, whereas the sign indicates whether the animal is attracted (positive) or repelled (negative) by the particular cue (Langrock et al. 2012). In our case, the BCRW model was built assuming that the movement directions $\omega_{[t]}$ are drawn from

a wrapped Cauchy distribution with mean direction $\mu_{[t]}$ and concentration parameter ρ and where $\mu_{[t]}$ reflected the compromise among 3 directions: 1) the direction of movement in time $t - 1$ (directional persistence, $\omega_{[t-1]}$), 2) the direction to the nearest point of the ash plume $\varphi_{\text{plume}[t]}$, and 3) the direction to the nest location $\varphi_{\text{nest}[t]}$ (Figure 1 and see Supplementary Appendix 1). Our main interest was in quantifying the effect of the ash plume in movement decisions but we included the possible bias given by the nest location to account for its potential role as a confounding variable. Given that we also expected that the strength of each movement bias was dependent on the distance to the corresponding cue, we defined the parameters $\beta_{\text{plume}[t]}$ and $\beta_{\text{nest}[t]}$ as follows:

$$\beta_{\text{plume}[t]} = \gamma_0 * \exp(-\gamma_1 * d_{\text{plume}[t]})$$
$$\beta_{\text{plume}[t]} = \kappa_0 * \exp(\kappa_1 * d_{\text{nest}[t]})$$

where $d_{\text{plume}[t]}$ and $d_{\text{nest}[t]}$ are the distance to the plume and nest, respectively (see Figure 1). Thus, as condors got closer to the ash plume, the $\beta_{\text{plume}[t]}$ could take large and negative values implying a strong repulsion bias. On the contrary, as condors moved away from it, the $\beta_{\text{plume}[t]}$ could be small implying that the plume was little important in determining the direction of movement. Correspondingly, the $\beta_{\text{nest}[t]}$ was set for increasing exponentially with the distance between the bird and its nest. Note that the parameters κ_1 and γ_1 governed the rate at which $\beta_{\text{plume}[t]}$ and $\beta_{\text{nest}[t]}$ went to zero as the birds moved with respect to the plume and nest, respectively. Our model was formulated as a hierarchical model where each individual got its parameters from Gaussian population-level distributions (except for parameter ρ where we used a Bet distribution, see Supplementary Appendix 1 for details). To fit this BCRW model, we selected all condor paths recorded during the 6 months after the outset of the eruption that were composed of at least 3 consecutive points hourly separated. To avoid spurious directional changes, we only used GPS locations from birds in flight (speed > 5 km/h). For the same period,
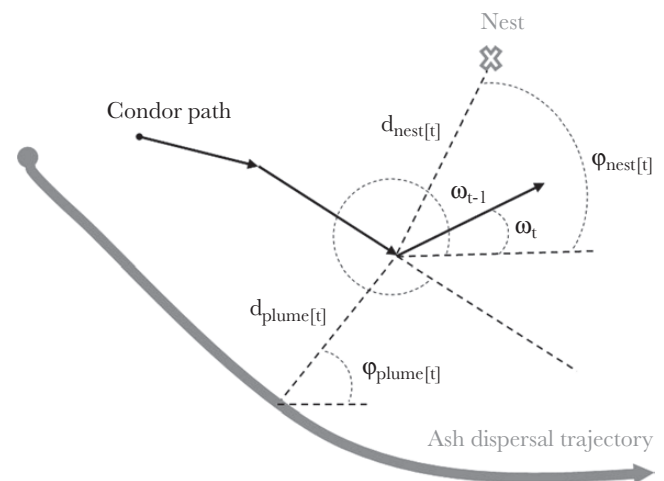
Figure 1
Representation of an Andean condor movement trajectory (solid black line) in relation to the location of the ash plume (solid gray line), and its nest (gray cross). It shows the set of movement variables measured at each time step (i.e., segment between 2 consecutive locations) and used to fit the hierarchical BCRW model. This model assumed that at a given time t, the condor movement direction ($\omega_{[t]}$) was influenced by directional persistence ($\omega_{[t-1]}$), the direction to the nest ($\varphi_{\text{nest}[t]}$) and the direction to the ash plume ($\varphi_{\text{plume}[t]}$). The strength of bias given by the nest and ash plume was modeled as functions of the distance $d_{\text{nest}[t]}$ and $d_{\text{plume}[t]}$, respectively.

