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Influence of stochastic processes and catastrophic events on reproductive dynamics of the endangered Maroon-fronted Parrot in Mexico

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Running head: *Stochastic and catastrophic events in parrots*

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Stochastic and catastrophic events may strongly impact the dynamics of wild populations. Evidence suggests that inter-annual fluctuations in rainfall may affect parrot populations, but few studies address the impact of other stochastic or catastrophic events on population dynamics. The Maroon-fronted Parrot *Rhynchopsitta terrisi* is an endangered species that nests colonially in cavities and crevices in limestone cliffs. From 1995 to 2010, we determined parrot attendance at nesting colonies throughout its breeding range, and reproductive output of nesting parrots from 1997 to 2010 at the two most important nesting colonies. There was significant variation among colonies in number of cavities occupied by parrots. The two nesting colonies produced an average of 1.6 fledglings per successful nest. Rainfall significantly influenced both the number of occupied cavities and productivity, which declined after severe dry years. Natural unpredictable events such as hurricanes impacting the nesting area did not modify nesting activity of Maroon-fronted Parrots at breeding colonies. However, wildfires increased in dry years, negatively affecting parrot attendance at breeding colonies. The Maroon-fronted Parrot may overcome the impacts of climatic variability, natural stochastic processes, and human-induced catastrophic events by employing nesting colonies as a network of nesting resources throughout the breeding range. Given the current trends in climate change, it is likely the species may suffer stronger and more frequent unpredictable catastrophic events, potentially putting at risk the persistence of the species in the long term.

Keywords: Cliff-nesting, ENSO, La Niña, *Rhynchopsitta terrisi*, Sierra Madre Oriental, wildfires

Stochasticity and environmental catastrophes may strongly impact the dynamics of wild populations to a point where large fluctuations in mortality and recruitment may drive populations to decline or extinction. The influence of these factors on population dynamics has been illustrated by theoretical models (Mangel & Tier 1993, Casagrandi & Gatto 2002). By comparison, empirical studies indicate that reproductive output and the effective population size are the main demographic measures that exhibit extreme fluctuations following stochastic or catastrophic events (Wiley & Wunderle 1993, Beissinger *et al.* 2008). Long-term studies are needed to more accurately understand population trends and how environmental stochasticity impacts population dynamics (Sæther *et al.* 2007).

Despite the fact that parrots represent one of the most threatened avian groups in the world (Bennett & Owens 1997), there have been few long-term studies on the factors associated with fluctuations in productivity and population dynamics of threatened parrot species. For three species of Mexico and South American parrots, reproductive output was influenced by interannual variation in rainfall caused by El Niño-La Niña cycle in the Pacific Ocean, likely due to an impact on food availability (Masello & Quillfeldt 2004, Renton & Salinas-Melgoza 2004, Sanz & Rodriguez-Ferraro 2006). The 1998-2000 La Niña event produced a severe drought that negatively impacted the survival of Burrowing Parrot *Cyanoliseus patagonus* nestlings in Argentina (Masello & Quillfeldt 2004), and the Yellow-shouldered Parrot *Amazona barbadensis* in Venezuela (Sanz & Rodriguez-Ferraro 2006). By contrast, in the central Pacific region of western Mexico, this event was associated with increased rainfall and reproductive output of the Lilac-crowned Parrot *Amazona finschi* in tropical dry forest (Renton & Salinas-Melgoza 2004). In addition, unpredictable events such as hurricanes may reduce shelter and food resources due to the destruction of key habitat, which makes parrots susceptible to predation, starvation or human trapping (Snyder *et al.* 1987, White *et al.* 2005).

Human activities, such as poaching and habitat modification, are widely recognized as the main factors impacting threatened parrot populations (Snyder *et al.* 2000). By comparison, the impact of natural stochastic or human-induced catastrophic events, such as wildfires, is less understood and their impact on the population dynamics of parrots has seldom been assessed (Davis *et al.* 2011). The scarcity of such studies may be due to the difficulty of gathering large datasets over a long time-span in this long-lived avian group. The little evidence available suggests that the impact of catastrophic events may be the primary driving factor affecting the survival of individuals in the wild, while environmental fluctuations play a secondary role that mostly impact reproductive output (Beissinger *et al.* 2008).

The Maroon-fronted Parrot *Rhynchopsitta terrisi* is an endemic and endangered species that inhabits temperate forests of the Sierra Madre Oriental of Mexico (Snyder *et al.* 2000, SEMARNAT 2010). Historical population estimates in the 1970's indicated a total of about 2000-4000 individuals in the wild (Lawson & Lanning 1981). Recently, approximately 3500 individuals were counted at a drinking waterfall in the wintering grounds (Valdés-Peña *et al.* 2008). Thus the wild population is at least 3500 individuals, though this may be an underestimate of the entire population as it is likely that not all the individuals of the population were present at that particular site. These two independent estimates suggest that the population of Maroon-fronted Parrots has remained stable over a 25 year period. The species nests colonially, using cavities and crevices in limestone cliffs several hundred meters in height in the northernmost region of its range. These nesting colonies are active during the breeding season from July to November. The cliff-nesting behaviour of the species has imposed some challenges for obtaining breeding information. Observations on the behaviour of nesting pairs suggest that eggs are laid by July-August. An estimate of the timing of hatching suggests that this may occur by August-September, while fledgling occurs by October-November (Valdéz-Juarez 2006). Once the fledglings leave the nest, the Maroon-fronted Parrots abandon their breeding grounds and move to their southern wintering range (Lawson & Lanning 1981, Enkerlin-Hoeflich *et al.* 1999). To date, however, no information exists on the breeding behaviour dynamics in these colonies, and whether they may be impacted by stochastic or catastrophic events.

Our objectives were threefold: (1) To determine how the effect of stochastic factors such as wildfire and rainfall influences Maroon-fronted Parrot attendance at breeding colonies (total number of cavities occupied per colony per year) over a 16-year period at 26 different colonies; (2) To evaluate the probability of occurrence of wildfires in the area of influence around Maroon-fronted Parrot colonies as a function of annual rainfall variability among years; and, (3) to determine reproductive output of nesting parrots over a 14-year time span for the two main colonies (El Taray and Los Condominios) identified from previous monitoring (Lawson & Lanning 1981, Macías 1998, Enkerlin-Hoeflich *et al.* 1999), and to evaluate how rainfall and wildfires influence the number of parrot fledglings as an estimator of productivity. Our study highlights the inter-annual variation in colony attendance and productivity of the Maroon-fronted Parrot and how climate and stochastic natural events, such as wildfires, may affect the breeding of this long-lived species.

