Factors affecting the distribution and abundance of the volcano rabbit *Romerolagus diazi* on the Iztaccihuatl volcano

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The volcano rabbit *Romerolagus diazi* is a localised endangered species with a range of less than 400km^2. It faces threats from habitat destruction, fragmentation and degradation, hunting and cattle grazing within national park boundaries and these were measured in relation to the distribution and abundance of the volcano rabbit. Faecal pellet counts were taken as a proxy of rabbit abundance in 1718 random 0.2m^2 quadrats at 859 point samples along 25 transects on the volcano Iztaccihuatl, covering an area of approximately 100km^2 between the altitudes of 3400m and 4000m. The presence of the species was significantly associated with: an absence of closed forest, an absence of long grass-types (not-bunchgrass), shallow inclines, no cattle grazing, lower altitude, low hunting pressure (measured by proximity to ranger station), an absence of bare ground, and, counter to previous findings, increased fire frequency. Within those habitats where the species occurs, it was significantly more abundant with a greater percentage cover of 'zacaton' bunchgrass, and short grass-types. It was significantly less abundant with increasing hunting (measured by proximity to ranger station) and cattle grazing. Key conservation priorities are therefore the protection of the sub-alpine zacaton bunchgrass dominated habitat type, strict enforcement of existing hunting laws and the immediate removal of livestock from relevant national park boundaries. However, the results suggest that fire frequency has significant positive effects on *R. diazi* occurrence through habitat improvement and this is often a consequence of anthropogenic management for cattle grazing.

The volcano rabbit *Romerlagus diazi* is an endangered species endemic to Mexico, with one of the most restricted ranges of any mammal (Granados, 1979; Thornback & Jenkings, 1984; Bell et al., 1985) and it is the focus of this study to identify the factors determining its presence and abundance so that its conservation can be facilitated (Portales et al., 1997). *R. diazi* is a small lagomorph endemic to the central Transmexican Neovolcanic Belt (TNB) distributed in a number of distinct populations on the uplands surrounding Mexico City. The species is currently distributed in discontinuous patches on the four volcanoes of Popocatepetl, Iztaccihuatl, El Pelado and Tlaloc (including Sierra Chichinautzin) (Fa & Bell, 1990). This is an exceptionally small range, covering approximately 386km^2 (Velázquez, 1994), the distribution is so limited partly because it has disappeared from some of its historical range in the central TNB, such as the Nevado de Toluca (Cervantes et al., 1990; Fa & Bell, 1990) and partly because its historical range was never very extensive (Cervantes et al., 1990). The most recent population estimation was approximately 7,085 (Portales et al., 1997). *R. diazi* is a sub alpine habitat specialist (Velazquez & Heil, 1996) and found at highest density in 'zacaton' bunchgrass communities dominated by *Festuca*, *Calamagrostis*, *Muhlenbergia*, *Agrostis* and *Stipa* genera (Velazquez, 1993). The greatest area of remaining suitable habitat is found within the boundaries of the Iztaccihuatl-Popocatepetl National Park (henceforth Izta-Popo) between 3400 - 4200m.

The volcano rabbit's habitat is decreasing mainly due to habitat destruction and degradation (Velazquez, 1993) through cattle grazing, encroachment of agriculture and property, logging, harvest of zacaton and anthropogenic fires (Fa & Bell, 1990; Portales et al., 1997). Its range is also becoming increasingly fragmented due to habitat loss and highway construction, causing the fragmented populations to become genetically isolated, increasing their risk of local extinction from random processes (Velazquez, 1993; Frankham, 1997), however genetic variation in *R. diazi* has been found to be similar to other more widespread and less fragmented Mexican rabbit genera such as *Sylvilagus* and *Lepus* (Cervantes et al., 2002). The species occurs within a number of protected areas, principally the Izta-Popo National Park, but hunting, cattle grazing, and grass burning persists within the park boundaries (Cervantes et al., 1990; Fa & Bell, 1990; Velazquez, 1993). Although the species is protected according to Mexican law there is a lack of local knowledge of the protected status and a lack of enforcement, consequently hunting may further decrease populations (Fa & Bell, 1990; Portales et al., 1997).

This study focuses on the slopes of the volcano Iztaccihuatl because it is one of the larger and potentially best protected areas of habitat. We consider the factors affecting populations of volcano rabbit at two spatial scales. On the large geographic spatial scale covering the entire volcano we aim to determine why it is present in some habitats and not in others. On the smaller spatial scale we aim to determine what predicts the abundance of the species within the habitats where it is present. This study therefore aims to derive conservation recommendations for the volcano rabbit *Romerolagus diazi* (see Portales et al., 1997) by assessing the importance of vegetation, hunting, cattle grazing, fire frequency and altitude on its (1) presence or absence (i.e. occurrence) and its (2) abundance in the areas that it does occur.

Methods

The study was conducted July-September 2011 on the Volcano Iztaccihuatl, located between the states of Mexico and Puebla, covering approximately $60km^2$ on the western slopes and $40km^2$ on the eastern slopes (Fig 1). It was not possible to include areas on the volcano Popocatepetl because it was active at the time of the study with an exclusion zone of 12km from the crater for safety reasons. On Iztaccihuatl, the eastern and western slopes were chosen because they allow the most rapid change in altitude. The study was carried out during the rainy season when volcano rabbits are breeding (Cervantes et al., 1990).

This study uses faecal pellets as a proxy both for species presence and abundance as validated by Velázquez (1994). Faecal pellet counts were used because *R. diazi* is crepuscular and shy (Cervantes et al., 1990), time of day does not affect pellet count data, and counts are temporally independent. Degradation effects on pellets were considered to be of minor effect because presence data simply require the presence of pellets, which is less affected by degradation, abundance data using pellet counts was only used as a proxy in habitats were the species occurred over a small scale, where factors affecting degradation rates are likely to be similar and because counts were not being used to ascertain population numbers or density but simply to allow an assessment of how abundance varied with various factors. Furthermore, Martinez et al. (2011) analysed the change in defecation rate with vegetation for *R. diazi* and concluded that faecal pellets can be used as a reliable index for this species.