ash dispersal trajectories were mapped on a daily basis using both satellite images from the MODIS sensor and the HYSPLIT track simulator (Draxler and Rolph 2013). Movement variables (Figure 1) were computed in ArcGIS 9.3© and models fitted using JAGS (Plummer 2003) via the package "jagsUI" for the R software (R Development Core Team 2012). We used vague priors for most parameters except for the variances of the population-level distributions where we used weakly informative priors. Five chains with 250000 iterations each were run, discarding the first 200000 as burn-in and assessing convergence using R-hat. Model inference was done based on the mean and credible intervals of posteriors (Gelman and Hill 2006).

To evaluate the degree to which the ash fall-induced livestock mass mortality affected the habitat preference of foraging condors, we adopted a use–availability design. For this, preference was defined as the likelihood of an animal using a particular foraging site when alternative sites were available (Beyer et al. 2010). As condors forage almost exclusively on the steppe (Lambertucci et al. 2014), GPS fixes located on this habitat were considered for the use–availability design. Availability was obtained by random points placed within the foraging ranges computed from a dataset that pooled GPS locations from all the 20 individuals. We used a map of ash-deposits that distinguished 10 categories of thickness as a proxy of the degree of affectation in the study area. The values of ash-deposits thickness for both control and data points were extracted using ArcGIS 9.3© (ESRI Inc., USA). Space use was then modeled as a Bernoulli process (0: control point, 1: data point), where the probability of success was a logistic function of ash thickness. In order to test if the effect of ash thickness changed the probability of use over time, we estimated a different slope α_1 for every m month in the period of study:

$$\text{logit}(p_{[i]}) = \alpha_0 + \alpha_{1[m]} * \text{ash.thickness}_{[i]}$$

This model was also constructed like a hierarchical model where each individual got its parameters from Gaussian population-level distributions (see Supplementary Appendix 2 for details). We fitted the model via Monte Carlo Markov chain techniques using JAGS (Plummer 2003) via the package "jagsUI" for the R software (R Development Core Team 2012). We used vague priors (i.e., normal with mean equal to zero and standard deviation [SD] equal to 10000), run 3 chains with 100000 iterations each discarding the first 50000 as burn-in. We evaluated convergence by means of R-hats and used the mean and credible intervals of posteriors for model inference (Gelman and Hill 2006).

RESULTS

Ten GPS telemetry units were deployed 7 months before the eruption and were active up to 26 months after the event. Ten additional units were deployed 6 months after the eruption and most of them worked over the entire studied period. The average number of locations obtained per bird was 4921 ± 2796 and the daily transmission intensity varied widely among the units (Supplementary Table S1). Before and after the volcanic eruption, birds moved mainly from their breeding grounds in the Andes Mountains to the foraging areas in the steppe (Figure 2; see also Supplementary Figure S2).