METHODS

Study area

We carried out our study in the breeding range of the Maroon-fronted Parrot in northern Sierra Madre Oriental, Mexico (100°16' W, 25°42' N to 99°50' W, 24°50' N). The Sierra Madre Oriental is a mountain range approximately 600 km long and 80 km wide, with elevations ranging from 1000 to 3500 m asl. All the known breeding colonies are located within a small area of about 100 km long and 20 km wide in this mountain range (Macías 1998). Environmental conditions vary with altitude along the Sierra, with an extremely dry to semi-dry climate at low elevations, and a cold climate at high elevations. The average annual rainfall throughout the breeding range is between 413 to 1020 mm (INEGI 2010). Most rainfall occurs during July - September with monthly averages from 67-262 mm. Minimum monthly rainfall has been reported in March, November and December with monthly averages as low as 8-26 mm depending on the year. Annual average temperature throughout the breeding range varies between 11 and 27°C (INEGI 2010).

The Sierra Madre is dominated by steep mountains, many of which have almost vertical limestone cliffs that are used by the Maroon-fronted Parrot for nesting. These ridges generally run parallel in a northwest to southeast direction. The vegetation is composed at high elevations of coniferous forests such as *Pinus-Abies-Pseudotsuga*, *Pinus cembroides*, *Quercus* spp, and mixed forests of *Pinus-Quercus*, *Quercus-Pinus;* other habitats include submontane shrub, microphyllous desert shrub, desert shrub, chaparral, grassland and agricultural zones (Ortiz-Maciel *et al.* 2010). Most pine forests in the region are relict from the Holocene period (Rea 1997), and regeneration is scant or absent once forests are destroyed by natural causes or timber extraction (Ortiz-Maciel *et al.* 2010). The diet of the Maroon-fronted Parrot is primarily based on seeds of pinion pines, especially those of *Pinus strobiformis, P. montezumae*, *P. greggii*, *P. cembroides*, *P. culminicola*, and in minor proportions, flowers and fruits of Agave *Agave gentryi*, and occasional soil consumption (Lawson & Lanning 1981, Enkerlin-Hoeflich *et al.* 1999, Valdés-Peña *et al.* 2008).

We included in this study wildfires reported in the Maroon-fronted Parrot breeding area during our study period to investigate the impact of unpredictable events on the breeding biology of the species. Analyses of the pattern of occurrence of wildfires in the Sierra Madre Oriental indicate that they are normally low-intensity wildfires occurring on average every 5-20 years (Fulé & Covington 1997, González-Tagle *et al.* 2005); however, in some areas they can be so rare that it is possible to find periods of up to 80 years with no wildfires (González-Tagle, *et al.* 2007). Wildfires have been found to influence densities of parrot populations in surveys in extremely dry environments (Davis *et al.* 2011), and the highly unpredictable pattern of occurrence of fires in the Sierra Madre could be a factor strongly impacting the Maroon-fronted Parrot. In addition, the breeding range of the Maroon-fronted Parrot is commonly used as a recreational area by people from the two nearby cities of Monterrey and Saltillo, which increases the likelihood of the occurrence of human-induced wildfires.

We obtained the total area burnt per year in the parrot breeding area for 1979, 1984-85, 1987-89, 1991-95 from Valdéz (2002) to obtain an evaluation of the historic mean. We then obtained an estimate of contemporary area burnt in 2006 and 2008, during our study by mapping hotspots obtained from MODIS images from the NASA-Fire Information for Resource Management System (NASA FIRMS 2012). Only wildfires recorded with over 60% confidence were counted. A polygon joining the outermost wildfires in a cluster of identified hotspots was created and the area burnt was estimated using ArcView GIS 3.2 (ESRI 1999). Additional information on contemporary area burnt for years 1998 and 1999 was obtained from Lozano (1998, 1999). Each polygon identified with burnt vegetation was overlapped on a map using

ArcView GIS 3.2 (ESRI 1999). The Maroon-fronted Parrot may travel up to 27 km daily over the breeding range (Ortiz-Maciel *et al.* 2010); therefore, a buffer area of 27 km radius was created around each colony to obtain the area in which a given parrot from a given colony could potentially travel during daily foraging movements. We defined this as the area of influence around the colony in which the occurrence of wildfires may impact individuals breeding in a given colony. We evaluated the presence or absence of wildfires within this area of influence. We also considered all hurricanes entering the Sierra Madre Oriental during the study period as an additional unpredictable factor affecting the species' breeding behaviour and productivity.

Nesting colonies

A nesting colony was defined as a group of more than one pair of parrots entering cavities on the same cliff face within 1 km of each other (Macías 1998). Nesting colonies can be detected by the loud vocalizations of Maroon-fronted Parrots. The first nesting colonies were reported in 1978 (Lawson & Lanning 1981), and since then additional colonies have been found by research expeditions of the Instituto Tecnologico y de Estudios Superiores de Monterrey (ITESM) and Universidad Autonoma Agraria Antonio Narro. To date, 28 nesting colonies have been located throughout the Maroon-fronted Parrot breeding range (Fig. 1). All known nesting colonies are included in this study, with the exception of two colonies found in 2008 (El Álamo and Lagunillas-Rumorosa). We studied 26 nesting colonies located in limestone cliff walls with varying orientations. Nesting cliffs had an average ± se height of 239.2 m ± 20.9 m (range = 90 - 420 m, n = 26) and were separated by a mean distance of 31 km ± 1.1 km (range = 1.7 - 98 km, n = 325 pairwise distances).

The two main breeding colonies, El Taray and Los Condominios, were 14 km apart, on opposite sides of the Sierra Potrero de Ábrego mountain range. The El Taray nesting colony is located in Arteaga, Coahuila (100° 28’ 57’’W, 25° 02’ 02’’N), in an escarpment of two south-facing cliff walls, each about 200 m high, and surrounded by chaparral (Ortiz-Maciel *et al.* 2010) in a 372-ha protected area created specifically to preserve this important nesting site. The Los Condominios colony is located in Santiago, Nuevo León (100° 20’ 29’’W, 25°21’14’’N), in the Cumbres de Monterrey National Park. This colony has a northwest orientation, four nesting cliff walls of 420 m height, surrounded by *Pinus-Abies-Pseudotsuga* forest. We obtained monthly rainfall data for the period of 1994-2009 from nine climate stations maintained by CONAGUA, pairing each colony with the closest available weather station. We considered the amount of rainfall in the previous year to nesting in our analyses, as this has been observed to influence the availability of food resources for parrots in the following year and hence productivity of nesting pairs (Renton & Salinas-Melgoza 2004).

