# Cascade effects of the ENSO cycle on a Neotropical felid

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# Abstract

Climate studies predict ENSO to double in frequency in the coming years. The effect of intense weather phenomena on higher trophic levels in the tropics remains unknown.

This study aims to explore the trophic cascade that occurs between rainfall events and predators, and determine the lag time between each effect.

Seven years' worth of rainfall, fruit-fall and camera trap data was collated from Barro Colorado Island in Panama and analysed as individual time series which were then cross correlated to establish the response time of populations after heavy rainfall.

It was found that the ocelot population was correlated to rainfall with a lag time of 93 weeks through fruit production and frugivore abundance. This was compared with the 61-week lag time between high sea surface temperature and the rise in ocelot abundance, suggesting that the ocelot population responds quicker during periods of low rainfall/high sea surface temperature.

This study suggests rainfall may cascade onto the secondary consumer level with a lag time may become longer with the predicted increased frequency of intense rainfall. This would result in the predator population growing at a slower rate due to the negative association of rainfall on fruit production effecting the prey species of the ocelot.

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# Introduction

ENSO, also known as the El Niño-Southern Oscillation, is an irregular climatic fluctuation between two states – a cold state (La Niña) and a warm one (El Niño) (Timmerman, 1999). Extreme instances of this pattern have had a significant impact on global weather patterns, and ensuing effects on ecosystems around the world (Cai *et al*, 2014). In fact, the ENSO cycle is the largest cause of inter-annual climate variability in the tropics (Lachniet *et al*, 2004). While these effects on the primary and secondary trophic levels in terrestrial systems have been investigated, little is known about the potential cascade into the higher trophic levels- the tertiary consumers (Grant *et al*, 2000; Condit *et al*1996; more references). As primary production is crucial in community structure and assemblage, the abundance and success of consumers is tightly linked to the status of primary production. Thus, consumers at higher trophic levels depend on this relative success (Hunter & Price, 1992; DeAngelis *et al*, 1996; Persson *et al*, 1996). This leads to the possibility that the increasing intensity of ENSO may lead to extreme changes that could have a consequential impact on the community structure of consumers (Jaksic *et al*, 1997; Holmgren *et al*, 2001).

Predator-prey relationships have been well-documented as exhibiting a cycling response pattern (DeAngelis *et al*, 1975), where the increase in prey populations leads to a lagged increase in predator abundance, as a response to the availability of food. This lag depends on growth rate and gestation time, making it species-dependent (Holling, 1973). A similar effect can be seen when prey numbers dwindle, leading to a corresponding decline in predators. This pattern suggests a bottom-up cascade, where primary production predicts prey abundance and prey dictate predator abundance. The classic study of snowshoe hare and lynx populations oscillating as a result of vegetation availability (Stenseth *et al*, 1997) highlights this community dependency on abiotic factors. Major changes in populations can modify the stability of an entire ecosystem, where a large decline in population of one trophic level can lead to an extinction cascade (Ameca y Juarez *et al*, 2012). This postulates that intense climatic events such as ENSO may put communities more at risk.

Given the current gaps in understanding the extent of ENSO effects and how it will be affected by the changing climate, further research is imperatively needed. The repercussions of changes to the climate have been explored at the primary and secondary trophic levels (Foster, 1982; Van Schaik *et al*, 1993; Wright *et al*, 1999; Milton *et al*, 2005), but whether this affects predator levels, is unknown. While a reduction in rainfall has been shown to modify the indirect effects of predators on lower trophic levels (Liu *et al*, 2016), these effects could be detrimental to ecosystems as predators maintain a balance. This is evident in predator-free forest fragments where the absence of predators leads to increased herbivory, reducing seedlings and saplings of canopy trees (Terborgh *et al*, 2001). Recent climate models predict the frequency of El Niño occurrences to double in the future (Cai *et al*, 2014) therefore, noting changes in predator prey cycles may aid in predicting populations in intensified conditions.

One particular location where ENSO effects in lower trophic levels have been well-documented is Panama's Barro Colorado Island (BCI) (Foster, 1982; Milton *et al*., 2005; Smythe, 1982; Wright *et al*, 1999). Here, during a strong El Niño event, it is relatively hot and dry with limited cloud cover. This alternates with periods of high rainfall. This change in weather conditions is thought to drive the fluctuations of fruit production on BCI, which is higher during a dry El Niño year, and lower during the ensuing La Niña year of high rainfall and less sun (Wright & Calderon, 2006). In fact, these lows can be so severe that die-offs in

frugivores reliant on fruit have been recorded, leading to a population 'bust' (Wright *et al*, 2009). For example, from January 1981 until January 1982, the *Sciurus granatensis* (red-tailed squirrel) population on BCI underwent a massive decline, possibly because *Dipteryx oleifera* and *Gustavia superba* (both critical fruit species for squirrels) had failed during this period (Milton *et al*, 2005). It has been noted that this alternates with the enhanced primary productivity during the sunny El Niño years, where mass fruiting occurs, leading to an increased birth rate and thus, higher abundances of frugivores (a 'boom') (Siriwardena *et al*, 1999; Wright *et al*, 1999; Neilsen *et al*, 2013). However, the flow on effects on to the tertiary consumer in this ecosystem, is unknown. It can be seen that when prey densities increase, predators tend to reproduce more successfully (Solomon, 1949). Thus, abundances of the consumer are predicted to increase after a boom in the abundance of frugivores.