Eight individuals in 2011 and 8 individuals in 2012 had enough locations to reliably estimate 3-month home ranges (i.e., they showed asymptotic values of their respective home-range areas). On average, these locations included 67 days (SD = 22.4) of tracking. Thus, a total of sixteen 3-month home ranges (8 in t_1 and 8
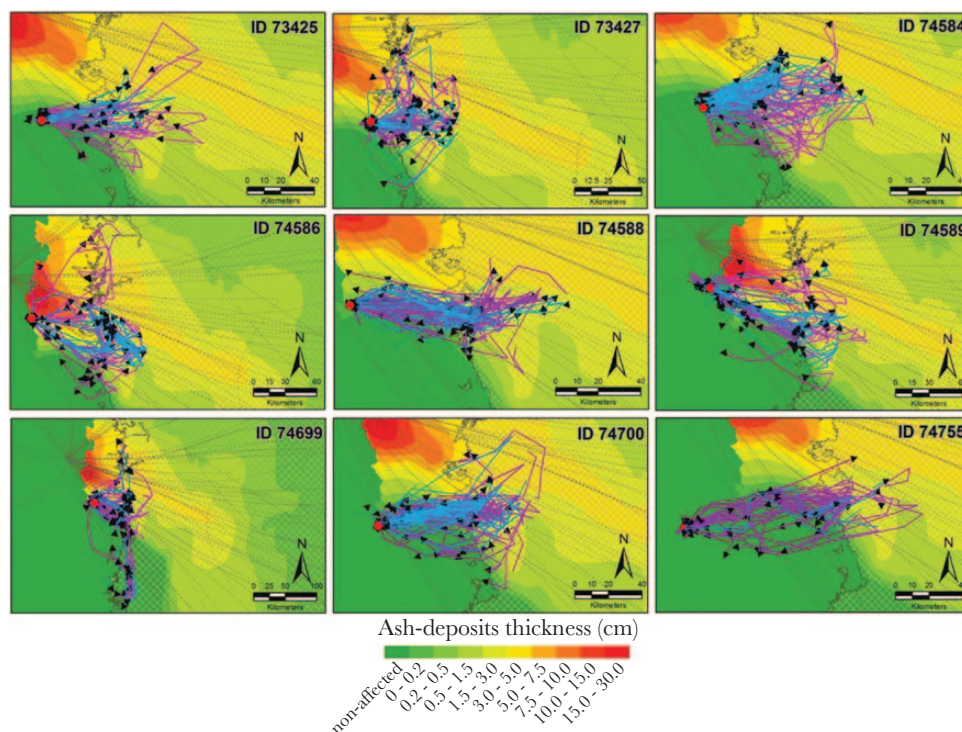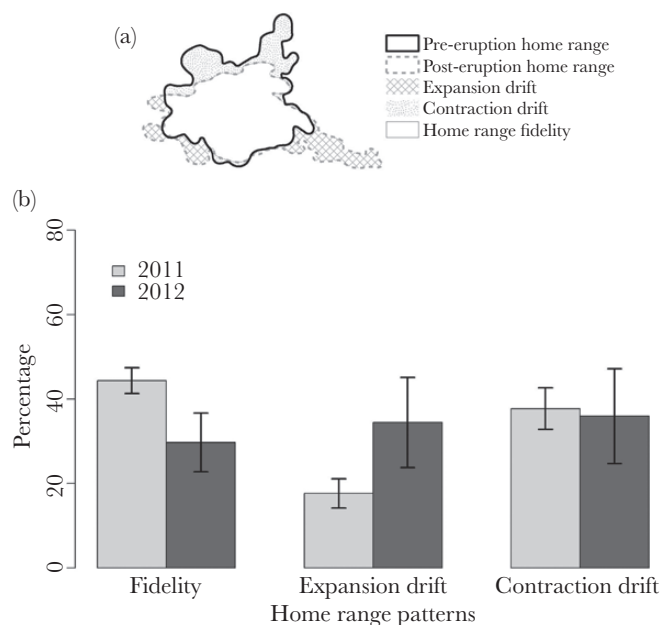
Figure 2
Movement paths of 9 GPS-tagged Andean condors during 3 months before (blue lines) and 3 months after (purple lines) the eruption of the Puyehue volcano (2011). Ash-deposits thickness is shown in a red–green gradient and daily ash dispersal trajectories by dotted gray lines. The grid pattern indicates the foraging areas used by condors and red dots their breeding sites.

in t_2) were calculated for 2011 from an average of 465 locations (range: 71–722) and 16 (8 in t_1 and 8 in t_2) for 2012 from an average of 766 locations (range: 60–2715). During the year of the eruption, home ranges in t_2 (i.e., after the eruption) were on average 22% smaller than in t_1, whereas for the same periods of the following year, they were on average 23% larger in t_2 than in t_1. However, these differences were not statistically significant (2011: $V = 31$, P value = 0.08; 2012: $V = 21$, P value = 0.74). During the year of the eruption, the area of contraction and home-range fidelity were similar to each other but higher than that of the expansion drift. However, all the 3 measures (i.e., contraction, expansion, and fidelity) were similar to each other 1 year after the volcanic eruption (Figure 3).