Colony surveys

We monitored all 26 Maroon-fronted Parrot nesting colonies during each breeding season (July-November) from 1995 to 2010. When no parrot activity was detected at a colony at the start of the breeding season, usually in the case of small colonies, we revisited the colony at least once more during the breeding season to confirm that no nesting pairs were present. Cavities used by parrots were located on photographs of the cliff face for the 26 colonies to assign each cavity a unique identifying numeric code. Observations were conducted with spotting scopes and binoculars at strategic lookouts at an average distance of 701.9 ± 98.6 m (range = 50 - 1920 m, *n* = 26) from the colony wall. Lookouts in the two main breeding colonies were approximately 50 m and 300 m from El Taray and Los Condominios nesting cliffs respectively. Lookouts were selected based on accessibility, and to ensure an unhindered view of the entire colony.

The interior of the nest cavities could not be accessed to check their contents, as these were located high on the cliff face, and direct inspections indicated they extended deep into the limestone cliff. Therefore, we applied indirect methods based on behavioural observations and rate of cavity attendance to determine the pattern of occupancy of the cavities at the 26 colonies. We considered a cavity as inspected by parrots if an individual perched at the edge of the cavity entrance. Inspected cavities were considered as occupied if all of the following criteria were fulfilled: (a) birds entered the cavity and disappeared from the observer's sight; (b) a single bird entered the cavity and two left, or vice versa; and, (c) parrots entered the cavity at least three times during the day, regardless of the time they spent inside the cavities. We determined the number of occupied cavities for each colony per breeding season.

Reproductive output

We recorded the number of fledglings leaving the nest by intensive observations at El Taray and Los Condominios from October to November. This period corresponds to the end of the breeding season and enabled us to obtain both the number of fledglings and successful nests. We performed simultaneous and continuous daily monitoring at both colonies from dawn to sunset. Fledglings were distinguished, with a high degree of reliability given the short distance of lookouts from the base of the cliffs, based on their begging calls, characteristic unskilled flight, and whitish beaks (Lawson & Lanning 1981, Macías 1988). Productivity data were obtained from the El Taray colony from 1997 to 2010, while productivity data from Los Condominios were recorded in the breeding seasons of 1998 and from 2002 to 2010.

Statistical analysis

Data on attendance at breeding colonies (number of occupied cavities per year and colony) and productivity (number of fledglings per year and colony) were analysed using Generalized Linear Mixed Models (GLMM), assuming Poisson error distributions. We analysed attendance for all colonies together, and separately for just the two main colonies of El Taray and Los Condominios. In addition, we evaluated whether the probability of wildfire occurrence in the area of influence of each colony was related to fluctuations in rainfall by fitting a logistic regression (wildfire presence vs. absence) with GLMM using a binomial error distribution (Bates *et al.* 2012). Because the consecutive counts of cavities and fledglings in the same colonies during the study period may cause temporal autocorrelation in our data, we used mixed effects models. These models are particularly useful in cases where there is temporal pseudoreplication or repeated measurements, as in this case (Pinheiro & Bates 2000, Crawley 2007). Thus the variance associated with the repeated measurement effect in the colonies over the years of study (C/Yr) was included as a random effect (Pinheiro and Bates 2000; Faraway 2005; Crawley 2007). Additionally, to account for the auto-regressive nature of the data, where counts close together in time are more likely to be correlated than counts further apart for a given site, we included log of cavities occupied as an offset in the mixed model (Zuur *et al.* 2009). As fixed factors, we included the following terms and their interactions: (i) annual rainfall prior to nesting as a proxy for the influence of environmental variation (AR); and, (ii) wildfires (WF, with two levels, presence and absence). For the case of cavities occupied and fledglings produced for the two main cavities, we also included the term Colonies (C, with two levels, Condominios and El Taray). We used the lme4 package (Bates *et al.* 2012) for R version 2.13.0 (R Development Core

Team 2013).

We first fitted saturated models, which included all possible interactions. Models were then simplified based on sequential removal of non-significant fixed effects and detecting significant changes in residual deviance at each step (Pinheiro & Bates 2000, Crawley 2007) as assessed by likelihood ratio χ^2 tests. The final model consists only of fixed significant terms (Pinheiro & Bates 2000, Faraway 2005). Results are expressed as means ± se.

RESULTS

We monitored an average of 22.6 ± 1.1 colonies per breeding season. The lowest number of colonies surveyed was 14 in 1995 and 1996, contrasting with 26 colonies in 1997 and with the 2003 to 2009 period. Colonies were monitored on average 132.5 ± 12.9 days per year (range = 42 - 219 days, *n* = 16 years). Observations were conducted for a mean of 7.4 ± 0.03 h per monitoring day (range = 0.8 - 13 h, *n* = 2120 monitoring days) at each colony, giving a total of 15 636 h of observations over the 16 years (977.3 ± 99.6 observation h/yr, range = 276 - 1467 h).

Colony attendance

The El Taray and Los Condominios nesting colonies were active in all of the 16 years of study, had the highest number of occupied cavities per year of the 26 nesting colonies (Supporting Information Table S1), and together represented 72% of all nesting activity of Maroon-fronted Parrots throughout the study period (Fig. S1). The total number of cavities occupied by parrots fluctuated greatly among years (334.9 ± 27.4 occupied cavities per year, range = 91 - 478) and throughout the breeding range (Fig. S1, Table S1). There was also temporal variation in the total number of occupied cavities per year over all colonies, with the highest total of 478 occupied cavities in 2008, and the lowest activity recorded in 1999 with a total of 91 occupied cavities (89 of which were at El Taray and two at Los Condominios), while the other colonies were deserted.

Productivity at El Taray and Los Condominios

During the 14-years of intensive monitoring from 1997 to 2010, we recorded a total of 511 successful Maroon-fronted Parrot nests at El Taray and Los Condominios combined. Half of these successful nests fledged one chick (261 nests, 51%), while 205 (40%) nests fledged two chicks, 41 (8%) nests fledged three chicks, and four (0.7%) nests produced four fledglings. For both colonies combined, 20.5% $\pm$ 1.9 % of occupied cavities successfully reared chicks. All 810 fledglings were reared from 174 unique cavities at the two main colonies over the duration of the study. Most of these cavities were used once (67 cavities) or twice (31 cavities). The most frequently used cavity was located at El Taray, and was used continuously over 13 years. Over the 14 years of nest monitoring, we registered the day of fledging for 387 chicks. Fledging occurred over a narrow six week period extending from 14 October to 24 November, with peak fledgling on 24 October when 33 fledglings left their nests.