The total sampling effort was 16 days (150 hrs) of data collection with an additional 3 days (20 hrs) of experimental study design in the field. The survey comprised 15 transects on the western slopes and 10 on the eastern slopes of Iztaccihuatl, running parallel to the altitudinal gradient which runs approximately East-West within an area of approximately 15 by 15km (Fig 1). Point samples were taken throughout each transect at every 20m altitudinal increment from 3400m to 4000m. The number of point samples per transect varied with the topography of the transect but most incorporated between 30 and 35 points (mean 37.2 ± 2.3 SE points per transect, N = 25 transects). Transects covered about 4.1 km ± 0.2 SE (N = 25 straight line distances from start to finish) and on average sample points were about 111.2 meters apart. The average distance between the 266 quadrats containing pellets on a transect was 223.0 m ± 13.4 SE, with 99 (37.3%) of these quadrats being separated by at least 223 m and 35 (13.1%) being separated by at least 334 m. Most distances between samples are likely to exceed the average range size (e.g. a pygmy rabbit *Brachylagus idahoensis*, slightly smaller than a volcano rabbit has a range of <0.3ha (Katzner &

Parker, 1997)). Point samples can therefore be considered to be reasonably independent. Furthermore the arrangement of points into transects was simply a consequence of logistics rather than a sampling issue (points could have been taken in random order and because of the short period of the study and the fact we counted pellets that do not move the results would have been identical). Nevertheless we explore the effects of sampling within transects on model results (see below).

At each point sample, two 0.2m x 0.2m quadrat samples were taken 5m apart perpendicular to the transect line and faecal pellet counts were taken for each quadrat and pooled into one point sample. In total, 1718 quadrats were taken in pairs at 859 point samples. Furthermore, at each point sample vegetation abundances were recorded according to percentage cover within a 10m radius. The vegetation abundances recorded in this way were zacaton bunchgrass, a sage (*Salvia*) species, a lupine (*Lupinus*) species, long grass types (not zacaton bunchgrass), short grass types, scrub bushes and small trees, and closed pine forest. Other variables recorded at each point sample in addition to the vegetation abundances include; the latitude, longitude and altitude using Garmin GPSmap 60CSX, incline of the site, cattle grazing pressure and fire frequency (see Table 1).

Selection of data was carried out in PASW Statistics 18 (2009. Chicago: SPSS Inc.). An additional variable was calculated using position data as follows; Northings and Eastings were used to calculate relative distance of all point samples to the only large ranger station on Iztaccihuatl, known as Alsomoni station. This variable, ‘Distance to station Alsomoni’, attempted to incorporate illegal hunting pressure on the species, the hypothesis being that less hunting occurs close to the station where gunshots can be heard and hunters seen more clearly. Hunters were seen on several occasions during fieldwork, and none of these were in proximity to the ranger station, nevertheless this spatial variable was not been explicitly linked to hunting pressure in our study. Analysis was performed using R-2.13.0. Six point samples had missing cases due to the malfunction of equipment and these were removed leaving 853 point samples. The first analysis concerned the factors determining the occurrence or distribution of the species on the large spatial scale while the second analysis concerned the factors determining the abundance of the species in the areas where it does occur.

For both analyses a full general linear model (GLM) of all possible variables affecting the species distribution was constructed that consisted of:

PelletCount ~ ClosedForest + DistancetoStationAlsomoni + Zacaton + Bareground + Altitude + SalviaSp + LupinusSp + LongGrasses + ShortGrasses + Scrub + FireFrequency + Incline + GrazingIntensity

For Analysis 1, a binomial regression model was used to analyse presence/absence: pellets were present in 266 point samples and absent at 587 point samples. For Analysis 2, only point samples where the species was present (i.e. points with faecal pellets in them) were included leaving 266 samples to determine factors affecting the abundance of the species. A natural log of the pellet counts was taken, allowing a reasonable fit of a quasi-Poisson distribution.

The full models were then simplified using the dredge command in R and a number of top models were averaged according to AIC weighting within a window of 2 (Akaike, 1974). The top models were then evaluated for both biological and statistical significance and these are reported in the results section of this paper. Residuals of the top models reasonably met model assumptions as demonstrated by the ‘plot’ command in R and according to criteria in Crawley (2007). However, note that any one of the suite of top models obtained from dredge, or the averaged parameter estimates could have been used and gave similar results both in relation to statistical significance and the biological effects.

For both analyses the variables Mature Pines, Juvenile Pines, Position and Transect, were excluded from the full models to remove autocorrelation and to simplify analysis within biological reason. Mature Pines and Juvenile Pines were logically excluded on the basis that they measured the same component of the vegetation as percentage closed forest. Position was excluded because spatial considerations are incorporated in the variables Distance to Station Alsomoni and altitude. Transect was tried in top models as a random effect (using Generalised Linear Mixed models in R, lmer), even though the clustering of samples within transects was unlikely to have biased pellet counts in any systematic way (transects were evenly distributed around the volcano – see Figure 1). The results for the random effects models indicated that there was some significant variance accounted for by some transects and so there was additional spatial variation in rabbit distribution that we were not accounting for that was captured by location of points along a transect. Nevertheless, all other variables retained in the model and their biological and statistical significance remained largely the same regardless of whether transect was included in the model (AIC mixed model = 878.7, AIC without transect = 879.2). We therefore removed transect from all subsequent models. Where biologically sensible (e.g. altitude), quadratic functions were also considered by including the square of variables in both full and top models. Models were not improved in any cases so quadratics were not retained in any models.