A total of 8 telemetry units provided enough data to be included in the hierarchical BCRW model. This dataset included a total of 3489 GPS locations with a mean of 436 ± 285 per individual. Our model shows that condors flying inside the ash plume (i.e., distance equal to zero) were biased away from it but that this effect disappeared as soon as the birds moved 400–500 m away. This is evident from the fact that the parameter $\mu_{\gamma1}$ was large enough to lead $\beta_{plume[t]}$ to reach zero rapidly (Table 1). Given that the plume had some few kilometers of width, our results suggest that the movement bias disappeared even when the birds were inside the ash plume. As expected, the model also indicates that the bias toward the nest was dependent on bird-nest distance, with the bias being stronger with increasing distance (Table 1).

The modeling of habitat preference included locations from all the 20 tagged birds and covered 26 months of monitoring. Areas

Figure 3
Home-range patterns of GPS-tagged Andean condors during the year of the eruption of the Puyehue volcano (2011) and 1 year after. (a) Example of computation of home-range fidelity (areas used in both pre- and post-eruption months), contraction drift (areas used in pre-eruption months but not in post-eruption months), and expansion drift (areas used in post-eruption months but not in pre-eruption months) performed from 95% KDEs. KDEs were computed for 3 months before and 3 months after the volcanic eruption and the same months of the following year. (b) Percentage of the different home-range patterns during the years 2011 and 2012. Bars indicate standard errors around mean values. KDEs, kernel density estimates.

with higher levels of ash-deposits were used in equal or greater proportion than expected by chance, and no signs of avoidance were detected, as indicated by the lack of negative α_1 values (Figure 4). Preference for the most affected areas seemed to reach a peak during the month of the eruption (i.e., June 2011) and tended to decrease gradually afterwards, which would be in line with the food pulse hypothesis. However, a similar pattern appeared the next year when the effects of volcanic ash were expected to be much less important (Figure 4).

DISCUSSION

This is the first detailed study, to the best of our knowledge, concerning the individual movement responses of a bird species facing a volcanic eruption. The eruption of the Puyehue volcano dramatically increased the concentration of airborne particles and altered the patterns of abundance and distribution of animal carcasses (Robles 2011; Flueck 2013). These factors have been shown to have large (and typically negative) effects on the spatial ecology of bird species. Examples include massive exoduses of gulls and forest birds from areas affected by ash fall (Hayward et al. 1982; Dalsgaard et al. 2007), anomalous changes in flight courses of trans-Saharan migrating raptors caused by dust storms (Strandberg et al. 2009), and changes of food-searching patterns in seabirds and old-world vultures when food sources become more predictable (Bartumeus et al. 2010; López-López et al. 2014). Interestingly, no strong eruption-induced effects were apparent on the movement behavior of the condors studied here. We expected to see important changes in home-range size after the catastrophe but these were only reduced (not significantly) in one-fifth of the original size. In line with this, condors did not avoid virtually the ash plume and did not show foraging patterns coincident with those expected under an increase in livestock mortality. Overall, our results suggest that the studied birds maintained their general movement patterns after the volcanic eruption and remained largely exposed to the conditions imposed by the catastrophe.

The eruption of the Puyehue volcano may not have actually imposed conditions extreme enough to result in a change of condors' movement patterns. The extremeness of an event is highly context dependent in terms of what a particular species have experienced in the past. Species that have been periodically exposed to high-impact events may have acquired physiological, behavioral, and ecological traits that confer resistance against future similar events (Kitzberger

Table 1

Estimates of population-level parameters of the hierarchical BCRW model

Estimates for group-level parameters (95% credible intervals)