The aim of this study is to investigate the cascading effect of weather on predators. In order to study whether weather oscillations affect tertiary consumers, I used BCI as my study area. The ocelot (*Leopardus pardalis*), a neo-tropical meso-predator and the largest resident predator on BCI, was used as the tertiary study species. Its prey species, *Dasyprocta punctata* (agouti)*, Cuniculus paca* (paca)*, Proechimys semispinosus* (Tome's spiny rat)*, Sciurus granatensis (*red-tailed squirrel) and unidentified mice species were used as the frugivores. As it has been shown that ENSO has a bottom- up effect (Jaksic *et al*, 1997; Meserve *et al*, 2003; Holmgren *et al*, 2001), it is predicted that the climatic conditions will alter primary production during El Niño years, hindering frugivore survival and subsequently, determining ocelot survival. Using the available data on rainfall and fruit mass collected on BCI as well, the relationships between the trophic levels were modelled as a means of examining potential ENSO effects. Time series analyses were used to establish whether there is an observed trend in the ocelot population correlated to altered prey availability in differing weather conditions. Therefore, the main objective of this study is to assess what the impact of weather oscillations are on the community on BCI, by examining the significance of correlation between trophic levels over time and the time delay of said effect. The following predictions will be tested:

1. The increase in fruit production will correlate with a delayed increase in herbivores - due to the high rainfall, low cloud cover, and warm temperatures which support vegetation growth, providing these herbivores with adequate resources
2. Ocelot population will correlate to the change in herbivore abundance (as there are initially more prey species due to the high primary production in El Niño years)

# Methods

<u>Study System</u>
The study site was Barro Colorado Island (9 09' N, 79 51' W), a 1500-ha biological reserve located in the Gatun Lake in Panama. The average annual rainfall of 2633±462mm (mean + 1 SD derived from 73 years of rainfall data) supports lowland tropical moist forest (Holdridge & Budowski, 1956). The dry season begins in December lasting until April. The average temperature on the island is 27°C with a seasonal variation of about 2.2°C (Leigh *et al*, 1996). The vegetation on the island is diverse, with 1369 species of vascular plants documented (Croat, 1978).

The largest resident predator on BCI is *Leopardus pardalis*, the ocelot, a 8-18kg neo-tropical felid (Moreno et al, 2006). Recorded in a range of habitats - mangrove forests, coastal marshes, savanna grasslands, thorn scrubs, and tropical and subtropical forest - structured vegetation cover appears to be essential to the ocelot as avoids open spaces (Nowell & Jackson, 1996). This diurnal and nocturnal predator preys upon some of the smaller species of mammalian frugivores found on BCI - red tailed squirrel, paca, agouti, mice species and the spiny rat (Wright *et al*, 1999) (arboreal mammals were excluded as they are not captured by camera traps, however the family Xentartha compromises ~20% of the ocelot's diet (Moreno *et al*, 2006)). Information regarding these species can be found in **Appendix 1**. According to a scat analysis (Moreno et al, 2006) the main species of prey found in BCI ocelots were rodents (62.6% of the scat samples) with sloths and primates also consumed but as this study only included terrestrial mammals this was not considered. Reptiles were also shown to be consumed but due to the inability of the cameras to capture reptiles accurately, this was also not considered.

Current knowledge regarding the ensuing effects that occur in response to extreme weather patterns ascertain that increased productivity associated with El Niño years results in increased fruit-fall. Contrastingly, this is followed by La Niña where there is low fruit-fall. (Milton *et al*, 2005). Inter-annually, the dry and wet seasons instigate fruit availability depending on the species (See Table 1). These species produce fruits which are commonly consumed by the terrestrial frugivores on BCI (Adler, 2000: Milton *et al*, 2005, Gliwicz, 1984; Forget *et al*, 1994). During periods of limited food availability, behavioural responses by these frugivores have been documented, such as affected birth rates. The general minimum and maximum offspring per individual of each species can be found in Table 3 (appendix 1), and can be used as a baseline to which deviations can be compared.

**Table 1**: Fruiting periods of focal fruit species (adapted from Gliwicz, 1984)

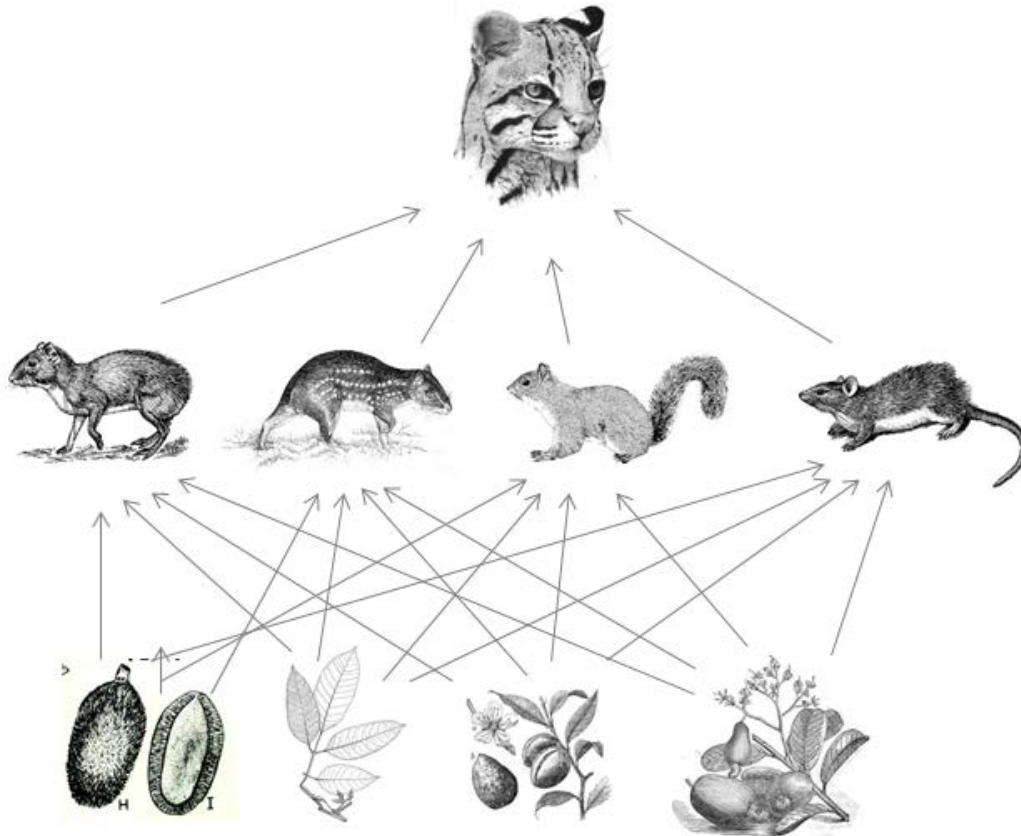| Plant species | Fruiting months | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **J** | **F** | **M** | **A** | **M** | **J** | **J** | **A** | **S** | **O** | **N** | **D** |
| *Dipteryx panamense* | + | + | | | | | | | | | | + |
| *Astrocaryum standleyanum* | | | + | + | + | + | + | + | | | | |
| *Anacardium excelsum* | | | | | | + | | | | | | |
| *Protium panamense* | | | | | + | + | | | | + | + | |

**Figure 1** A food web of the study system. The fruit trees are evident in the bottom room as the primary producers, followed by the primary consumers in the second row - the agouti on the left, paca and squirrel in the middle and the spiny rat on the right and the secondary consumer - the ocelot at the top tier.