Results

Analysis 1 for presence/absence resulted in 15 models within 2 AIC of the top model (Table 2) and the best model retained 7 significant variables (Table 3). The probability of occurrence of the species decreased with increasing closed pine forest cover, cattle grazing intensity, long grass type cover, incline of the site, hunting pressure, and altitude; the probability of occurrence increased with increasing fire frequency (Fig. 2, Table 3). As the percentage cover of closed pine forest increased from 0-100% the probability of the species' occurrence decreased by 97.1%. As the cattle grazing intensity increased from low to high the probability of the species' occurrence decreased by 57.9%. As the percentage cover of non-zacaton long grass-types increased from 0-80% the probability of the species' occurrence decreased by 82.4%. As the incline of the site increased from shallow to steep the probability of the species' occurrence decreased by 78.5%. As the distance to ranger station Almosoni increased from 0-12km the probability of the species' occurrence decreased by 44.4%. As altitude increased from 3400m to 4000m the probability of the species' occurrence decreased by 48.3%. As fire frequency increased from low to high the probability of the species' occurrence also increased by 39.3%. The percentage cover of scrub was also included in some top models but had no significant effect on the occurrence rabbits in the top model.

Analysis 2 for abundance resulted in 10 models within 2 AIC of the top model (Table 4) and the best model retained 4 significant variables (Table 5). In general the species is more common as the percentage of zacaton and short grass-types increase and less common as grazing intensity and hunting pressure increase, assuming hunting increases with distance to ranger station Alsomoni (Fig. 3, Table 5). As the distance to ranger station Almosoni increased from 0-12km the species' abundance decreased by 72.2%. As the percentage cover of zacaton bunchgrass increased from 0-95% the species' abundance increased by 124.2%. As cattle grazing intensity increased from low to high the species' abundance decreased by 46.6%. As the percentage cover of short grass-types increased from 0-70% the species' abundance increased by 220.6%. The percentage cover of scrub and percentage cover of *Lupinus* sp. were also retained in the top model but they had no significant effects on the abundance of the species.

Discussion

Our study provides reasonably statistically robust results that volcano rabbits are present where closed forest, long grass-types, cattle grazing, hunting, bare ground and slope incline occur at low levels, and where fire frequency is higher. Within those areas where the species occurs, increased abundance occurred with increasing cover of ‘zacaton’ bunchgrass, and short grass-types, and lower levels of hunting and cattle grazing. It is important to note, however, that our measure of presence and abundance is an index based on faecal pellets and so may have been subject to false negatives due to degradation, fire presence only measured recent fire effects, and our estimate of hunting pressure rested on an untested assumption that there was proportionally less hunting closer to where the park rangers are based. Nevertheless we believe all of these potential problems do not introduce a systematic bias and are likely to render our hypothesis tests more conservative, thus strengthening the significance of any effects we identify.

Closed forest dominated by *Pinus hatwegii*, also known as highland temperate forest (Galicia & García-Romero, 2007), has a very strong biological effect because as the habitat changes from open to completely closed forest cover the chance of the species’ occurrence falls to near zero. This supports the current understanding of the dependence of the species on the sub-alpine zacaton grassland habitat found above the forest edge (Velazquez & Heil, 1996). In many cases the transition zone between highland temperate forest and sub-alpine grassland habitats can occur as low as 3400m, and this may be dependent on anthropogenic effects on the forest (Fig. 4). Although little can be done about the abiotic altitudinal upper limit to the rabbits range, its occurrence at lower levels is constrained by forest occurrence which can be managed.

Another vegetation variable to have a significant effect on the distribution of the species is the percentage cover of non-zacaton long grass-types. As can be seen (Fig 2), the probability of the species’ occurrence decreased by 82.4% as long grass-types increased from 0-80%. At first, this can seem like a large biological effect, however the majority (91%) of sample points have less than 20% long grass-type cover and the total mean cover in the sub-alpine habitat above the forest edge is only 4.5% (SE=0.41 N=554). However in the transition zone between this and sub-alpine habitats (3400m - 3600m) percentage cover increases dramatically after which it decreases with increasing altitude to less than 1% cover by 4000m (Figure 5). Therefore, the effects of this vegetation component will follow this pattern; a greater negative impact on species occurrence in the transition zone just above the forest edge, especially below 3600m, and reduced effects with increasing altitude.

The current scientific consensus is that fire frequency has a negative effect on *Romerolagus diazi* (Hoth et al., 1987; Velazquez, 1989; Fa et al., 1992; Velázquez, 1994). However, our study finds the opposite, at least for recent fires. In support of our result, it is recognized that bunchgrasses generally are adapted to and encourage a frequent fire regime to remove competition and permit new growth (Ellsworth & Kauffman, 2010). This suggests that fire could be important in the conservation of the sub-alpine habitat through the promotion of the dominant zacaton bunchgrass and at the very least does not warrant a policy of active fire suppression (Keating, 2007). Zacaton bunchgrass is the main dietary component of *R. diazi* (Cervantes et al., 1990; Cervantes & Martinez, 1992). Therefore, maintaining its dominance through a frequent fire regime while promoting new growth should benefit *R.*diazi in turn. However, the effects of fire frequency need to be considered in conjunction with cattle grazing because human induced fires are an attempt to encourage new pasture growth explicitly for cattle grazing (Fa & Bell, 1990; Portales et al., 1997).

An increase in cattle grazing intensity had strong negative effects on both the species' distribution and abundance. The results of cattle grazing from this study agree with the findings of much of the published literature (Hoth et al., 1987; Velazquez, 1989; Fa & Bell, 1990; Fa et al., 1992) and so conservation recommendations are reiterated here that cattle should be removed from the sub-alpine habitat, especially within park boundaries. However the negative impact of cattle grazing has possibly been overestimated in other studies due to the possible positive impact of increased fire frequency as a result of pastoralism that we identify here. If cattle are removed from the national park, then the positive effects of fire frequency may also be reduced because 98% of fires are human induced to promote grazing. However, this does not mean that pastoralism should continue because the negative effects of cattle grazing probably outweigh the positive effects of the associated increased fire frequency: fire results in a 39.3% increase in species' occurrence over the range of the study whereas cattle grazing results in a 57.9% decrease over the same range. Furthermore, the removal of cattle could cause an increase in the frequency of natural fires through the restoration of native bunchgrass species abundances and growth patterns. The increased build-up of plant debris due to reduced grazing pressure might then increase fire frequency without anthropogenic intervention.