Modeling of β_{nest}	$\mu_{\kappa0}$	0.002 (0.000, 0.007)	$\sigma_{\kappa0}$	0.002 (0.000, 0.007)
	$\mu_{\kappa1}$	−0.11 (−0.14, −0.08)	$\sigma_{\kappa1}$	0.02 (0.001, 0.06)
Modeling of β_{plume}	$\mu_{\gamma0}$	−2.34 (−13.45, 3.97)	$\sigma_{\gamma0}$	2.37 (0.10, 4.85)
	$\mu_{\gamma1}$	12.21 (2.45, 26.68)	$\sigma_{\gamma1}$	2.37 (0.12, 4.85)
Modeling of ρ	a_ρ	4.91 (1.43, 11.52)	b_ρ	12.42 (3.51, 29.17)

The parameters β_{plume} and β_{nest} measure the importance of the nest and ash plume location in determining the mean direction of movement, whereas the parameter ρ measures the dispersion around this mean value. The parameters β_{plume} and β_{nest} were modeled as negative and positive exponential functions of the distance bird-ash plume and bird-nest, respectively, and where γ_1 and κ_1 represented the rate of change. Note that the population-level estimate for γ_1 (i.e., $\mu_{\gamma1}$) was large enough to result in β_{plume} declining rapidly to zero as distance to the plume (kilometer) increased.
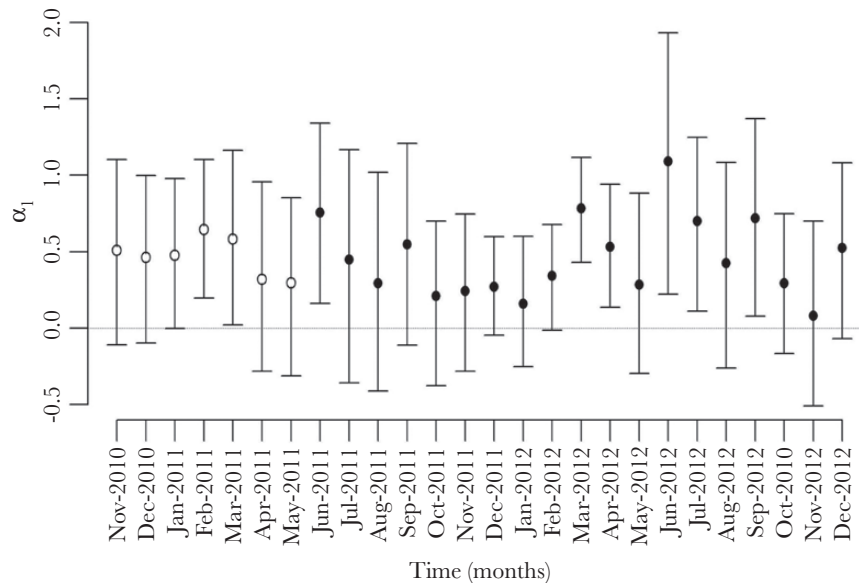
Figure 4

Andean condor foraging habitat preference in relation to ash-deposits thickness and time of the year. The parameter α_1 measures the importance of ash-deposits in determining the probability of use of a certain foraging area. Positive α_1 values indicate preference of areas containing high levels of ash-deposits, whereas negative α_1 values indicate avoidance. White and black dots indicate pre- and post-eruption months, respectively. Bars correspond to 95% credible intervals around mean values. Note that there were no extreme positive α_1 values during the months immediately following (July 2011–September 2011) the volcanic eruption, neither negative values in medium term and long term, as it was expected to occur under a scenario of food superabundance.

2013). The fossil record suggests that *Vultur* species reached South America during the mid-Pliocene when the Andes region was already the principal area of volcanism in the continent (Emslie 1988; Tilling 2009). Since then, Andean condors have been strongly linked to the Andes probably because of the good flying, roosting, and nesting conditions they provide (del Hoyo 1994; Shepard and Lambertucci 2013). Based on this close link, it is reasonable to think that these birds went through a process of natural selection that currently allows them to address the most severe and immediate effects such as respiratory infections that are known to appear after exposition to volcanic ash (Monick et al. 2013). Even if not specialized structures evolved to this end, certain anatomical structures such as nictitating membranes and feathers made of melanic keratin (Bonser 1995) may have played a key role in buffering the abrasive effects of fine-grained ash particles. The extent to which the overexposure to these particles translates into medium- and long-term physiological costs is unknown but, for instance, silicosis or chemical contamination can be expected to occur (Baxter 1990).