Productivity of fledglings per year differed between the two main nesting colonies (χ^2_1 = 13.3, $P < 0.001$), with a higher mean of 33.8 ± 4.3 fledglings per year for El Taray compared with 28.1 ± 6.5 fledglings per year for Los Condominios. However, productivity was similar when considering fledglings per successful nest (El Taray = 1.7 ± 0.04, range = 1 – 4, n = 13 years, 283 successful nests; Los Condominios = 1.5 ± 0.04, range = 1 – 3, n = 11 year, 228 successful nests). These two colonies combined produced a mean of 1.6 ± 0.02 fledglings per successful nest. Productivity, measured as the number of fledglings per year by colony, varied greatly over the 14-yr study period, ranging from 0 to 79 fledglings per colony. The highest productivity of fledglings was recorded at El Taray in 2004 with 64 fledglings, while the highest productivity at Los Condominios occurred in 2006 with 79 fledglings. No fledglings were produced at either colony in 1999.

Occurrence of wildfires and hurricanes

We found wildfires to be infrequent events that were scattered throughout the breeding range of the Maroon-fronted Parrot during the study. We found a mean historic burnt area of 354 ha/yr, ranging from 10.01 ha in 1989 to 1412 ha in 1988. In four years of our study (1998, 1999, 2006 and 2008), the amount of area burnt by wildfires exceeded the historic mean by between 6883 ha and 12880 ha (Lozano 1998, 1999). In particular, 1998 was an exceptional year as the average number of wildfires occurring within the 27 km radius of colonies was 2.23 wildfires per colony (range = 1 - 3 wildfires in the influence area).

Four hurricanes were recorded during the study period: Hurricane Erika in 2003, Hurricane Emily in 2005, Hurricane Dolly in 2008 and Hurricane Alex in 2010 (NOAA 2012a). Hurricane Erika (Category 1 on the Saffir–Simpson scale; NOAA 2012b) hit Sierra Madre Oriental on 17 August. That year, 442 cavities occupied by parrots were recorded. In 2005, Hurricane Emily (Category 3) formed in the Atlantic Ocean and hit the Sierra Madre Oriental on 20 July. On 7 June 2005, we observed Maroon-fronted Parrot activity at nesting colonies prior to the hurricane, but by 11 July all of the previously active colonies had been abandoned. However, by 2 August 2005, breeding activity had re-started, and the total number of 416 cavities occupied over all colonies after re-initiation was higher than the annual average of occupied cavities for all years. Hurricane Dolly (Category 2) passed north Sierra Madre Oriental on 25 July in 2008, but parrot breeding activity was high with a total of 478 occupied cavities from all colonies that year. Finally, Hurricane Alex (Category 2) hit the Sierra Madre Oriental in June 2010. There were 373 cavities occupied by parrots recorded at all nesting colonies after the hurricane had passed.

Effects of environmental variability and catastrophic events

Breeding activity of the Maroon-fronted Parrot was influenced by a number of factors. The GLMM demonstrated that attendance differed significantly among all colonies and that annual rainfall explained some of this variation (Table 1). Specifically, we found a negative relationship between colony attendance and rainfall. However, the GLMM also found a significant interaction between rainfall and wildfires (Table 1), where the effect of rainfall was stronger (i.e. steeper slope) in wildfire-free colonies. By contrast, colonies with presence of wildfires showed a *c*. 5-fold decrease in the number of cavities, as indicated by the intercept (Fig. 2). Considering only El Taray and Los Condominios, rainfall had a contrasting effect to that when considering all colonies (Fig. 3). Rainfall had a significant positive effect on the number of cavities (Table 1), with similar slopes for both colonies, but higher number of cavities for El Taray (Fig. 3). In general, El Taray recorded a more homogeneous rainfall pattern during the study period (260-632 mm) than Los Condominios (268-1915 mm).

We also found that the overall probability of wildfire occurrence within the area of influence of a colony was significantly related to the amount of rainfall prior to the breeding season ($\chi^2_1 = 75.5$, $P < 0.001$). The logistic regression model indicated that those colonies with < 300 mm of rainfall had the highest (0.44) probability of wildfire occurrence, while those colonies with ≥ 700 mm of rainfall had less than a 0.10 probability of recording a wildfire within the area of influence (Fig. 4).

Furthermore, the number of fledglings produced in the two main colonies was positively related to rainfall prior to the breeding season, with a greater number of fledglings in years of increased rainfall ($\chi^2_1 = 5.5$, $P < 0.01$, Fig. 5). One of the wildfires in March 2006 consumed 545 ha of standing trees around the El Taray nesting colony (CONAFOR 2006a, 2006b) destroying > 70% of the El Taray Reserve (Manzano 2006); however, neither wildfires nor the interaction with rainfall had any effect on the number of fledglings at the two main nesting colonies. Prior to 2006, the El Taray colony had been the most productive colony, but after the 2006 wildfire at El Taray, Los Condominios experienced a two-fold increase in fledglings, and produced more fledglings than El Taray (Fig. S2).

DISCUSSION

We have presented the first long-term evaluation of reproductive dynamics for the endangered Maroon-fronted Parrot at 26 of the 28 known nesting colonies of this species. Our results have demonstrated large fluctuations in attendance at breeding colonies and in productivity of Maroon-fronted Parrots that may be influenced by stochastic processes, climatic variability, and human-induced catastrophic events such as wildfires. The results also highlight the importance of the two main nesting colonies of El Taray and Los Condominios, and their contribution to productivity and long-term persistence of this endangered parrot.

Impact of unpredictable events on breeding colonies

We found temporal fluctuation in colony attendance and productivity of the Maroon-fronted Parrot related to inter-annual variation in rainfall, although the results varied according to which colonies were included in the analysis. For all colonies, there was a negative effect of rainfall on nesting activity: however, when the two main colonies were analysed separately there was increased nesting activity after periods of high rainfall, and a decline in nesting activity after dry years. It is clear that these colonies are very important for the species' overall reproductive output, hence we believe the real impact of climatic variability on parrot nesting activity may be masked when all colonies are combined in the analysis due to the inclusion of a large number of colonies with only a few breeding pairs. This may also imply movement between colonies and a greater reliance on the two main colonies in wet years (see below).