An increase in hunting pressure also had negative effects on both the species' distribution and abundance. Hunting pressure was estimated using the distance from the conspicuous ranger station Alsomoni because hunting of the species, which is illegal under Mexican law, should be less where there are enforcers. Consistent with this assumption is the observation that there was a marked change in abundance at approximately 3km (see Fig 3), coinciding with the limit of visibility and reduced audibility from the ranger station caused by a large ridge running east to west. The negative impact of hunting pressure on volcano rabbits is also supported by previous studies (Hoth et al., 1987; Velazquez, 1989; Fa & Bell, 1990; Fa et al., 1992).

Zacaton bunch grass and short grass also affected abundance, which is consistent with Zacaton bunchgrass being the main dietary component of the rabbit as well as providing cover (Cervantes et al., 1990; Cervantes & Martinez, 1992). From the model, the effect of short grasses appears to be more important biologically, however in the sub-alpine habitat where the *R. diazi* is distributed, the short grass type has a mean cover of 3.7% (SE=0.45, N=554) compared to zacaton bunchgrass which has a mean cover of 57.3% (SE=0.97, N=554). Furthermore, in 80% of the habitat, short grass types are not present at all (see Fig. 3). Therefore, zacaton bunchgrass, although less biologically significant over the full range of the study, is more important to species' abundance because it is the dominant grass type. Therefore, conservation effort in the sub-alpine habitat should be focused on maximizing the zacaton abundance.

Conservation recommendations

Habitat destruction is perhaps the greatest potential threat facing the species, for example destruction of the sub-alpine zacaton bunchgrass dominated habitat would be disastrous (Portales et al., 1997). The effects of this threat have been notably reduced due to the long established Izta-Popo National Park as a protected area since 1935. This protection has led to a low rate of habitat loss over time (0.35% per decade) in comparison with other unprotected areas in Mexico (3% per decade) (Ochoa-Gaona & González-Espinosa, 2000; Galicia & García-Romero, 2007). The position of the national park boundary at 3600m is well placed to protect the current distribution of the species. But if the sub-alpine habitat is put at risk, there would be a bigger impact on species' abundance than either hunting pressure or cattle grazing intensity. So protecting the largest available area of habitat the Izta-Popo National Park is the key component to this species' survival.

Habitat creation could also be considered. The potential of higher population densities due to more short grass-types and the effects of altitude could suggest that the species has greater abundance in highland temperate forest clearings. Further research of the species' abundance and distribution in these forest clearings is recommended to ascertain how important these are to potentially increasing populations of the species.

Another priority concern should be the enforcement of the existing laws prohibiting the hunting of the species (Portales et al., 1997). Also, education and awareness programmes are necessary for local people (Portales et al., 1997) who, as one author (MH) found, are often not aware of the species' existence or indeed protected status. Furthermore, if possible, the establishment other obvious symbols of park authority vigilance should be considered. A suitable example site would be an outcrop near the flat plateau above San Rafael, relatively far away from the existing station at Alsomoni, to maximise the area of new ground that would be protected.

R. diazi is endemic to a very limited area of less than $400km^2$, one of the smallest mammalian ranges in Mexico. Its largest contiguous area of habitat is in the Izta-Popo National Park, on the volcanoes Iztaccihuatl and Popocatepetl which together cover just 0.02% of Mexico by area but contain over 10% of all Mexican mammalian species (Velázquez et al., 2001). The Transverse Neovolcanic Belt, within which the Izta-Popo National Park lies, also has an exceptionally high level of endemism with 52% of Mexico's endemic mammalian species and all of Mexico's endemic mammalian genera represented (Koleff et al., 2004). Therefore it is likely that, in protecting the habitat of one indicator species, in this case the volcano rabbit, a number of other species would also be conserved.

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Table 1: The variables recorded at each of 859 point samples on Iztaccihuatl.

Variable Name	Description
Pellet count	The total number of pellets at each point sample is a sum of two 0.2m x 0.2m quadrats taken 5m apart which were recorded separately and then later amalgamated.
Position	Latitude and longitude using a Garmin GPS map 60CSX recorded to <10 m accuracy.
Altitude	Altitude recorded using a Garmin GPS map 60CSX to determine the position of point samples at 20m intervals in altitude to the nearest metre.
Transect	The line traversed parallel to the altitudinal gradient running from approximately 3400m to 4000m (1 to 25 transects).
Zacaton	The percentage cover of zacaton bunchgrass within 10m radius of the point sample, this grass-type includes the genus *Festuca*, *Calamagrostis*, *Muhlenbergia*, *Agrostis* and *Stipa*, major components of the *R. diazi* diet.
Salvia sp.	The percentage cover of a Salvia or sage species within 10m radius of the point sample, this is a conspicuous plant with purple flowers, a measure of the vegetation composition.
Lupinus sp.	The percentage cover of a *Lupinus* species within 10m radius of the point sample, this is a large bush with light blue/cream flowers, a measure of the vegetation composition.
Long grasses	The percentage cover of grasses >=20cm (zacaton bunchgrass not included) within 10m radius of the point sample, these grass-types possibly compete with zacaton bunchgrass.
Short grasses	The percentage cover of grasses <20cm within 10m radius of the point sample, these grass-types are a potential food source for *R.diazi* and a possible sign of cattle grazing.
Scrub	The percentage cover of bushes and small trees <3m in height within 10m radius of the point sample (*Salvia* and *Lupinus* not included), a measure of the vegetation composition.
Bare ground	The percentage area of bare ground within 10m radius of the point sample. Another measure of the vegetation composition and indication of fire or grazing or other factor.