In our study, movement responses were not consistent with those expected under a pulsed resource scenario or a similar context of food superabundance. Soon after the ash fall, large numbers of live-stock carcasses were available to scavengers in a short-time window and concentrated in the most affected farms (Robles 2011). These conditions are known to shape spatial ecology of animal species and commonly enhance individual fitness (Oro et al. 2013). In particular, scavenging birds have been found to realign their food-searching patterns by making more directed movements toward areas with predictable food and also by foraging over smaller ranges (Bartumeus et al. 2010; López-López et al. 2014). The trend to increase the home-range fidelity after the volcanic eruption might be understood as evidence in favor of this idea. However, it is also reasonable to think that they were efforts to prevent the overexposure to volcanic ash, possibly because these particles were not innocuous for the birds.

Contrary to the movement responses expected under a context of abundant and spatially clumped food, our model of habitat preference indicates that condors did not select highly ash-affected areas in the short term (when they were rich in livestock carcasses) nor did they avoid them in medium–long term (when livestock carcasses were reduced). Instead, condors maintained their foraging grounds throughout the duration of the study possibly because food supply is not a limiting factor in the study area (Speziale et al. 2008).

Condors may have been subject to a compromise between being exposed to unhealthy conditions and losing valuable resources derived from familiarity with the physical and social environment. Individuals capable of storing information regarding the location and quality of foraging and breeding sites may benefit from the familiarity with a site, showing highly stereotyped movement behaviors even when they are no longer convenient (Biro et al. 2004). On the other hand, individuals familiar with their neighbors or with other members of their social groups may benefit, for example, by having information about their dominance statuses and fighting abilities (Eason and Hannon 1994). Condors are large-bodied, socially complex birds that rely on landscape energy to fly among breeding, roosting, and feeding sites which in our study area are located several dozens of kilometers apart (Shepard et al. 2011; Shepard and Lambertucci 2013; Lambertucci et al. 2014). Thus, staying in a familiar area possibly allows them to wader their home ranges without incurring high energetic costs and keeping their social context. Finally, site fidelity may be especially important for this species because long-lived animals that are territorial in the breeding area, commonly deal with low rates of turnover in breeding sites (Carrete et al. 2006). Thus, the abandonment of a breeding area could mean the potential loss of a scarce and highly valuable resource for condors.

Owing to the unpredictability of natural catastrophes and the difficulty of conducting field surveys under such conditions, researchers are often faced with undesirable methodological issues

(e.g., lack of solid precatastrophe data, low sample size, very coarse-scale approaches) that commonly lead to studies with low statistical power. In such cases, it is then difficult to determine if a lack of response is due to a methodological weaknesses or due to a genuine lack of effects (Jennions and Møller 2003). We had the unique opportunity to document and analyze animal movement patterns from a solid dataset that included pre- and post-eruption high-resolution telemetry data. This dataset enabled us to conduct a case–control study and accurately assess mechanistic links between individual responses and the consequences of the eruption. This suggests that our results are due to a genuine lack of strong movement responses rather than to our inability to detect them. We acknowledge, however, that other important carry-over effects on health, reproductive biology, and population dynamics may have occurred and that future studies should address these issues.

In a world that is undergoing global change, the study of the effects of catastrophic events on organisms has an increased interest in ecology and conservation, and detailed studies are needed to improve our predictive power (Easterling et al. 2000; Smith 2011). Despite the fact that natural catastrophes are traditionally seen as drivers of abrupt ecological changes, paleoecological and experimental studies suggest that many populations are able to maintain numerical and functional stability (Botkin et al. 2007). This capacity to persist in disturbed environments, however, is expected to be possible by altering fitness-related traits (Moritz and Agudo 2013). Here, we showed that the movement patterns of Andean condors were not largely altered by an explosive volcanic eruption, with condors showing the capacity to persist in areas affected by the volcanic eruption. These movement decisions may expose condors to sublethal effects such as silicosis or chemical contamination (Baxter 1990), thus silently affecting the fate of individuals, the demography of the population, and eventually the evolution of the species.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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