The severe drought recorded in 1998 could have resulted from the 1998 La Niña phase of ENSO, impacting the reproduction of the Maroon-fronted Parrot indirectly. The El Niño and La Niña ENSO events affect rainfall patterns, which in turn may influence plant productivity (Holmgren *et al.* 2001, Magaña *et al.* 2003, Pavia *et al.* 2006). La Niña has been associated with dryer conditions in northwestern Mexico (Magaña *et al.* 2003), potentially also resulting in lower precipitation in the Sierra Madre Oriental in 1998. This could have resulted in reduced seed production, negatively affecting attendance of nesting pairs of Maroon-fronted Parrots at breeding colonies in 1999, in the same way that the 1998-2000 La Niña impacted the reproduction of other parrot species at southern latitudes (Masello & Quillfeldt 2004, Sanz & Rodriguez-Ferraro 2006).

We found that rainfall negatively influenced the probability of occurrence of wildfires affecting breeding colonies of the Maroon-fronted Parrot. The historic record in the Sierra Madre Oriental indicates that wildfires may be a regularly occurring phenomena at low intensity, but with some considerable wildfires occurring intermittently (Fulé & Covington 1997, González-Tagle *et al.* 2005, González-Tagle *et al.* 2007). We recorded four years during our study (1998, 1999, 2006 and 2008) in which the degree of influence of the burnt areas from wildfires may have strongly impacted nesting areas of the Maroon-fronted Parrot. Mexico recorded a severe season of wildfires with over 580 000 ha of burnt vegetation in 1998 (DOF 1998), when intense wildfires were recorded in the Sierra Madre Oriental associated with a severe drought. This drought may potentially have resulted in a dramatic reduction in colony attendance by breeding pairs of Maroon-fronted Parrots, with zero productivity of fledglings in 1999.

The reason for the shift in parrot attendance recorded between the two main colonies is unclear. This shift could be related to the massive wildfire in 2006 close to El Taray, which could have made individuals from El Taray to move to Los Condominios to breed. However, the post-fire reduction in El Taray was not as marked as may be expected, and Los Condominios was already showing a trend of continuous increase even before the wildfire. Alternatively, this shift could be associated with fluctuations in parrot population dynamics at Los Condominos, resulting from flux of individuals from minor colonies.

Unpredictable events may not only influence nesting colony attendance and parrot productivity, but also the pattern of regional movements. Maroon-fronted Parrots could disperse to forage in new areas not previously visited as a strategy to overcome stochastic and catastrophic events, as they were observed in 2008 feeding on seeds of pines in the city parks of Saltillo and Arteaga after a fire devastated > 7300 ha in Santiago, Nuevo León (Ortiz *et al.* 2009). These two cities are within the range of the species, and could easily have been visited during daily movements. Australian parrots in cities can fluctuate in numbers during drier periods or after the occurrence of wildfires, possibly due to fluctuations in resources or the mortality of individuals (Davis *et al.* 2011). Fluctuation in resources has been suggested as the main driver predisposing the evolution of long-distance movements in Neotropical birds (Levey & Stiles 1992), and may modify the pattern of local movements (Rey 1995, Renton 2001, Saracco *et al.* 2004). Hence, this event may have triggered the displacement of Maroon-fronted Parrots to new areas if resources were scarce after 2008 wildfires.

Our data suggest that population dynamics of Maroon-fronted Parrots are also able to withstand effects of hurricanes. Parrots may be able to relocate to areas unaffected by hurricanes in insular environments, returning when conditions improve (Snyder *et al.* 1987, White *et al.* 2005). However, both the topography of the Sierra Madre Oriental, and the distance from the coast (290 km to the closest colony) could have reduced the impact of this climatic phenomenon in comparison to the more exposed coastal areas. Visual inspection of the habitat after Hurricane Emily in 2005 suggested that the hurricane did not have a strong impact, as we noted minimal numbers of cones on the ground and the canopy was largely undamaged. The lack of a strong impact of hurricanes on nesting Maroon-fronted Parrots is further supported by the return of parrots to colonies and the successful rearing of young in 2005 after Hurricane Emily.

Breeding colonies as a network of nesting resources

Our results highlight the importance of the two nesting cliffs of El Taray and Los Condominios for Maroon-fronted Parrot reproduction and population dynamics. The fact that these two nesting cliffs are preferred over the other 24 suggests that individuals attending these colonies are acquiring higher fitness benefits than parrots in other colonies. In addition, the inconsistency in our results on the impact of rainfall on attendance when analysing all colonies together and the two main colonies independently could suggest that colony attendance may be dependent on the environment, as conditions for nesting at main colonies could improve in wetter years due to an increase in the availability of food resources. This situation could motivate breeding pairs from minor colonies to move to main colonies for nesting. We further observed an increase in attendance and productivity at Los Condominios. This data further supports the idea of movement of individuals among colonies, possibly new recruits attending this nesting colony. The 26 colonies throughout the breeding range could be seen as a network of nesting resources that allow the parrots to cope with catastrophic and unpredictable events, such as wildfires and local food shortages. Access to alternative breeding sites could play an important role in the species' population dynamics, in which not only the main nesting cliffs but also minor nesting cliffs could provide alternative nesting resources. Records of wildfires since 1975, which destroyed extensive areas up to *c*. 12 000 ha of pine forests yearly (Lawson & Lanning 1981, Lozano 1998, 1999, Brown *et al.* 2000, CONAFOR 2006a, 2006b, Ortiz *et al.* 2009), indicate that the breeding range of the Maroon-fronted Parrot in the northern Sierra Madre Oriental may have been altered considerably. The movement of individuals among colonies could buffer the effects of catastrophic and stochastic events throughout the breeding range.

Implications for conservation

Our long-term data on the dynamics of Maroon-fronted Parrot nesting colonies indicate the susceptibility of the species to natural stochastic processes and human-induced catastrophes. Considering current trends of climate change, the probabilities of wildfire occurrence in the future may increase, and this change may also affect the regional availability of the food supply (Dore 2005). Our research also highlights the link between habitat preservation and wildfire prevention actions within the species' range to ensure the long-term viability of the species.

Human-related factors such as poaching and habitat modification are the two main threats to parrots (Snyder *et al.* 2000). It seems from our study and from that of Davis *et al.* (2011) that wildfires could be added to this list; however, these trends may be only observed given the length of the monitoring of both studies.

The proximity of the two main colonies of El Taray and Los Condominios means that the breeding dynamics of these two and the other colonies may be interconnected. The protection not only of the main colonies but also of the minor colonies is required for the species to withstand stochastic and catastrophic events impacting on the species breeding performance. Our study suggests that these actions also need to consider reducing wildfires close to at least the two main breeding colonies.

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Table 1. Fixed effects of generalized linear mixed models (GLMMs) to assess the role of climatic variability and wildfires on attendance (occupied cavities) of Maroon-fronted Parrots at different breeding colonies. Results for all colonies and for the two main colonies of El Taray and Los Condominios are presented. $LRT\chi^2$: chi-square from the likelihood ratio test, *df:* degrees of freedom and *P*: probability. The - denotes factors and interactions that were not significant in the analysis and were excluded from the final model.

	All colonies			**For the two main colonies**		
Fixed factor	$LRT\chi^2$	***df***	***P***	$LRT\chi^2$	***df***	***P***
Annual Rainfall	116.8	2	< 0.001	3,44	1	<0,01
Wildfire	172,6	2	< 0.001	-	-	-
Colony	-		-	10,6	1	0.001
Annual Rainfall:Wildfire	57.6	1	< 0.001	-	-	-

Figure 1. Map of the study area showing the breeding distribution of the Maroon-fronted Parrot and the 28 known nesting colonies indicated by the white dots in Sierra Madre Oriental, Mexico.1 Aguajito de Adentro, 2 Banco de Abajo, 3 Canoas, 4 El Álamo, 5 El Arbolito, 6 El Calabozo, 7 El Mimbral, 8 El Pajonal, 9 El Taray, 10 La Boca, 11 La Huasteca, 12 La Zacatosa, 13 Lagunillas-Rumorosa, 14 Las Navajas, 15 Las Tijeras, 16 Las Trancas, 17 Los Condominios, 18 Los Sierrales, 19 Los Tomates, 20 Mediodía, 21 Pablo L. Sidar, 22 Potreritos, 23 Puerto El Hondable, 24 Rancho Las Boquillas, 25 San Antonio de la Osamenta, 26 San Isidro, 27 San Lorenzo, 28 Santa Cruz.

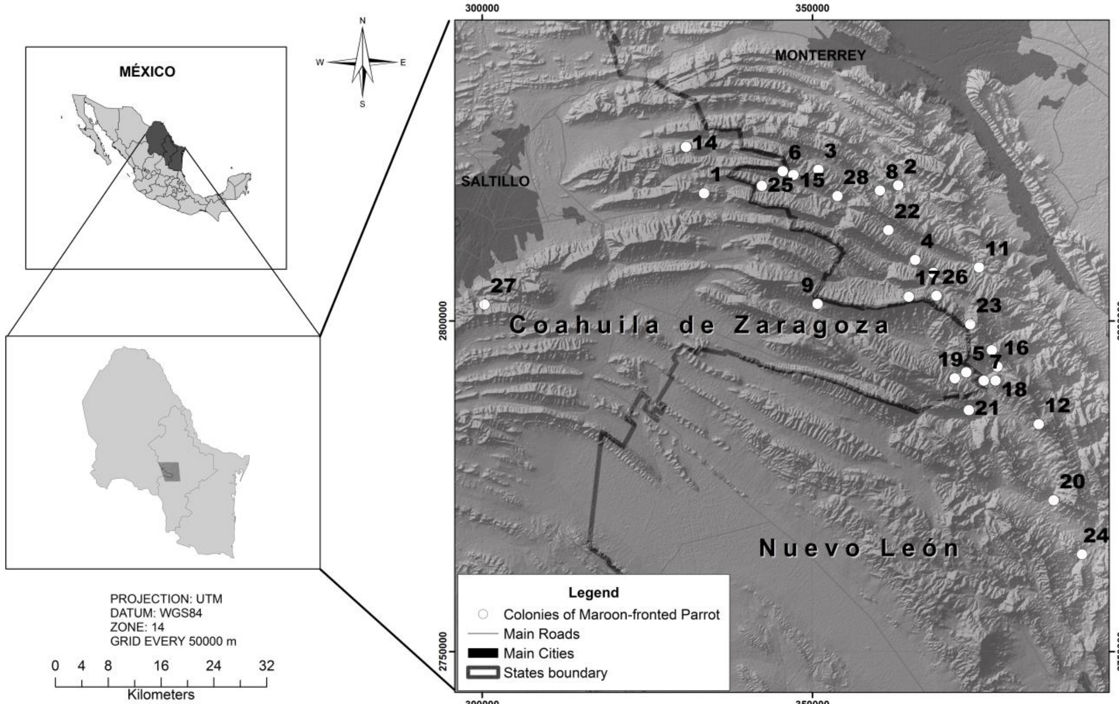
Figure 2. Influence of annual rainfall prior to the breeding season and occurrence of wildfires on colony attendance by Maroon-fronted Parrots (number of cavities occupied) at 26 colonies during the 1995-2010 period. Regression lines were obtained from the GLMM Poisson model. Dashed line indicates the regression line for free fire colonies.

Figure 3. Effects of rainfall on attendance (number of cavities occupied/colony) of Maroon-fronted Parrots for the two main colonies during the 1995-2010 period. Regression lines were obtained from the GLMM Poisson model. Dashed line indicates the regression line for the El Taray colony.

Figure 4. Probability of a wildfire occurring within the area of influence of a colony as a function of annual rainfall (mm). Open circles represent sites with fire present within a 27 km radius, while closed circles represent absence of wildfires. The regression line was obtained from the GLMM binomial model.

Figure 5. Relationship between productivity (fledgling/colony/year) and annual rainfall (mm) for the two main nesting colonies of Maroon-fronted Parrot during the 1995-2010 period. Regression lines were fitted from the GLMM Poisson model.

Figure 1.


MÉXICO
N
W
E
S
PROJECTION: UTM
DATUM: WGS84
ZONE: 14
GRID EVERY 50000 m
0 4 8 16 24 32
Kilometers
300000
350000
MONTERREY
SALTILLO
Coahuila de Zaragoza
Nuevo León
2800000
2750000
14
1
6
3
25
15
28
8
2
22
4
11
17
26
9
27
23
16
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5
7
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12
20
24
Legend
Colonies of Maroon-fronted Parrot
Main Roads
Main Cities
States boundary

Figure 2.