Closed forest	The percentage cover of a closed forest habitat dominated by the Mexican mountain pine *Pinus hartwegii* (highland temperate forest) within 10m radius of the point sample.
Mature pines	The number of mature dominant pines within 10m radius of the point sample, the species is almost exclusively *Pinus hartwegii*.
Juvenile pines	The number of juvenile pines below the canopy level within 10m radius of the point sample, the species is almost exclusively *Pinus hartwegii*.
Incline	The greatest average incline of the slope over the 20m diameter around the point sample was measured using inclinometer and recorded as degrees from the horizontal.
Fire frequency	The time passed since last fire burn within 10m radius of the point sample was recorded on a scale of 0-3. The evidence of a very recent fire such as trees and other vegetation burnt to the ground with regrowth of <20cm would be scored the maximum 3, no sign of fire would be scored 0 and a continuum was used between these extremes. Note that our index can only detect signs of fires occurring within 1-2 years.
Grazing pressure	The cattle grazing pressure within 10m radius of the point sample was recorded on a scale of 1-5, 1 being no discernible signs of cattle in the immediate area and 5 being strong evidence. Cattle faeces, grazing of the pasture and individuals within sight and/or earshot were used as indicators.

Table 2: Analysis 1 predicting presence/absence model averaged parameter estimates and their relative weighting (i.e. inclusion) in the top models for all models (15) included within 2 AIC of the best model.

	Coefficient	SE	Relative var. importance
(Intercept)	7.1	2.83	
Altitude	-0.00152	6.77E-04	1.00
% closed forest cover	-0.0346	1.01E-02	1.00
Distance to station Almosoni	-0.000151	5.32E-05	1.00
Fire frequency	0.264	1.16E-01	1.00
Cattle grazing intensity	-0.393	8.78E-02	1.00
Incline of site	-0.0435	1.25E-02	1.00
% long grasses cover	-0.0223	1.27E-02	0.90
% bare ground cover	-0.0124	1.33E-02	0.64
% short grass cover	0.0104	1.19E-02	0.59
% cover Zacaton	0.00725	9.10E-03	0.59
% *Lupinus* cover	-0.00214	7.98E-03	0.36
% scrub cover	-0.00534	8.79E-03	0.36
% *Salvia* sp.	0.00615	1.22E-02	0.30

Table 3: The results of the top binomial regression GLM describing the distribution of the species. The variables that are included in the model are shown along with the estimates, standard errors and p-values from the model output. The percentage change in the probability of the species' occurrence over the range of the study for each variable is shown as a measure of biological significance using median values for all other parameters.

Variable	Estimate	S.E.	P value	Mean % change in occurrence
Percentage closed forest cover	-4.2 e-02	5.7 e-03	<0.00001	-97.1
Cattle grazing intensity	-3.7 e-01	8.1 e-02	<0.00001	-57.9
Percentage long grasses cover	-3.0 e-02	7.7 e-03	0.00011	-82.4
Incline of site	-4.5 e-02	1.2 e-02	0.00018	-78.5
Distance to station Almosoni	-1.7 e-04	5.2 e-05	0.0013	-44.4
Altitude	-1.9 e-03	6.5 e-04	0.0043	-48.3
Fire frequency	2.9 e-01	1.1 e-01	0.0096	39.3
Percentage bare ground cover	-2.1 e-02	1.1 e-02	0.045	-57.4
Percentage scrub cover	-1.3 e-02	7.7 e-03	0.091	

Table 4: Analysis 2 predicting abundance. Model averaged parameter estimates and their relative weighting (i.e. inclusion) in the top models for all models (10) included within 2 AIC of the best model.

	Coefficient	SE	Relative var. importance
(Intercept)	1.21	5.60E-01	
Distance to station Almosoni	-1.72E-04	3.07E-05	1.00
Cattle grazing intensity	-1.55E-01	5.47E-02	1.00
% short grass cover	1.07E-02	7.12E-03	0.85
% cover Zacaton	4.77E-03	4.45E-03	0.68
% scrub cover	5.53E-03	7.03E-03	0.49
% closed forest cover	-3.63E-03	5.79E-03	0.40
% *Lupinus* cover	3.38E-03	5.33E-03	0.37
% long grasses cover	-2.38E-04	2.71E-03	0.16
Altitude	-2.47E-05	1.25E-04	0.09
% bare ground cover	-7.84E-04	3.32E-03	0.08

Table 5: The results of the top quasi-Poisson regression GLM model describing the abundance of the species. The variables that are included in the model are shown along with the estimates, standard errors and p-values from the model output. The percentage change in the species' abundance over the range of the study for each variable is shown as a measure of biological significance using median values for all other parameters.

Variable	Estimate	S.E.	P value	Mean change in abundance (%)
Distance to station Almosoni	-1.7 e-04	3.0 e-05	<0.00001	-72.2
Percentage zacaton cover	8.5 e-03	2.9 e-03	0.004	124.2
Cattle grazing intensity	-1.6 e-01	5.3 e-02	0.0037	-46.6
Percentage short grasses cover	1.6 e-02	5.4 e-03	0.0089	220.6
Percentage scrub cover	1.2 e-02	5.8 e-03	0.053	
Percentage *Lupinus* sp. cover	8.7 e-03	4.7 e-03	0.12	

Figure legends

Figure 1. (a) The location of the study site and transects in Mexico, where the white rectangle shows the location of (b) within the central Transverse Neovolcanic Belt. (b) The four sites where the volcano rabbit occurs near Mexico City: 1, El Pelado; 2, Tlaloc; 3, Iztaccihuatl; 4, Popocatepetl. The grey rectangle indicates the location of (c), the study area on Iztaccihuatl. (c) The white area indicates the extent of the forest/grassland habitat where the volcano rabbit occurs on Iztaccihuatl and includes the transect locations. The central grey areas mark the largely unvegetated summit of the volcano; the peripheral grey areas are farmland and urban areas.