Data collection

*Climate data*

Rainfall data were taken from the STRI Environmental Monitoring Program (http://www.stri.org/tes). Daily precipitation is recorded both manually (tipping bucket) and electronically. For this project, weekly averages of rainfall were used. Rainfall measured daily was recorded and compiled into a weekly total. BCI has an average annual rainfall of 2633 mm of per year, but this can depend on the ENSO phase. Weekly data from 2009 until 2015 was used. Weekly solar radiation data was not available. Sea surface temperature (SST) was used as it is a common indicator of ENSO periods, this was downloaded from (http://www.cpc.ncep.noaa.gov/data/indices/wksst8110.for).

*Fruit densities*

Data of annual fruit production was calculated as dry mass fruit production in grams per square meter per week. This data has been collected since 1987 until present, from 200 traps, randomly placed within a 50-ha plot (collected by Wright *et al*, 2005). Traps are 0.5m$^2$ in size with 1mm mesh screen mounted 80-100cm above the ground. Seeds (>1mm in diameter) caught within these traps were counted weekly. Species were identified by reproductive parts, the presence of flowers was recorded and fruits/seeds were counted (Wright *et al*, 2005). For this study, data was only used from 2009 until 2015 and of the following species – *Dipteryx panamensis*, *Astrocaryum standleyanum*, *Protium panamense* and *Anacardium excelsum* as these are sources of food for the focal frugivore species and can be used as a proxy of fruit

abundance (see Table 1 for fruiting their periods) (Adler, 2000: Milton *et al*, 2005, Gliwicz, 1984). In an attempt to limit the number of fruit species used for this study as fruit species have different fruiting periods throughout the year which could indicate a constant (albeit low) supply of fruit on BCI year-round which could deduct from fluctuating fruiting trend. Therefore, I used species that have been noted in previous studies on BCI to be consumed by all of these four frugivores.

These fruit-fall traps do lend to some data collection error as this is only a sample and is not representative of all fruiting trees on the island. This is also why fruit mass/sqkm was not used as this would only be representative of the 50ha plot. Also fruit consumed by animals (both before it falls and once in the trap) is not counted and can lead to a misrepresentation of total fruit count. However the main interest of this study is the fluctuations in fruit fall, therefore as this is the case over the entire study this fluctuation can still be monitored.

*Mammals*
For this component of the study I used (Giacalone, unpublished) data of on-trail camera traps, which have been active since 1995. This study used data from 2009-2015. During this time, there were, on average, 18 un-baited camera placed 30cm above ground. (Figure 2). Cameras were Reconyx PC900 and RC55 trail cameras distributed across the island insuring a capture probability of >0 (based on Karanth, 1995). All traps were programmed to stay active 24h and photographs were set 1 min apart. The total grid size of the camera traps was 10.18km$^2$. Photos were collected from the cameras, then uploaded to a database (http://cameratraplab.org/) which groups pictures taken within three minutes of each other, representing one observation. Afterwards, species, age and sex can be identified for each photo. Photo sequences were considered independent if they were an hour apart.

Data of every observation since 2009 from the trail cameras (137,886) was filtered by species – paca, red tailed squirrel, agouti, spiny rat and mouse (79,445 observations) and then converted into weekly counts for each species. The number of cameras active every week determined the capture rate used to estimate the relative prey biomass captured each week for each of the focal species. The mass of each species from Eisenberg & Thorington (1973). This method does not account for camera trap. Firstly, detection distance variation and activity level variation are dependent on weather and can suggest certain trends that may not be the case. For example, the detection distance during high rain is lower, so the rainy season may result in less captures of frugivores, but this does not infer that there are less frugivores, just the probability of capture is lower. Activity levels can also affect capture rates as some animals may need to forage more during a period of low resource availability, triggering cameras, and suggesting higher abundance of animals when the animals are merely more active not more abundant.

To establish the ocelot population size, mark-recapture was used as the unique spot patterns on the flank of each individual can be used. Each camera station contained one camera, therefore only one side of the animal was captured, so for individual ocelot recognition, a catalogue was used that contains all named individuals that have been identified since the beginning of the original long term study. By determining when the first and last observation of each individual was captured, a timeline of overlap can be composed indicating the minimum total population size. This was scaled to determine the population size weekly.
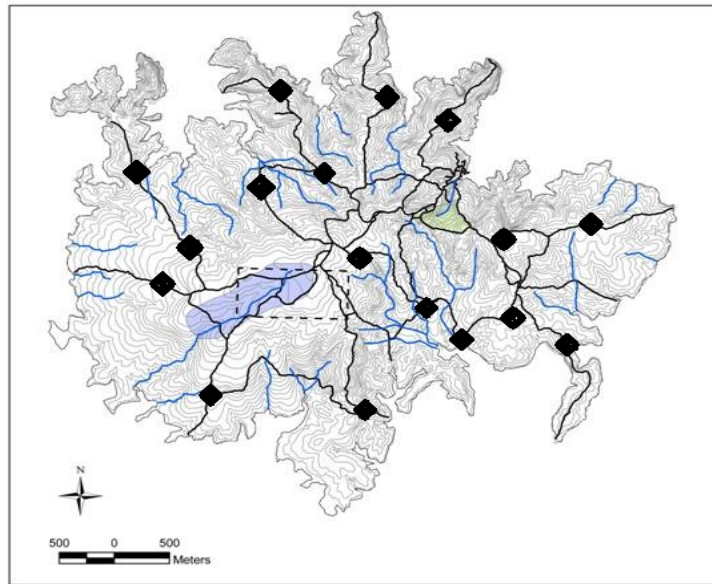
**Figure 2** Map of BCI marked with trails (black lines), streams (blue lines) and on-trail cameras (black diamonds).

Data Analysis

I used R 3.3.2 (R Development Core Team 2011) to statistically analyse and model the time series data.

Time series models were used as the data collected expands a seven-year period and in order to determine the change over time and the relationship between the variables it deemed visible. The variables mentioned (rainfall, fruit production, prey abundance and ocelot population) were examined independently as time series and then paired for analysis - rainfall and fruit, fruit and frugivore, frugivore and ocelot. By using this pairing system, I attempted to reduce multicollinearity that may be present as each trophic level has a complex and dynamic relationship so by evaluating the effect between each trophic level rather than an overall look, I tried to tease appear the effects of each predictor.

This was done with a cross correlation analysis, which calculates the correlation between two different time legs and plots the significance across time lags. This method is thought to be an effective way of analysing the comparative behaviour of two time series that are stationary (Shumway & Stoffer, 2011) and was therefore used in this study to examine the lag time delay between the trophic levels. A cross correlation function (CCF) between two time series examines the possibility that $y_t$ may be related to $x$ in past lags. It determines which lags of the $x$ may be correlated to $y_t$. A strong correlation for a negative lag indicates that $x$ is leading $y$ by so many lags (Platt & Denman, 1975; Li *et al*, 2001). Whilst this employs components of multicollinearity, it is not an issue here because I am not assuming perfect correlation, I am simply aiming to determine the degree, if any, of correlation between the time series.

Time series should be tested for stationarity (Athanasopoulos & Hyndman, 2013). By testing stationarity with the autocorrelation function, I can establish if there is serial correlation in the time series data by determining if observations within a time series affect each other. The autocorrelation functions (ACF) uses the value of $x_s$ to linearly predict the series at time $t$. It is a ccorrelation coefficient that assesses the correlation between values of the same variable. This can be used to determine whether or not the series is stationary by using the first lag (Bolker, 2008). After visual inspection of the ACF, two unit-root tests – ADF and KPSS were completed to test the series for stationarity (Dennis & Taper, 1994; Phillips & Perron, 1988). The KPSS test has a large Type 1 error so an additional test- Augmented Dickey Fuller was done to test for unit roots in these time series (Kennedy, 2003). In the event a time series is not stationary, a time series can be manipulated by computing the differences between consecutive observations.
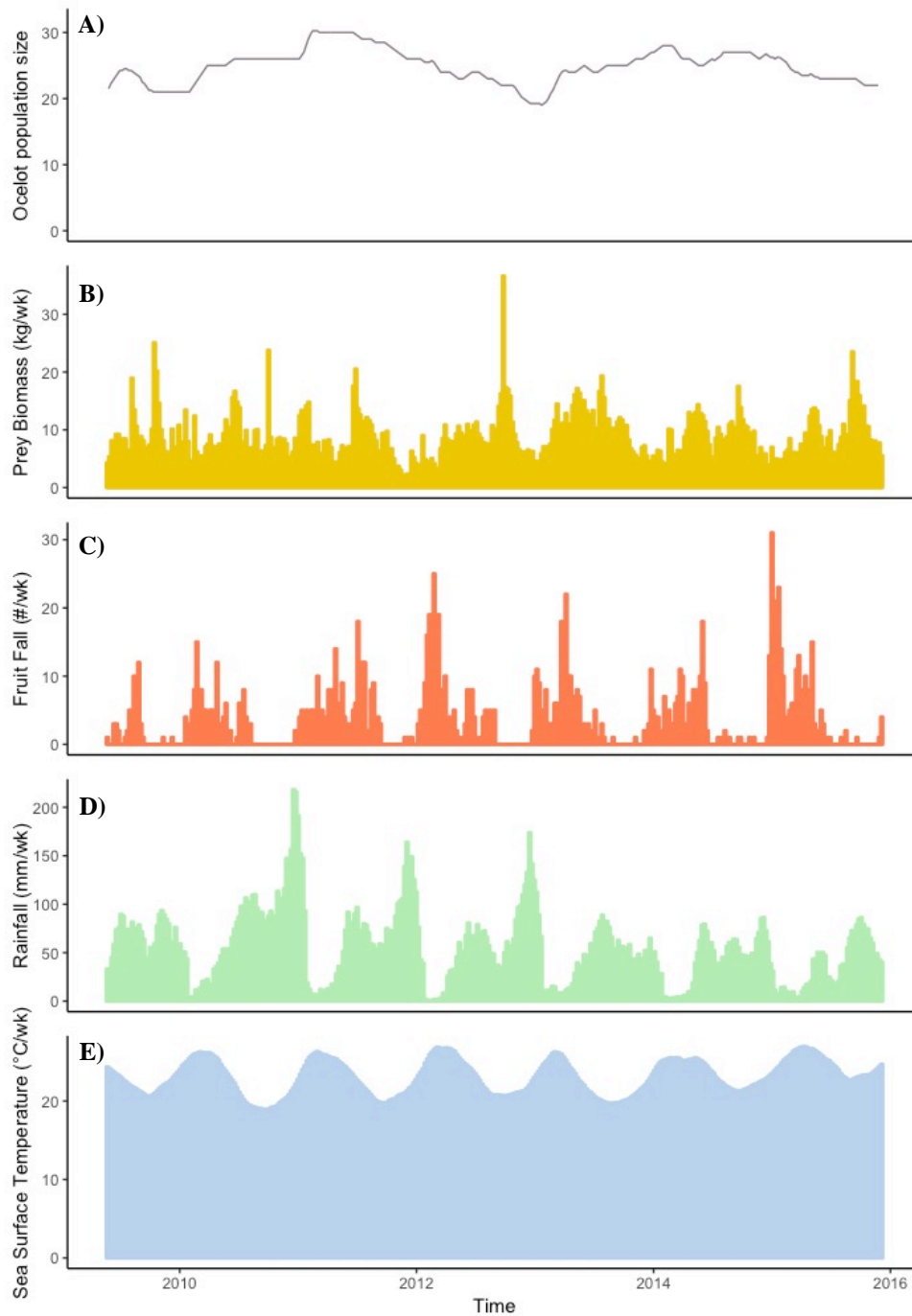
# Results



**Figure 3** Graphs depicting each trophic level over the seven-year study period by week. **A)** Total ocelot population size (coefficient of variation of 10%) **B)** Relative abundance of prey biomass measured in kilograms (coefficient of variation 43%) **C)** Number of fruits counted in the fruit fall traps in the 50ha plot (coefficient of variation 143%) **D)** Total rainfall measured in millimetres (coefficient of variation 110%) **E)** Sea Surface Temperature measured in degrees (coefficient of variation 9%) **B), C), D), E)** are all depicted as histograms while **A)** is displayed as a line. Moving averages were calculated for each time series to smooth the data for this graph

Figure 3 shows the data, stacked to allow for comparable examination of the trophic levels. It appears that the high in SST correlates with a low in rainfall. Periods of high rainfall also appear to correlate with low fruit production.