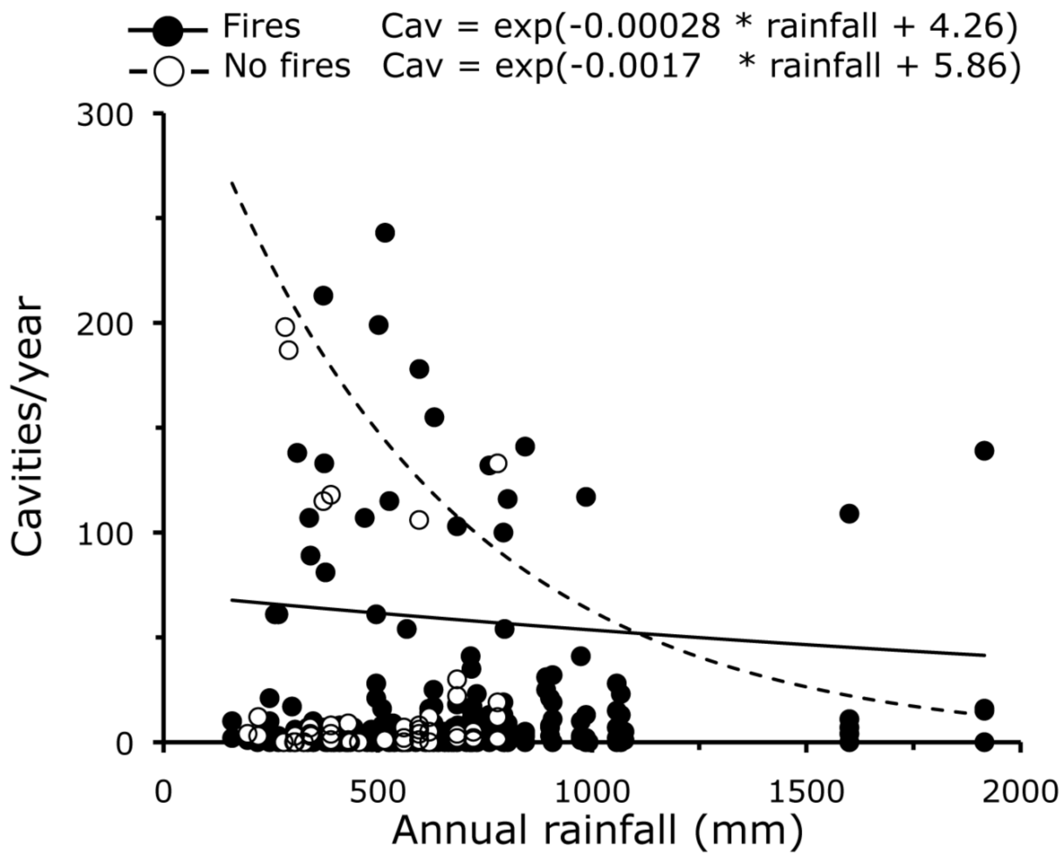

Fires Cav = exp(-0.00028 * rainfall + 4.26)
No fires Cav = exp(-0.0017 * rainfall + 5.86)
Cavities/year
300
200
100
0
0
500
1000
1500
2000
Annual rainfall (mm)

Figure 3.

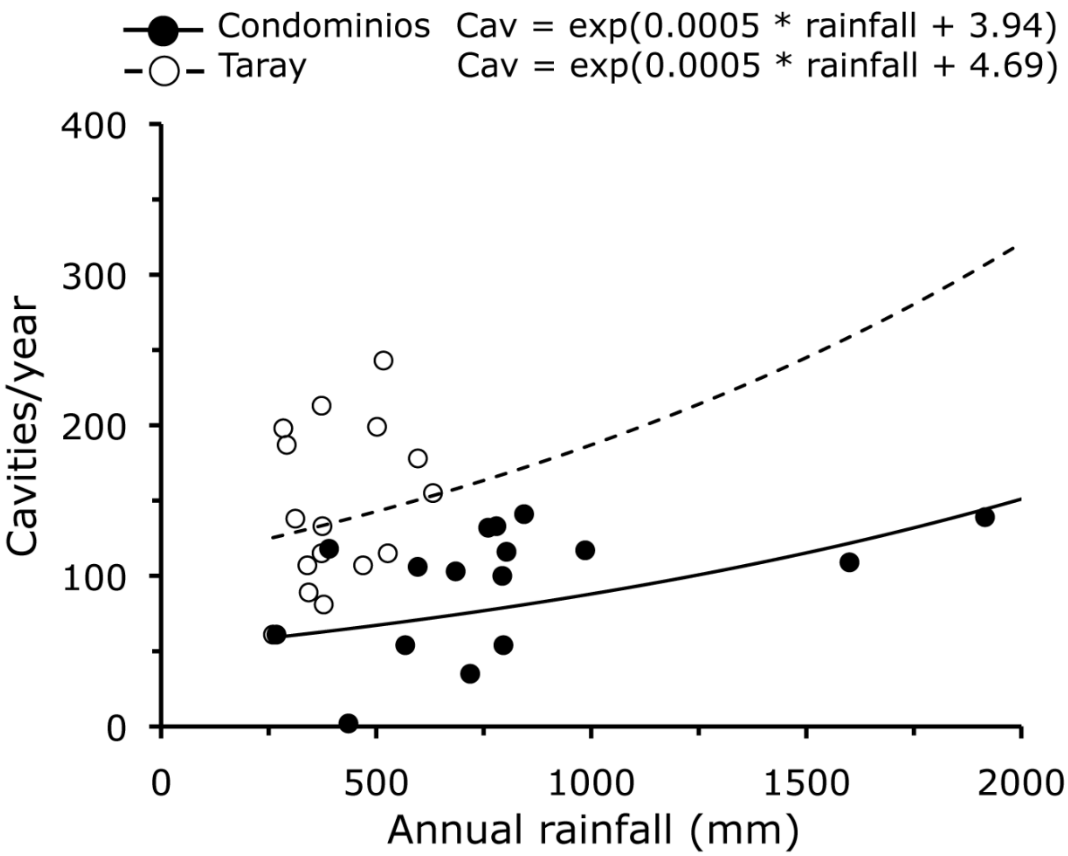

Condominios Cav = exp(0.0005 * rainfall + 3.94)
Taray Cav = exp(0.0005 * rainfall + 4.69)
Cavities/year
400
300
200
100
0
0
500
1000
1500
2000
Annual rainfall (mm)

Figure 4.

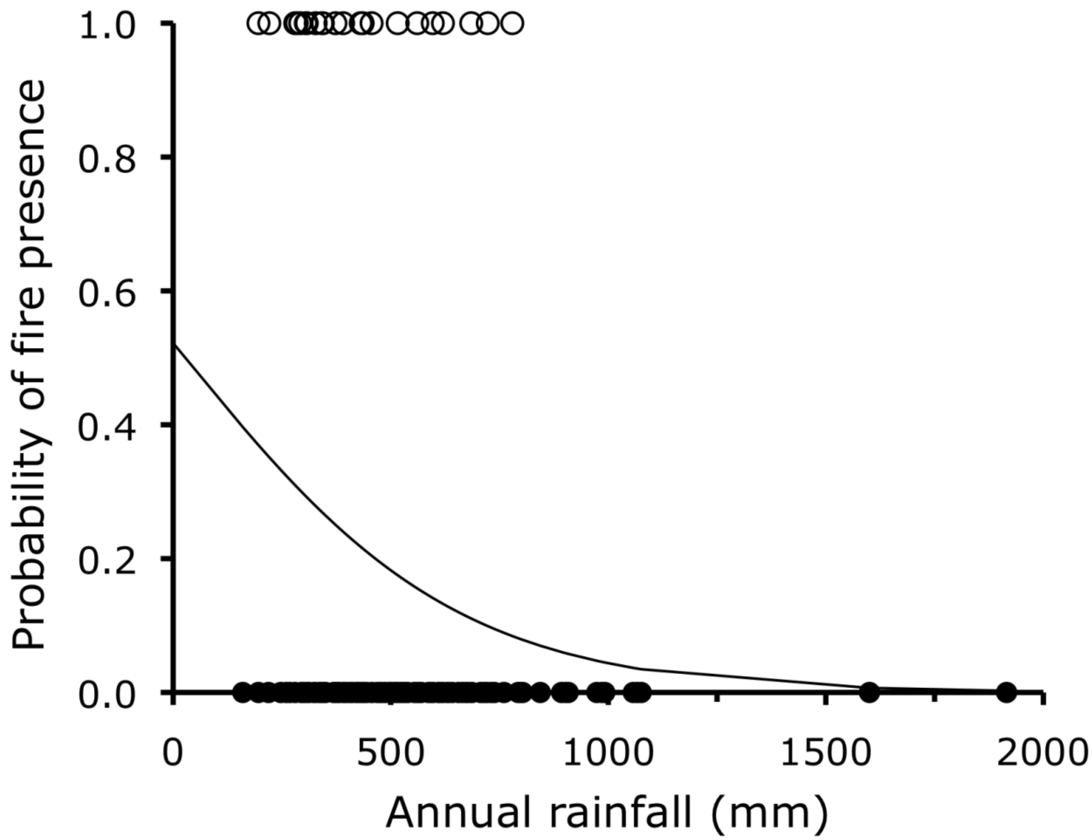
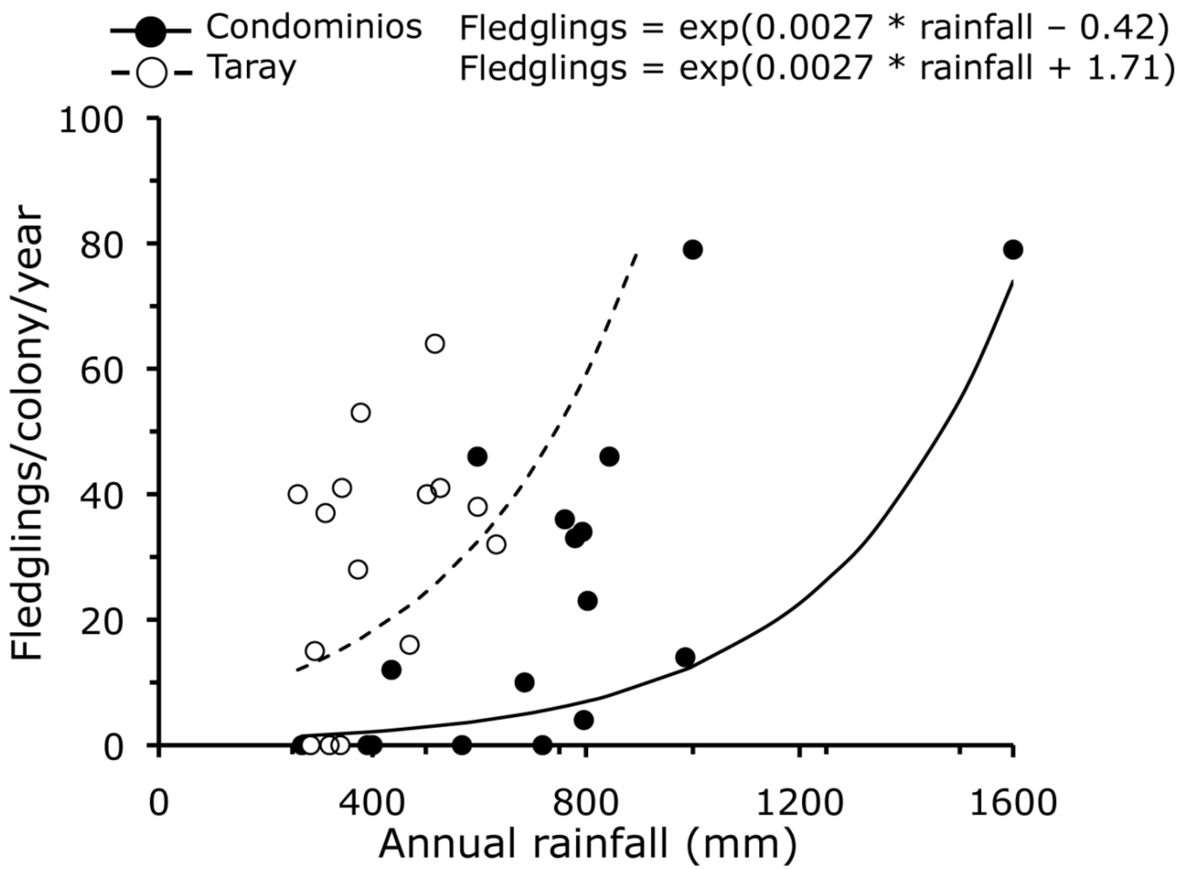

1.0
0.8
0.6
0.4
0.2
0.0
Probability of fire presence
0
500
1000
1500
2000
Annual rainfall (mm)

Figure 5.


Condominios
Fledglings = exp(0.0027 * rainfall – 0.42)
Taray
Fledglings = exp(0.0027 * rainfall + 1.71)
100
80
60
40
20
0
Fledglings/colony/year
0
400
800
1200
1600
Annual rainfall (mm)