Figure 2: Sunflower plots showing the significant biological effects acting on the distribution of the volcano rabbit *Romerolagus diazi* using data from 853 random point samples with faecal pellets as a proxy of the species' presence and absence on the volcano Iztaccihuatl. The raw data are plotted as 'petals' which represent the number sample points. Lines are the predicted values from an optimal binomial regression (GLM) using median values for all other variables, solid lines represent mean predicted values and dashed lines 95% confidence limits.

Figure 3: Scatterplots showing the biological effects acting on the abundance of the volcano rabbit *Romerolagus daizi* on the volcano Iztaccihuatl using data from 266 random point samples with faecal pellet counts as a proxy. Each point represents a single point sample with associated values of log transformed count data. Lines are the predicted values from an optimal quasi-Poisson regression (GLM) using median values for all other variables, solid lines represent mean predicted values and dashed lines 95% confidence limits.

Figure 4: Scatterplot of data for altitude against the percentage closed highland temperate forest

dominated by *Pinus hartwegii* below 3400m highland temperate forest dominated by *Pinus hartwegii*, above 3600m sub-alpine grassland dominated by zacaton bunchgrass, between 3400m and 3600m is a transition zone between the two habitats depending on exact location and local conditions.

Figure 5: The percentage cover of long grass types between 3200m and 4000m. Data separated into bins of 100m intervals in order to show abundance change with altitude. Mean values are used for each bin. Note below 3400m highland temperate forest dominated by *Pinus hartwegii*, above 3600m sub-alpine grassland dominated by zacaton bunchgrass, between 3400m and 3600m is a transition zone between the two habitats depending on exact location and local conditions.

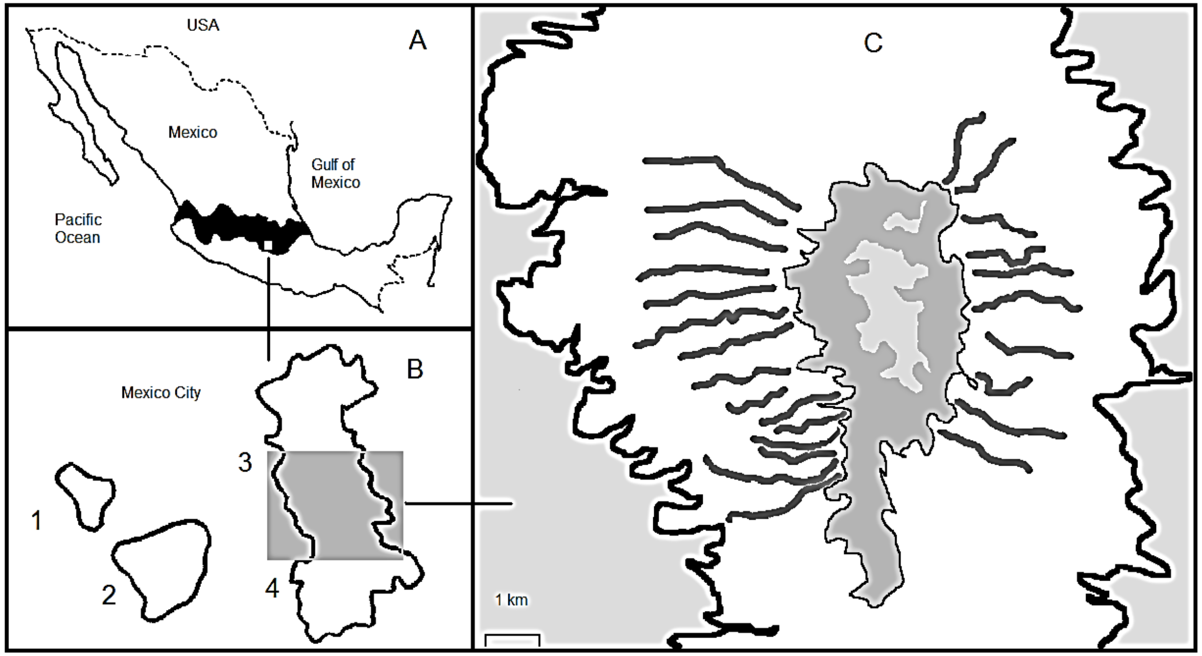
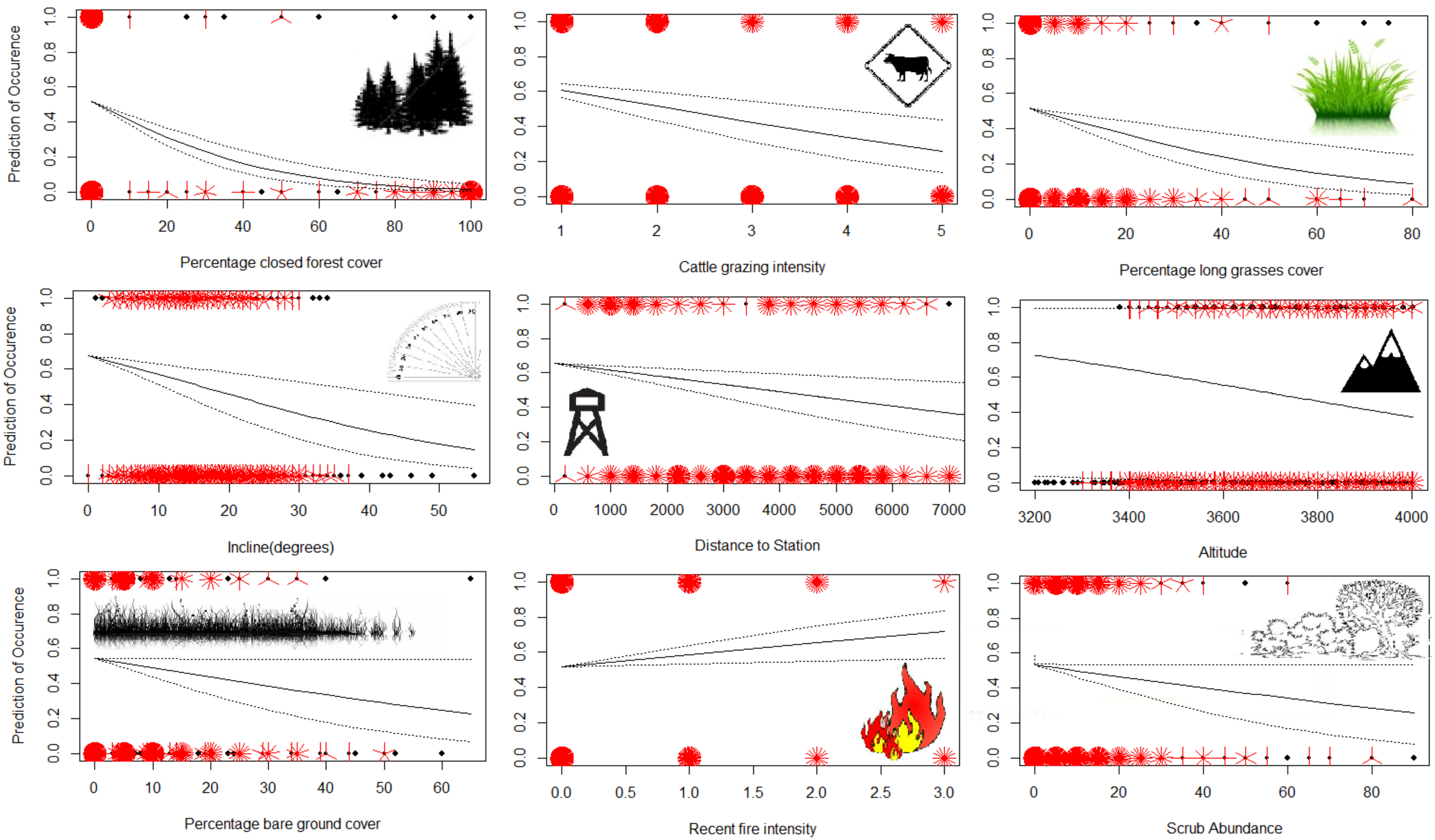