Autocorrelation Function (ACF)

The ACF of each series (**Figure 2**) quantifies the stationarity of each series. Each time series shows a significant drop off after lag 1, indicating stationarity (Hyndman & Khandakar, 2008). The raw ocelot data demonstrated non-stationarity (Appendix 2) and therefore had to be manipulated in order for it to resemble the plot now visible in Figure 4. The drop off after the initial lags is reminiscent of stationarity. Critical values at any given lag are 5% with the hypothesis that the autocorrelation is asymptotically standard.
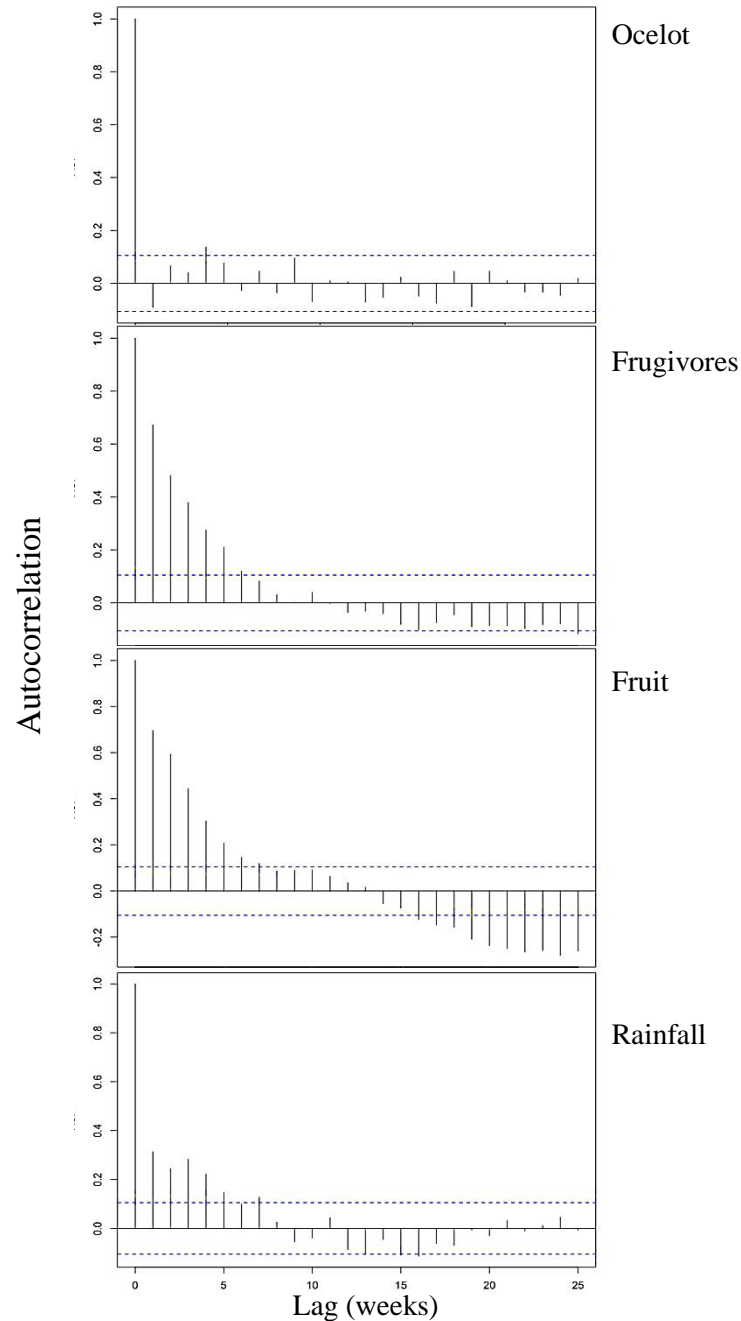


**Figure 4** ACF plots of each time series. Vertical axis is the correlation value and horizontal axis is the lag number. The plots for each time series indicate stationarity by exhibiting a drop off in significance after the intial lags. The significance level is indicated by the dashed black line.