USA
A
Mexico
Gulf of
Mexico
Pacific
Ocean
B
Mexico City
3
1
2
4
C
1 km

Figure 1



Prediction of Occurence
Percentage closed forest cover
Cattle grazing intensity
Percentage long grasses cover
Prediction of Occurence
Incline(degrees)
Distance to Station
Altitude
Prediction of Occurence
Percentage bare ground cover
Recent fire intensity
Scrub Abundance

Figure 2:

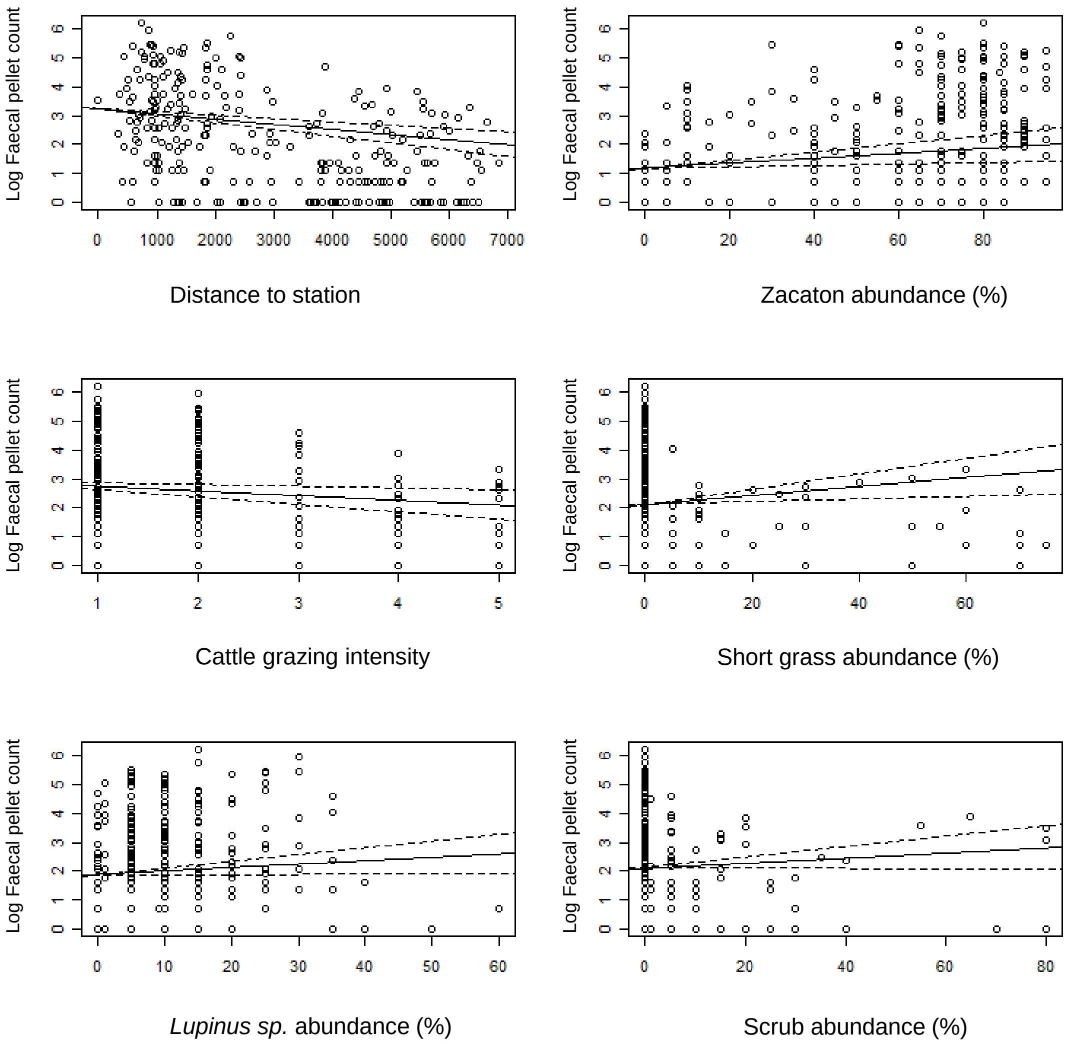

Log Faecal pellet count
0
1
2
3
4
5
6
0
1000
2000
3000
4000
5000
6000
7000
Distance to station
Log Faecal pellet count
0
20
40
60
80