ADF test and KPSS test

Initially, the Kwiatkowski–Phillips–Schmidt–Shin (KPSS) test was used for each of the time series and the frugivore and fruit data were stationarity (p 0.1). The rainfall data and ocelot data returned KPSS values of 0.03 and 0.05 respectively, rejecting the null hypothesis that these times series were not stationary. The Augmented Dickey Fuller test (ADF) for the rainfall time series rejected the null hypothesis that there is a unit root for the time series (p 0.01). Howbeit, the ocelot time series (p 0.5) still suggested a unit root, indicating non-stationarity. (Figure 1D). After manipulation, the p value for the ADF test was 0.01. This meant that the time series could then be used for further analysis.
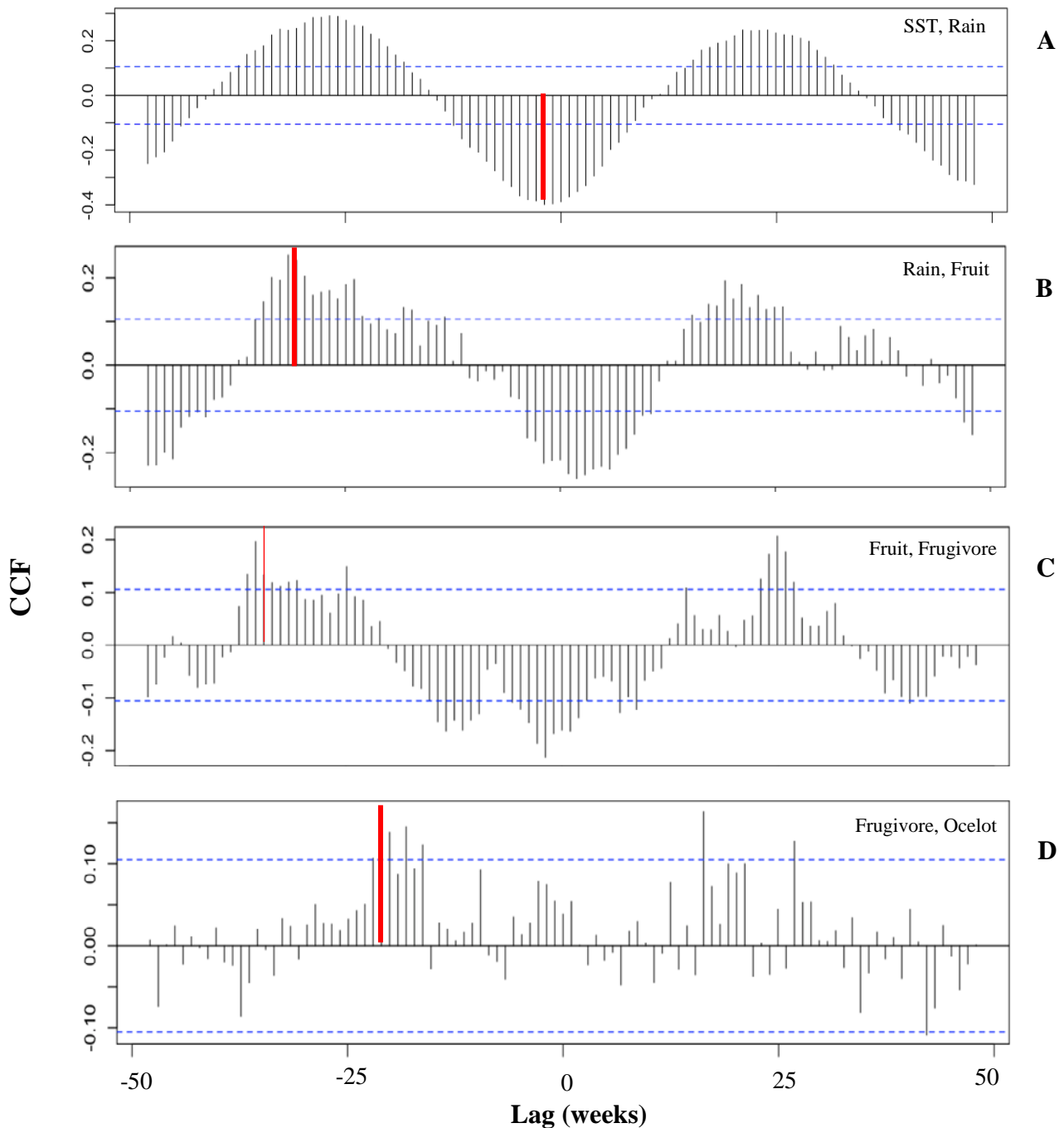
Cross Correlation



**Figure 5 A)** *Sea Surface Temperature and Rainfall,* **B)** *Rainfall and Fruit,* **C)** *Fruit and Frugivore,* **D)** *Frugivore and Ocelot*
Each correlation plot includes the most significant correlations for each time series, marked in red and confidence levels
indicated with blue dashed lines. Negative correlations suggest that the high in series *x* is followed by a low in series *y*. Each lag
has a correlation, but the most significant one is used as an indicator for the lag time between the highest in *x* and either the
lowest or highest in *y*.

There was a significant negative correlation coefficient (-0.39) at lag 2 indicating that sea
surface temperature at its peak is followed by a low in rainfall 2 weeks later (Fig 5A). 5B)
shows a strong correlation in negative lag. There is a maximum correlation at lag 33 with a
correlation of 0.25. This suggests that the above average of rainfall leads to a 6-month delay
in the above average in fruit. At time *t* there is also a strong correlation coefficient indicating
that high in rain is about 3 weeks before the low in fruit. C) showed the most dominant

correlation (0.212) for lag -3 indicating that when fruit is high, it is followed by a low in prey species three weeks later. However, it takes 40 weeks before prey peak after the high fruit period. Whilst D) indicates that there is a 21 week lag between the above average of prey to the above average of ocelot (lag = -21 and correlation=0.165). These significant correlation coefficients indicate that to a certain degree (varying depending on the trophic level) these time series are collinear.

## Discussion

The impending threat of intensified weather phenomena, coupled with the unclear effect on terrestrial ecosystems has lead this study to examine the correlation between rainfall and predators. Using BCI in Panama as a case study, cross correlation of trophic levels were analysed to explore the accumulative lag phase of rainfall into the consumer levels. The results of this study suggest that ENSO may indeed produce a trophic cascade to the top predator level. Firstly, fruit production peaks around 30 weeks after heavy rain. Secondly, it takes a further seven months for the frugivores to be at their above average after this fruiting boom. Lastly, it takes five months before there is an ocelot increase.

Rainfall and fruit were inversely correlated, as fruit production is reliant on solar radiation (Wong *et al*, 2005; Wright & Calderon, 2005) this suggests that the high in rainfall is followed by high fruit fall 38 weeks later. This can be explained by the raining season (April – December) inhibiting the fruiting period, peaking in November being followed by the peak fruiting season in June. Although, as Flemming *et al* (1987) suggest, the more seasonality in rainfall, the larger the lag phase between the highs and lows of annual fruit production, which exemplifies the threat to this system influenced by more frequent hydrological effects.

Fruit abundance has been shown to regulate populations of frugivores (Foster 1982, Terborgh 1986, Bodmer 1990, Adler 1998, Wright *et al*. 1999). In this study, there is a cyclic pattern between the fruit production, where there is a 33-week delay between the peak in fruit production and peak in prey. Smythe (1986) alludes that the lean period of neo-tropical terrestrial frugivores is at the end of the wet season which seemingly corresponds to the cyclic pattern observed in this study.

The litter sizes and gestation times of each of the focal prey species also explain some of the time delay between the peak in frugivores and the peak in fruit. This may also explain why the initial lag phase suggests that the high in fruit is accompanied by an apparent low in frugivores a few weeks later, as it requires more time for the effects of the fruiting period to become apparent. Moegenburg & Levey (2003) similarly found in Brazil that frugivore diversity and abundance was higher post-harvest. As smaller mammals (rodents) tend to breed in more optimal conditions – such as the dry season, increased and more frequent periods of rainfall could reduce abundance (Lima *et al*, 1999). Other frugivore populations have been correlated to the fluctuations in climate, the Norwegian red deer and south American rodents in Chile (Forchhammer *et al*, 1988; Lima *et al*, 2001). This indicated that even though there is high fruit fall, populations don't respond straight away. In fact, there are even some species that have alternate measures that enable them to survive when there is not much food supply available during these periods. Agoutis cache seeds so for this reason during periods of low fruit the change in agoutis might not be so apparent (Asquith *et al*, 1997).

There was about a five-month delay from the above average peak of prey until the ocelot population to reach its above average. This time lag could be the result of the average ocelot gestation time (two months), coupled with the ocelot mother bringing food back to the den for her kittens for the first couple of months. Therefore, the youngest age at which young are caught on camera is about 2-3 months. The population estimate for the ocelot is dependent on camera sightings, therefore new kittens (indicating the rise in population) will only be sighted about 5 months after the peak in prey numbers as seen in the CCF plots. The rise in prey numbers could be providing ocelots with the opportunity to reduce search and handling time, leading to increased birth rates (Sinclair, 2003). This is supported by a study from Karanth *et al* (2004) which suggested that prey density is the most defining factor of large felid abundance. This is not the first time weather has previously shown to affect these cats, they have been previously recorded to have higher abundances during the dry season in Brazil (Maffei et al, 2005).

These results indicate that climatic fluctuations do cascade through this food web. Also seen in a recent study by Morris & Letnic (2017) which demonstrated that fluctuations in primary productivity as a result of irregular rainfall leads to a flow on effect in the biomasses of plants and consumers. Marine predators have been reported to die off after die offs of plankton and fishes (Stenseth et al, 2002; Bost et al, 2015;). Similarly, taking into account all the cross-correlation analyses from this study, it could be interpreted that it takes 33 weeks after high rainfall before fruit fall peaks. This high fruit fall correlates with high observation rates of prey biomass 40 weeks later, after this peak, there is a 21-week lag before there is an increase in ocelots, leading to a projecting 94-week lag between high rainfall and a rise in the ocelot population. This fits the aforementioned hypothesis that rainfall will correlate with a lagged response in ocelots. This implies that more intense ENSO patterns that increase rainfall, could have a negative effect on the ocelots by reducing the frugivores after unfavourable fruiting conditions leading to a population bottleneck. Adding to this, predation rate could be low during periods of increased rainfall as there are higher thermoregulatory costs for small mammals, potentially limiting their above-ground activity thereby reducing their predation risk. Also, small rodents may go by unheard, concealed by the sound of raindrops on dry litter or undetected as scent trails become washed away (Vickery & Bider, 1981; Terraube *et al*, 2016).

Limitations
There are some limitations with this study. First, solar radiation should have been used instead of rainfall. This is positively correlated with fruit fall and would make the results easier to analyse, unfortunately this was not possible as only monthly data was available and time series must have the same frequency for cross correlation analysis. Also using flowering period, as this could account for some lag time before fruit production peaks (Singh & Kushwaha, 2006). *Attalea* was not used for this study, however it is a common resource of frugivores on BCI (Wright & Duber, 2001, Forget *et al*, 1984, Wright, 2003) this was due to the dataset I used. Competition between the frugivores was not taken into consideration, yet it is an important component of therefore if one species was able to survive better during low fruit periods, due to some competitive advantage (e.g. agoutis caching seeds) this wouldn't be evident in the analysis. This could alter prey preference for the ocelot during different seasons.

Arboreal and avian frugivores and reptiles, as important components of the ecosystem, were unable to be included in this study, but understanding their role in this trophic relationship would increase the validity of this study. Arboreal prey species, which are thought to account

for at least 20% of the ocelot's diet (Moreno *et al*, 2006). The response for these species and fruit fall may have been stronger that what was seen with rodents and fruit fall. It is predicted that there would be relationship between these arboreal frugivores and the ocelots as well. In an attempt to not include too much – all possible prey species and all possible fruit species – as this might dilute possible relationships with too much fluctuation and noise, may have resulted in not enough or not the right species being chosen.

Also, the absence of top predators (jaguar and puma) from this study location also means that recently there is a larger populations of frugivore species (Terborgh & Wright, 1983) therefore reductions in population size may not be as dire as they have been in previous ENSO years, as seen by Milton *et al* (2005). This may result in the lower correlations of the CCF analysis as ocelot population fluctuations may not be as harshly impacted as there is still adequate resources available to sustain a viable population. Therefore, the results from this analysis may not demonstrate the true effect and rather the ocelot population is still stabilizing.

Whilst there has been some use of CCF for trophic cascade correlation (Tian et al, 2014; Li *et al*, 2007) there hasn't been a prolific amount, making it hard to compare previous results and analysis. This approach does not take into account the interactions happening within each cohort and could be seen as a minimalistic approach to this problem. Perhaps the CCF should be used after a more in-depth look into the interactions between fruit species and frugivore species. This may provide insight into which species directly affect each other and perhaps would be better used in the analysis.

Further research
To further this study, there are a few suggestions. Firstly, a proportion of the original data set extending back to 1999 is based on camera trap photos that are on film which have yet to uploaded to the main server with the photos from the digital cameras. This shortens the time series and removes two ENSO cycles. Extending this could improve the validity of the study and provide new insights. Also adding additional levels to this study, weekly solar radiation and flowering may account for more of the lag time effects. Moreover, there are still 430 unidentified ocelot sequences on the database (not all photos present a clear image of an individual's flank) this could increase the minimum population size.

Convergent Cross Mapping has been used to determine whether there is causation or correlation in ecological time series (Clark *et al*, 2015). The CCFs only provide information regarding the correlation between x and y, so it isn't possible to see if there is causality in the system. This could provide important information regarding whether there is a top down or bottom up effect in this ecosystem.

What was not considered in this study was pinpointing the carrying capacity of these populations as this would help further improve these claims by understanding what the natural state of these species are under ideal conditions and then examining whether there is a significant change in this under weather pressure. To do this would require Lotka-Volterra modelling of each species and then examining these populations change under intensified conditions. Resource availability and predation play important roles in ecological regulation and requires species to adapt in order to survive (Hiltunen & Laakso, 2013). ENSO could be a disturbance that alternates this community from a stable state to a transient one and the fluctuations in populations sizes could be a mechanism of species survival rather than a direct effect from predator to prey. Another area of further research could then perhaps be to

examine specific cohorts of the ocelot populations to see if birth rate is correlated with frugivore abundance. This could provide insight into whether there is a life history trait trade-off for ocelots regarding lower birth rate during periods of low resource availability (Charnov & Ernest, 2005).

Conclusion
The results from this study support the first prediction as there is a delayed onset in frugivore abundance after the fruit peak. Similarly, ocelot abundances appear to correlate with frugivore abundances, as they increase only after frugivores are at a peak. However, this only seems to occur when fruit production is at its highest during periods of low rainfall.

This study suggests that there is a prolonged lag phase before which the population appears to increase after wet weather conditions. Rainfall adds a six-month delay to the ocelot population increase, when compared with no rainfall (high SST) where fruit fall is at its highest. This is an indication that intensified weather fluctuations may have an effect on the top predator. Periods of extreme or prolonged rainfall, already predicted to double in the coming years, could mean that ocelot populations take even longer to rise. This could lead to a population bottle neck with an estimated population size of 25 individuals. This could have larger implications as large felids are considered keystone species, vital in the conservation of entire ecosystems (Moreno et al, 2006; Eisenberg 1980; Miller and Rabinowitz 2002; Sanderson et al. 2002). Already, the absence of apex predators has meant frugivores abundances are larger than ever, which may change the forest structure, and impact the whole ecosystem.

Communities are made up of complicated processes and interactions - predation, competition and resource availability are interconnected and dynamic and to understand a whole trophic system and its functioning, requires extensive research (Hiltunen & Laakso, 2013; Chesson, 2000; Hardin, 1960; Chase et al, 2002). This approach attempted to examine the community fluctuations over time, as a result of these factors. Perhaps, these species were not the best representation of this community and perhaps this approach is too simplistic and requires modification, however it still suggests a difference in time delay between alternating weather patterns and should be seen as a start in this examining the effects of ENSO on top predators. The decline in large predators already exceeds those of other groups of species (Ray *et al*. 2005; Wilmers & Post, 2006), coupled with the impinging climate threat, further necessitates the need to examine other ecosystems that could similarly be affected by this bottom-up cascade. Therefore, it is suggested that further research is conducted to establish and model how these populations may respond to more frequent and intense ENSO events and whether they will be able to survive. This would have implications on conservation management as predators are often top-down regulators and without their presence, localised extinction could cause massive changes to ecosystems.

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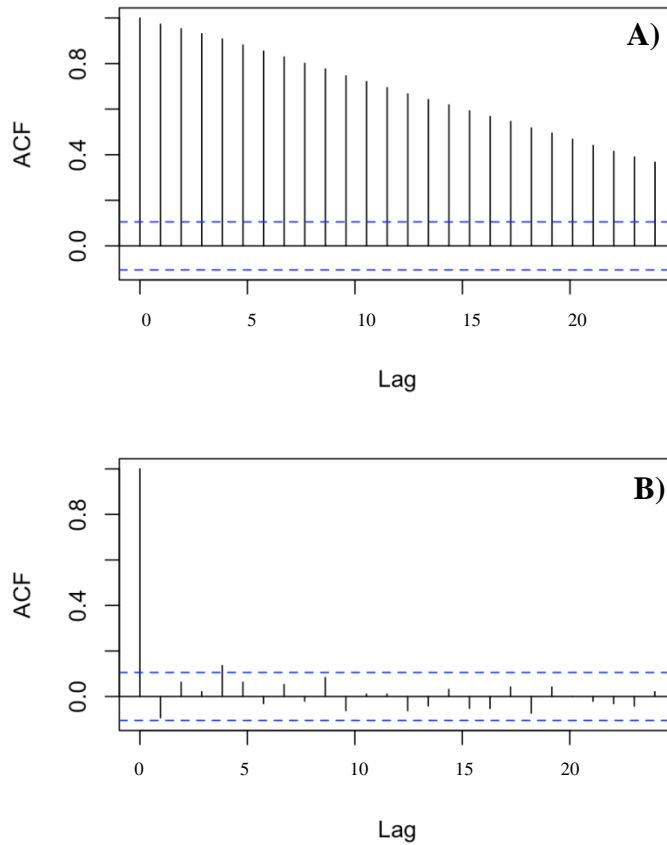
Madeleine van der Poel

## **Appendix 1**
Breeding behaviours

**Table 3: Prey species brooding behaviours**

| Species | Litters per year ( min-max) | Size per litter (min-max) | Fecundity (yr$^{-1}$) (min-max) | Gestation length (days) | Body mass (kg) |
|---|---|---|---|---|---|
| **Rat** | 4-6 | 4-8 | 16-48 | 65 | 0.3 |
| **Agouti** | 2-3 | 1-2 | 2-6 | 120 | 1-4 |
| **Paca** | 1-2 | 1 | 1-2 | 110 | 7-12 |
| **Squirrel** | 2 | 2-4 | 4-8 | 34 | 0.25 |
| **Unidentified mice** | 5-10 | 6-8 | 30-80 | 20 | 0.19 |

# Appendix 2
ACF plots of ocelot data



ACF plot of the original ocelot time series (A) and the differenced series (B). The slow decrease in the top plot indicates non stationarity and the quick drop to zero on the bottom ACF plot is more complacent of stationary data. The vertical axis is the correlation coefficient, and significant is indicated by the dashed blue lines. The horizontal axis indicates the number of lags in weeks.