Zacaton abundance (%)
Log Faecal pellet count
1
2
3
4
5
Cattle grazing intensity
Log Faecal pellet count
0
20
40
60
Short grass abundance (%)
Log Faecal pellet count
0
10
20
30
40
50
60
Lupinus sp. abundance (%)
Log Faecal pellet count
0
20
40
60
80
Scrub abundance (%)

Figure 3:

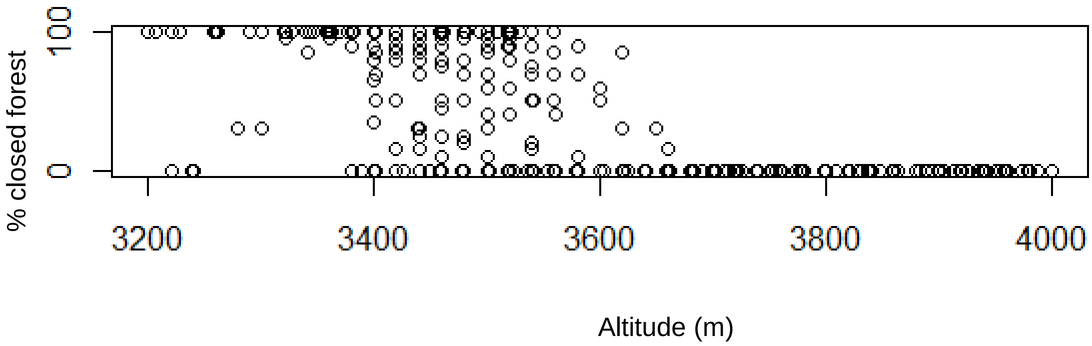
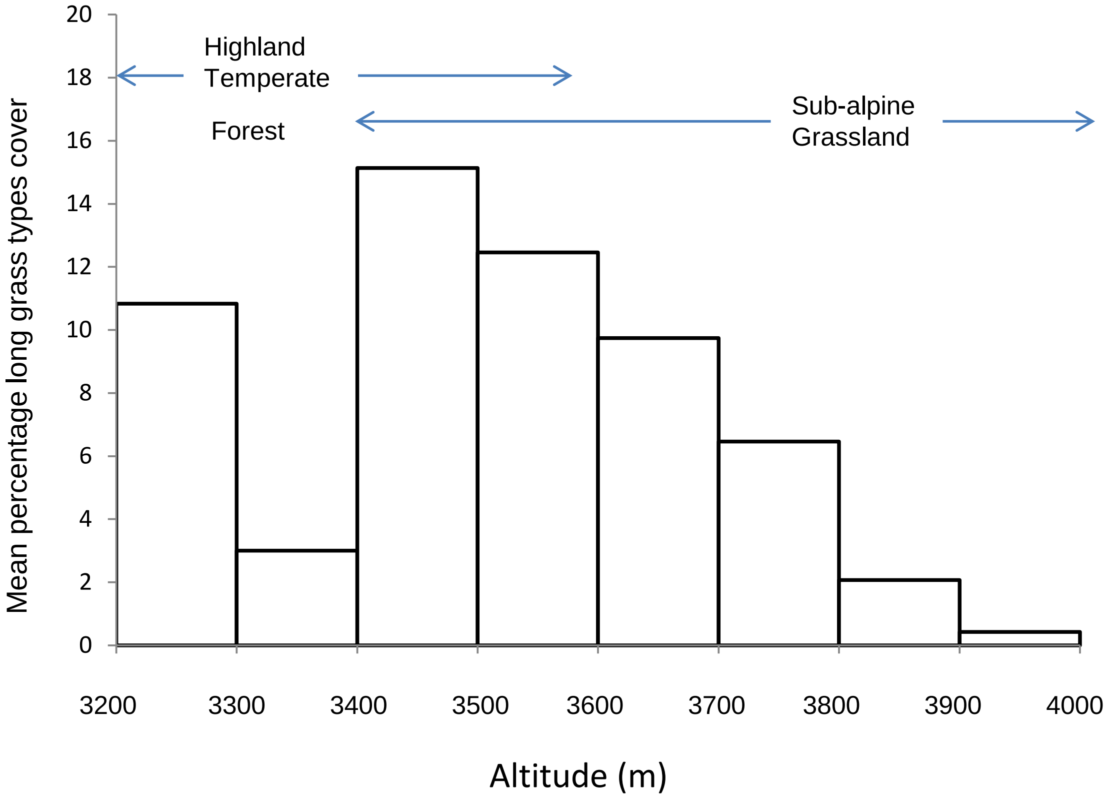


Figure 4:



Mean percentage long grass types cover
20
18
16
14
12
10
8
6
4
2
0
Highland
Temperate
Forest
Sub-alpine
Grassland
3200
3300
3400
3500
3600
3700
3800
3900
4000
Altitude (m)

Figure 5: