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Analysis of 5-years of data from Rio Bravo Conservation and Management Area (RBCMA) and one year of data from Gallon Jug/Yalbac Ranch, on trap rates and occupancy for predators and prey, including jaguar density estimates in unlogged versus sustainably logged areas

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EXECUTIVE SUMMARY

Very few studies exist on the impacts of timber harvest on large predators such as wild cats and their prey. The few studies that do exist have conflicting results regarding the compatibility of production forests with wildlife conservation. To examine the impacts of timber harvest on wildlife biodiversity, we used remote camera surveys from 2008-2013 in La Milpa (unlogged) and Hill Bank (sustainably logged) and in 2013, at Gallon-Jug-Yalbac (sustainably logged). We calculated trapping rates over time and estimated occupancy for multiple predators and prey, and we estimated density for jaguars at each site. We found trap rates of most species to be stable through time, but ocellated turkeys may be showing a decline in activity at the Hill Bank site. White-tailed deer and pumas appeared to have higher trapping rates in Hill Bank but not in all years. White-lipped peccaries appeared to have higher trap rates in La Milpa. Jaguars, pumas, and ocelots had a higher proportion of area occupied in La Milpa and Gallon Jug than in Hill Bank, while red brocket deer occupied more area at La Milpa. Jaguar densities were calculated in multiple ways using traditional and spatially explicit methods, but there was little evidence for differences among the sites. Jaguar densities fluctuated, especially at La Milpa, and spatial estimates were lower in 2013. Continued monitoring will allow determination of trends through time and eventually enable survival and recruitment analysis, important demographic parameters that could give us more insight into the viability of these populations in the long term. Our results lend support to the concept that production forests can be compatible with conservation but we have not considered impacts on rare or very specialized species.

Introduction

The term "sustainable logging" usually refers to the attempt to maintain long-term timber supplies on a logging site (Pearce et al. 2001). It implies that harvesting trees in the present does not significantly impair future harvests (Mallory & Brokaw 1995). Thus, the vast majority of studies evaluating sustainable forest management focus only on the timber supply without taking into consideration the effects that timber harvests may have on overall biodiversity. There is a great need to understand the conditions under which logging can be compatible with conservation goals (Clark et al. 2009) and that requires investigating how logging affects forest biodiversity (Brook et al. 2006; Wright and Muller-Landau 2006 a, b). Numerous forestry companies have adopted a paradigm of sustainable forest management that, in theory, promotes biodiversity conservation (ITTO 2005; FSC 2006). But given our limited understanding of how logging affects biodiversity, we need to test the idea that production forests can meet both forestry and conservation goals.

While there have been some studies on the impacts of logging on birds and primates (Johns 1985, 1992), there have been very few studies on the impacts of timber harvest on large predators such as wild cats and their prey. To date, the only studies on the impact of logging on wild felids come from Asia and include: the tiger (large felid), the clouded leopard (medium-sized felid) and the leopard cat (small felid). Tigers showed a preference for primary over degraded forest in Sumatra (Linkie et al. 2008), but in Peninsular Malaysia tigers had high relative abundance in secondary forest with logging activity, but that may have been due to little other available habitat (Azlan and Sharma 2003, 2006). Clouded leopards in Borneo had high detection rates in undisturbed forests compared to a logged forest (Brodie and Giordano 2012), while another study in Borneo found no difference in clouded leopard densities between an unlogged and a reduced impact logging site (Wilting et al. 2012). In contrast, the leopard cat in Borneo had higher densities in the more disturbed reserves with higher impact logging than in the sustainably managed forest (Azlan et al. 2013). Also in Borneo, the small carnivore species known as civets where all found to occur in disturbed forest, but the overall density was drastically lower in the logged than in the primary forest (Heydon and Bulloh 1996).

Given the number of areas in the Neotropics conducting sustainable forestry or reduced impact logging, it is surprising that there have been no published studies comparing mammal fauna biodiversity relative to logging intensity. Here, we report our preliminary results of 5 years of study in the Rio Bravo Conservation and Management Area and 1 year study in Gallon Jug Estate and Yalbac Ranch and Cattle Company, where we compare trapping rates, occupancy, and density of mammals, with a particular focus on the jaguar.

In terms of previous density estimates for jaguars, studies in Cockscomb Basin Wildlife Sanctuary (Silver et al. 2004) and in the Chiquibul Forest Reserve (Kelly 2003), obtained jaguar densities of 8.80 ±2.25 jaguars 100 km^2 in Cockscomb , and 7.48 ±2.74 jaguars 100 km^2 in the Chiquibul (Silver et al. 2004). These estimates had overlapping standard errors suggesting that there was little difference in the density of jaguars between logged (Chiquibul) and unlogged (Cockscomb) sites. However, the study sites have very different elevation, rainfall, and history.

This study investigates the impact of sustainable logging on jaguars by comparing jaguar density among three sites of similar habitat, elevation, and climate at two sustainably logged sites (Hill Bank and Gallon Jug-Yalbac) and an unlogged forest site (La Milpa) in Belize, Central America. We also present the trapping rates and occupancy rates for several other carnivores and numerous potential prey species, and we compare traditional density estimation techniques with newly developed techniques to evaluate whether there is a difference in jaguar densities among the sites.

METHODS

Study Sites

Rio Bravo Conservation and Management Area

The RBCMA has two field stations, La Milpa and Hill Bank, which have been owned and managed by PfB since 1982 (Figure 1). The La Milpa Field Station is situated in a large block of broadleaf forest and is near the commercial farmlands of Blue Creek in the northern Orange Walk District. La Milpa is the center of archaeological research at RBCMA and is located only three miles from the third largest archaeological site in Belize (PfB 2008). Due to the tourism potential for this site, the forest of La Milpa has been set aside for strict conservation, and logging is not conducted in its interior. However, logging does occur up to the edge of reserve in the "secondary forest products zone."

Hill Bank was a logging camp for mahogany harvesting for over 300 years until stocks were depleted and the camp was abandoned in 1982 (PfB 2008). Presently, it is a working conservation field station, which was established in 1995. Hill Bank is now the site of experimentation and trials in sustainable logging. PfB hopes "to manage timber in a way that allows for income, yet also provides for rehabilitation of forest quality while retaining the full array of biodiversity and other environmental goods and services" (PfB 2008). In 1997, sustained yield timber harvesting was initiated (PfB 2008). During the same year, PfB began sustainable forest management in accordance with guidelines established by the Forest Department (Bird 1998). All timber extracted from the site is certified under the rules of the Forest Stewardship Council (FSC) and by the Rainforest Alliance (PfB 2008).

At Hill Bank 750-1000 ha per year are harvested on a 40 year rotation, producing about 500,000 board feet per year. For every 100 ha logged, 20 mahogany seed (mature) trees and 10 seed trees of other species are retained. However, while the practice is closely monitored for "sustainability" with respect to timber supplies, the impact on wildlife, including the jaguar, has not been studied. Thus, the implications of logging for jaguar conservation at the site are unknown, and it is unclear whether the logging practices are capable of sustaining healthy jaguar populations.

Gallon Jug Estates

Gallon Jug borders RBCMA to the south and also has a history of logging similar to Hill Bank. In the mid-1980s Belize Estates Company was purchased by Barry Bowen who retained the 130,000 acre parcel. Farming efforts at Gallon Jug began in the mid-1980s. A cleared area of less than 3,000 acres is now focus of coffee, cacao, and a cattle project using English Hereford bloodlines to improve local stock. It is hoped that these agricultural activities will allow the remainder of the land to remain forested. Chan Chich Lodge was also built in the late 1980s.

Gallon Jug is divided into 500 ha compartments and 2 compartments per year are selective logged. Output is approximate 600,000 board feet of the main commercial species: mahogany and cedar. The rotation is also 40 years as per Forest Department regulations for obtaining a Long Term Forest License (LFL40 yrs), which also requires development of a Sustainable Forest Management Plan (SFMP). Seed trees also must be left standing with minimum diameter classes for all timber species being felled.

Yalbac Ranch and Cattle Company

Yalbac Ranch borders Gallon Jug to the south, and Yalbac recently purchased a large parcel from Gallon Jug Estates such that the current ownership, where our study takes place, includes both Gallon Jug and Yalbac lands.

Yalbac follows very similar logging rotations as the other sites logging 900-1000 ha per year, but in 2014 only 150,000 board feet were produced due to extensive hurricane damage from Hurricane Richard in 2010. The past 3 year of salvage logging worked off of 1300 ha. Up until the hurricane, Yalbac was producing 1,000,000 board feet per year. They too follow the 40 year rotation and leave a minimum of 20 seed trees standing and are certified by FSC for sustainable logging.

Study Design and Data Analysis

Set-up

Camera trapping is now an established method for surveying wildlife, specifically medium and large carnivores such as pumas, ocelots, and jaguars (Silver et al. 2004; Dillon and Kelly 2007; Kelly et al. 2008). Recently, camera trapping has been used to study jaguars in Belize for the estimation of population density and abundance following the methods originally developed for tiger in India (Karanth 1995; Karanth and Nichols 1998). This technique is very useful when the target species are large, elusive predators which are difficult to physically capture and handle. Instead, motion sensitive cameras “capture” animals in digital images. Because all spotted/striped cats are individually identifiable by their coat patterns, this technique utilizes photographic captures to create capture histories for each individual animal and applies capture-recapture analysis to estimate population abundance (White et al. 1982). Our methodology follows previous studies on jaguars in Belize (Kelly, 2003; Silver et al. 2004; Harmsen 2009).

Cameras operated 24 hours a day for a period of 2-3 months per survey. Data collection occurred in 2008, and then yearly from 2010-2013 in La Milpa and yearly from 2009-2013 in Hill Bank. The first survey in Gallon Jug-Yalbac was in 2013. Within each of the three study sites 20-40 camera stations were spaced roughly 3 kilometers apart in an approximated grid pattern. Cameras were set up in pairs on opposing sides of main roads, old logging roads, old trails, new trails, and also on trails near water bodies such as Irish Creek. Cameras recorded date and time of each photograph. Stations were checked ~10 days for proper functioning and maintenance.

Trapping rates

Because most prey and other predator species photographed by our camera stations do not have unique coat patterns that enable us to distinguish individuals apart, we determined trapping rates for these species. We calculated trapping events as the number of distinct individuals photographed within each 30 min time period regardless of the number of photographs. This means that we only counted a single fox in front of the camera over a 30min time period as one single capture event, even if there were many photographs of that fox. This is a fairly standard procedure used in many remote camera projects (Kelly et al. 2012).

We then divided the number of events by the number of trap nights that each camera station was operational. We considered a station operational as long as one of the two cameras was still functional at that site. That way we could compare capture rates from stations that had different numbers of trap nights. We then averaged (and calculated standard errors for) the traps rates across all the stations within each site. We multiplied the trap rate by 100 because numbers are often very low and this allows easier interpretation. For example, if we obtain an average trap rate at one site of 5.0 photo-events per 100 trap nights, that is equivalent to obtaining 5 photographs in 4 nights (if we have 25 stations operational per night).

It should be noted that trapping rates should probably not be used as a measure of relative abundance until they have been calibrated to abundance through some in-depth study. This is because some species are more detectable by camera stations than others even though densities of different species could be very similar. For this reason we describe trap rate as a measure of activity level – noting that even activity level could be influenced by one particularly active individual. However, given the similarities in our camera placements across the sites, we feel that trap rates could give us an indication of activity trends over the long term at each site.

Occupancy

Presence and distribution of a species can be assessed using “occupancy modeling” techniques. Occupancy surveys can be used to evaluate the spatial distribution or estimate the proportion of a given area occupied by jaguars and their prey (MacKenzie et al. 2002, 2003, 2006). Occupancy is scaled from 0 to 1 such that a site with a 0.5 occupancy rate means that the species occurs at about ½ of the sites surveyed (in our case about half of the camera stations). Occupancy is more accurate than simply counting the stations where the target animals occurred (called naïve occupancy) because it takes into account imperfect detection and corrects for detectability in the final estimation of site occupancy.

To measure detectability, occupancy surveys consist of detection/non-detection surveys repeated at a number of sample units over a number of repeat visits. These models account for imperfect species detection, i.e. the fact that a sample unit might be occupied, but we fail to detect the species during our surveys. Detection of the species of interest at each site during each repeat visit, or occasion, is denoted with a ‘1’, meaning the species was detected, and ‘0’ if it was not detected. We used our camera stations as our detectors and combined each 7 day (1-week) time period as our detection occasion for all predators and prey. So if we detected our target species within a week of camera trapping it got a “1” for detected. If our survey ran for 8 weeks, we would have a serious of 8 detection/non-detection occasions for each survey.

We present trapping rates and occupancy probabilities for carnivores: jaguars, pumas, ocelots, gray foxes, and coatis; for potential prey species: white-tailed and red brocket deer, white-lipped and collared peccaries, agoutis and pacas; and for two potential bird prey: curassow and ocellated turkeys. We also present these values for tapirs.

Jaguar Density Estimation

Because the study sites were different sizes and varied in size from year to year within a site, abundance estimates must be divided by the area surveyed to estimate jaguar density. We dividing the abundance of jaguars derived from programs mark recapture analysis in programs CAPTURE and MARK by the effective sample area (Rexstad and Burnham 1991; Otis et al. Wilson and Anderson 1985). The effective sample area is the area that the cameras covered along with a buffer surrounding the area to account for animals living on the edge of the grid and beyond. To determine the area surveyed, we placed a circular buffer surrounding each camera trap and dissolved areas of overlap. We used traditional methods of calculating the buffer by using the average (mean) of the maximum distance that each jaguar moved among camera traps (MMDM). The MMDM was then divided by 2 (for ½ MMDM), which gave the radius used to create circular buffer around each camera station using ArcGIS buffer tools in ArcMap 10. Once this area surveyed was determined, jaguar abundance was divided by area surveyed to determine density (jaguar per 100km^2), and the results were compared among sites. We estimated standard error in density using the delta method (following Karanth and Nichols 2002).

There are several limitations to these traditional photographic CMR techniques. The first limitation is that the area from which animals are sampled is generally unknown (O'Brien and Kinnaird 2011; Royle et al. 2009); density is therefore estimated ad hoc, typically by adding a buffer area around the trap array (Karanth and Nichols 1998; Parmenter et al. 2003; Wilson and Anderson, 1985). There are different methods to define the width of that buffer, thus, the precise definition of the effective trapping area is generally uncertain (Borchers and Efford 2008; O'Brien and Kinnaird 2011) and density estimates are somewhat arbitrary. A second limitation is that the spatial component of capture data is not directly incorporated into CMR analyses (Gopalaswamy et al. 2012). The location of camera traps is important because an individual jaguar's capture probability depends on the overlap of its home range with the trap array (Efford 2004; Royle et al. 2009). Consequently, the lack of spatial information in traditional CMR analysis also may impact density estimates.

Due to these problems associated with estimating density via traditional methods, we also used recently developed spatially explicit capture-recapture (SECR) models implemented in Programs DENSITY and SPACECAP (Borchers and Efford 2008; Efford 2004; Royle et al. 2009), to address the limitations of traditional mark-recapture techniques. In SECR modeling capture probabilities are modeled as a function of the distance among camera trap locations and an animal's activity center. The location of activity centers is unknown, but the spatial coordinates of the camera traps where individual animals were photographed provide some information about this location (Borchers and Efford 2008; Royle et al. 2009). The SECR technique uses the locational data of the captures to estimate where the home range centers should be and to estimate how many home range centers there should be in the entire study area. The number of home range centers is then considered the as the number of jaguars in the area. In practical terms, SECR models may also be advantageous over CMR methods because their performance is less dependent on the spatial set-up of the camera stations (Noss et al. 2012; Sollmann et al. 2012). Spatially explicit capture-recapture models, however, still require that all photographed animals are uniquely identifiable, but see new techniques for animals like pumas, where some of the population are individually identifiable (Rich et al. 2014).

RESULTS

Set up

We initially established 40 camera stations in La Milpa in 2008 only, and from then on used approximately 20-22 stations from 2010-2013 (Figure 1, Figure 2). In Hill Bank we established 20-26 stations. In Gallon Jug we established 28 camera stations (Figure 2).

Between 2008-2013 we accumulated 7540 trap nights in La Milpa, and between 2009-2013, 6525 trap nights in Hill Bank for a total of 14065 from the 2 sites combined (Table 1). In our first Gallon Jug-Yalbac survey in 2013, we accumulated an additional 2017 trap nights. Yearly survey effort was similar among the sites. We counted up all photos and photo-events of all animals at La Milpa, Hill Bank and Gallon Jug-Yalbac and present them in Tables 2-4. We obtained a grand total of 17,313 events (in 52,516 photographs) across all years at La Milpa 9,738 events (in 39,961 photographs) at Hill Bank across all years and 5,915 events (in 24,424 photographs) in the first year at Gallon Jug-Yalbac. It should be noted that human photos were included in these numbers, which substantially increases the number of photographs and events. Concerning wildlife only, we photographed similar numbers of mammal species at all 3 sites, but photographed many more birds at Hill Bank than the other 2 sites, likely due to its proximity to the large Hill Bank lagoon.

Trapping rates

Trapping rates for jaguars were remarkably similar from 2008-2012 at Hill Bank and La Milpa. In 2013, however, we had a much higher jaguar trapping rate at Hill Bank than La Milpa and Gallon Jug-Yalbac was in between the two (Figure 3). Interestingly, we had a higher trapping rate of pumas at La Milpa than Hill Bank until 2013 when rates converged. Gallon Jug had the highest puma trapping rate, but standard errors overlapped with La Milpa only. Ocelots tended to have a higher trapping rate in La Milpa compared to Hill Bank especially in year 1, 3 and 5, but numbers were similar in years 2 and 4. Gallon Jug had much higher ocelot trapping rates than the other 2 sites in 2013.

For prey species, white-tailed deer tended to have higher trapping rates at Hill Bank and Gallon Jug than at La Milpa, while the numbers were similar for red brocket deer among all 3 sites (Figure 4). Collared peccaries had similar trap rates at all 3 sites, while white-lipped peccaries had higher trapping rates at La Milpa in all years except 2013 when numbers were similar at all 3 sites. Agoutis and pacas had higher trap rates in La Milpa than Hill Bank except in the first 2 years and Gallon Jug-Yalbac had similar rates to La Milpa in 2013 (Figure 5). Curassow and ocellated turkey trapping rates were similar between La Milpa and Hill Bank except in 2013 when both species showed a spiked increase in La Milpa (Figure 6). Gallon Jug-Yalbac had a much higher turkey trapping rates than the other sites in 2013. There has been a steady decline in in turkey trapping rates in Hill Bank, however, we did survey Hill Bank in a different season than La Milpa in 2013.

Finally, Baird's tapir showed only slightly higher trapping rates in Hill Bank, and Gallon Jug had the lowest tapir trapping rate, but standard errors overlapped indicating little difference. Gray foxes had the highest trapping rate of any species in Hill Bank, but this declined in 2012, and in 2013 Gallon Jug and La Milpa had higher trapping rates. White-nosed coati had similar trap rates over time and only in 2013 did La Milpa have higher trap rates than Hill Bank and Gallon Jug-Yalbac.

Occupancy

Our occupancy analysis for 2012 (La Milpa and Hill Bank) and 2013 (Gallon Jug-Yalbac) revealed that jaguars occurred at ~70% of the sites at La Milpa, ~50% of the sites at Hill Bank, and 100% of the sites at Gallon Jug-Yalbac (Figure 6). A similar trend was found for pumas. For ocelots, both La Milpa and Gallon Jug had 100% occupancy. Gray foxes had high occupancy at La Milpa and Gallon Jug. Coatis were the only carnivore that had lower occupancy at Gallon Jug than at the other sites.

For prey species in 2012 La Milpa had 100% occupancy for collared and white-lipped peccaries and tapir, while Hill Bank had 100% occupancy for only collared peccary. No white-lipped peccaries were photographed in Hill Bank in 2012 and hence they had 0% occupancy for that year. In 2013, Gallon Jug had 100% occupancy for only pacas and tapirs and, in general, had lower occupancy than the other sites for collared peccaries (Figure 6).

Jaguar Density

Jaguar density estimates from 2008-2013 from traditional methods of CMR (i.e. Programs CAPTURE and MARK) always had overlapping standard errors among all 3 sites, except for in 2013 when Hill Bank and Gallon Jug were higher than La Milpa only for Program CAPTURE but not MARK (Figure 7). The range was from ~1.5 to 6.5 jaguars per $100km^2$ depending on the year and method.

For the recently developed SECR techniques, Program DENSITY produced a similar range of jaguar density estimates, but had lower density estimates for La Milpa in years 2010, 2012 and 2013 than the other methods. The estimates from DENSITY were in the same range as the traditional methods except for 2013 where estimates were lower from Program DENSITY. Program SPACECAP, on the other hand, tended to produce lower jaguar density estimates overall ranging from 1-4 jaguars per $100km^2$. In years 2012 and 2013 estimates were lower from La Milpa than the traditional methods but similar to the other SECR method.

Jaguar density estimates for Hill Bank remained remarkably stable over the 5-year time period of this study regardless of the technique used. La Milpa seems more variable and low density in 2013 may be concerning. To date, 3 jaguars captured at Gallon Jug were also captured at La Milpa or Hill Bank, making enormous movement across the landscape, indicating that previous studies may have underestimated jaguar home range size (Rabinowitz and Nottingham 1986). Jaguars have been recorded in photographs mating at both Hill Bank (2012) and Gallon Jug-Yalbac (2013).

DISCUSSION

This report represents our preliminary analyses of the impacts of selective logging on jaguar densities and also on the trapping rates and occupancy rates of prey and other predators, providing information relevant to overall biodiversity conservation. There is a tendency to perceive selectively logged forest as having limited conservation value (Rayan & Mohamed 2009). Yet other studies in Asia have shown that selective logging may actually improve tiger habitat (Miquelle et al., 1999) as the disruption of the forest canopy increases sunlight to the forest floor, increasing browse availability for ungulate prey species (Linkie et al. 2008; Davies et al. 2001). However, other research has shown that species exhibiting generalist-oriented feeding strategies fare better in disturbed forests (Johns 1985, 1992) than specialist species or extremely rare species.

In this study, we did not find dramatic differences among the sites in terms of species assemblages, trapping rates, or occupancy. Excluding humans and domestic animals, we photo-trapped 27, 24, and 25 mammal species in La Milpa, Hill Bank, and Gallon Jug-Yalbac, respectively. White-tailed deer did tend to be trapped more, and occupy more area, in the logged areas of Hill Bank and Gallon Jug-Yalbac, while white-lipped peccaries tended to be trapped more and occupy more area in the unlogged site, La Milpa. Pumas tended to have higher trapping rates and occupy more area in the unlogged area, except in 2013 when they had highest rates in Gallon Jug-Yalbac. Red brocket deer occupied more area in the unlogged site, but had similar trapping rate among all sites.

There were very few trends in trapping rates over the 5 years. Most species trapping rates remained relatively constant or varied by year with no particular pattern. The only exception may be the ocellated turkey in Hill Bank which has shown a steady decline in trapping rate since 2009. This site was surveyed at a different time of year in 2013, but La Milpa has also been surveyed at variable times of year and has not shown a similar trend. Turkeys in Gallon-Jug however, are photo-trapped at 5 times the rates of the other sites and are the most photographed species in that site. This is likely due to the fact that turkeys congregate in large numbers (as do white-tailed deer) in the 3000acre cattle clearing in Gallon Jug.

Despite the fact that we used multiple methods to estimate jaguar densities, we found very little difference among the 3 sites in density estimates. The only potential differences out of the 4 density techniques we used all showed lower jaguar density estimates in the unlogged site, La Milpa, in year

2010 (for the 2 SECR techniques), year 2012 (for 1 SECR technique), and year 2013 (1 traditional technique and 2 SECR techniques). Density estimates for Hill Bank were very stable through time, were somewhat variable for La Milpa, and never produced the lowest estimate for the first survey of Gallon Jug-Yalbac. Overall we do not find any strong evidence that sustainable logging has negatively impacted jaguar densities.

We must offer a few caveats with our initial findings. Due to differences in season of surveys and habitat differences including water availability, these results should be cautiously received. Hill Bank, with its permanent water source (the New River lagoon), may be preferred jaguar habitat. In contrast, La Milpa, which is at a slightly higher elevation, typically has less water availability. If this is the case, Hill Bank may perhaps provide better habitat for jaguars regardless of the disturbance caused by logging operations, and the higher density estimates obtained for Hill Bank may simply be a factor of preferred water availability.

Other studies have shown severe declines in biodiversity of large mammals following logging, primarily due to increased hunting/poaching or the encroachment of shifting agriculture into such areas (Johns 1985). The point is made by Frankel & Soule (1981) that multiple-use management of tropical rain-forest is potentially compatible with conservation of wildlife only where hunting is absent or carefully controlled. This point must be taken seriously if we are to conserve wildlife species in a production forest. The fact that similar numbers of species, similar trapping and occupancy rates, and similar densities occur across our study sites is testament to the limited access and protection afforded by the logging companies. Full-time, manned gates with strict permissions for accessibility and border patrolling occurs at these sites and it is likely a necessity for any production forest to maintain viable populations of wildlife.

Finally, our findings that many species survive well in a disturbed environment, should not be used to justify further disturbance. This problem has arisen particularly in South-east Asia, perhaps because studies of the effects of logging have concentrated on a few larger species, coincidentally successful ones (Johhs,1982). This could lead to wildlife population collapses as disturbance increases. There also could be rare and/or specialist species that do not do well in disturbed environments that we have missed in our study. Additionally, due to the nature of logging in Belize, we note that all of our study sites have similar logging history and it could be that La Milpa is still in a regenerating stage and has not yet reached, mature, virgin rainforest status yet since it was last logged.

Future directions

We plan to complete occupancy analysis for all prey and predators for all years, adding to the one year we have completed thus far. In combination with our trapping rates, this will give us a clearer picture of whether negative trends in species activity or distribution exist. In addition, we can identify ocelots by their distinct coat patterns and will estimate their densities at the sites for all years. With the development of new models that allow us to estimate densities for animals with a portion of the population marked (Rich et al. 2014), we will estimate puma densities for each site and year as well.

With repeated camera trapping through time, it will be possible to take our camera trapping work to the next level and determine jaguar survival, recruitment, and longevity. Jaguar survival rate would be a particularly useful demographic parameter because there is very little known about jaguar survival in the wild. High survival could indicate that resident jaguars do well in sustainably logged areas. Conversely, poor survival could indicate that jaguars are moving into logged areas from surrounding habitat and dying, indicating that logged areas could be a population sinks and thus detrimental to jaguar populations.

The habitats at our sites are not static, but rather are subject natural forces such as hurricanes, fires, and floods. It is interesting to note that jaguar densities in Hill Bank did not appear to decline in 2011, the year after Hurricane Richard and subsequent fires, but appear to have increased slightly or remained stable. Long term monitoring will be essential to determine how jaguar populations respond as ecosystems recover from natural disasters. We still advise conducting camera trapping at all sites to build a premier data sets on jaguar population dynamics and to continue to assess the impacts of sustainable logging on biodiversity. This study will serve as a unique area for disturbance ecology and serve as a model system for other timber operations in other parts of the world to follow. Given that protected areas alone are not likely large enough or numerous enough to protect jaguar populations across their range, it is essential to assess how jaguars fare in multi-use landscapes over the long term and enact management guidelines that promote biodiversity conservation in production forests.

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Table 1: Summary of dates, # nights, # stations, and # trap nights of effort for jaguar camera trapping surveys in Rio Bravo Conservation and Management Area and in Gallon Jug Estates and Yalbac Ranch and Cattle Company Lands.

Rio Bravo Conservation and Management Area

	Survey Code	Begin date	End date	# nights	# stations	#Trap nights	Notes
Survey #1	1RB	10-Jan-2008	09-Apr-2008	90	40	2579	La Milpa
Survey #2	1RBHB	20-Jun-2009	09-Sep-2009	81	20	890	Hill Bank
Survey #3	2RBLM	16-Jun-2010	11-Sep-2010	87	20	776	La Milpa
Survey #4	2RBHB	22-Jun-2010	28-Sep-2010	98	20	1069	Hill Bank
Survey #5	3RBHB	13-Mar-2011	02-Jun-2011	81	20	1541	Hill Bank
Survey #6	3RBLM	02-Jun-2011	04-Aug-2011	63	20	1173	La Milpa
Survey #7	4RBHB	12-May-2012	01-Aug-2012	81	20	1419	Hill Bank
Survey #8	4RBLM	30-May-2012	09-Aug-2012	71	20	1347	La Milpa
Survey #9	5RBLM	26-May-2013	13-Aug-2013	79	22	1665	La Milpa
Survey #10	5RBHB	05-Nov-2013	13-Jan-2014	69	26	1606	Hill Bank
					Total trap nights	**14,065**	

Gallon Jug - Yalbac

	Survey Code	Begin date	End date	# nights	# stations	#Trap nights	Notes
Survey #1	1GJYB	20-May-2013	12-Aug-2013	84	28	2017	Gallon Jug Yalbac
					Total trap nights	**2,017**	

Table 2: Summary of all photo data from La Milpa from 2008-2013. Number of independent events consists of a photographic event of each distinct animal within a 30 minute time period regardless of the number of photographs. The number of photographs just adds up all photos of these animals even if the same individual was lingering around the camera station.

La Milpa	2008		2010		2011		2012		2013	
Species (common name)	# indep events	# photos	# indep events	# photos	# indep events	# photos	# indep events	# photos	# indep events	# photos
Mammals										
Baird's Tapir	17	52	9	11	10	28	8	35	19	81
Bat			3	3			3	3	17	22
Central American Agouti	93	106	13	20	163	429	120	350	97	297
Collared Peccary	26	37	1	2	33	80	8	24	24	88
Coyote									2	8
Domestic Dog	96	169	13	91	12	46	4	7	5	10
Gray Four-eyed Opossum					1	1				
Gray Fox	124	200	67	139	80	182	97	224	163	304
Human	4579	8727	923	2222	1050	3421	2748	13172	2735	10488
Jaguar	67	157	20	36	21	66	53	140	40	121
Jaguarundi	3	3			1	1			1	3
Margay	17	21	1	1	12	45	3	8	6	13
Nine-banded Armadillo	4	5	1	1	3	7	7	17	29	73
Northern Raccoon							1	1	1	3
Northern Tamandua	2	2			1	2	1	2		
Ocelot	126	238	41	81	75	246	61	176	78	233
Opossum	18	26	13	8	1	1	26	49	19	31
Paca	25	28	35	80	62	167	59	212	73	229
Peccary (unknown)							3	9		
Puma	67	119	44	81	80	225	100	292	84	267
Red Brocket Deer	46	70	11	19	28	100	20	65	37	176
Spiny Pocket Mouse					8	10	1	1	1	3
Squirrel	9	13	1	3	9	30	3	7	2	6
Striped Hog-nosed Skunk	4	7			2	4			2	5
Tayra	6	9	1	1	3	7	2	6	1	3
Unknown Cat					2	2	1	4		
White Hog-nosed Skunk									1	5
White-lipped Peccary	30	46	56	95	20	146	35	203	33	112
White-nosed Coati	13	22	1	1	9	24	13	34	40	90
White-tailed Deer	10	27	31	114	50	165	37	113	71	242
Yucatan Black Howler							1	3		

Table2 continues on the next page….

Table 2 continued from previous page.

La Milpa	2008		2010		2011		2012		2013	
Species (common name)	# indep events	# photos	# indep events	# photos	# indep events	# photos	# indep events	# photos	# indep events	# photos
Birds										
Blue-crowned Motmot							1	3		
Cedar Waxwing					1	1				
Common Pauraque									5	12
Crested Guan	5	6	10	11	4	4	3	39	5	23
Dove	53	59	3	6	45	132	40	116	31	104
Gray-necked Wood-rail					4	7	2	2	1	2
Great Black-hawk									1	15
Great Curassow	131	201	71	157	74	300	50	220	227	1056
Great Tinamou			1	3					11	26
Hawk (unknown)							1	2	1	7
Limpkin									1	3
Ocellated Turkey	292	513	114	332	129	358	90	226	274	1234
Plain Chachalaca	19	14					1	1	5	6
Tinamou (unknown)	36	43	2	3	14	33	1	3	4	8
Turkey Vulture			1	34			1	3		
Unknown Bird	10	13	1	1	5	12	8	27	2	5
Vermiculated Screech-Owl									1	3
Other										
Frog									19	310
Insect						1	3	1	14	49
Snake									1	3
Unknown	6	6	19	21	16	20	23	31	22	87
Totals	**5,934**	**10,939**	**1,507**	**3,577**	**2,027**	**6,303**	**3,639**	**15,831**	**4,206**	**15,866**

Grand total (events)	**17,313**
Grand total (photos)	**52,516**

Table 3: Summary of all photo data from Hill Bank from 2009-2013. Number of independent events consists of a photographic event of each distinct animal within a 30 minute time period regardless of the number of photographs. The number of photographs just adds up all photos of these animals even if the same individual was lingering around the camera station

Hill Bank	2009		2010		2011		2012		2013	
Species (common name)	# indep events	# photos	# indep events	# photos	# indep events	# photos	# indep events	# photos	# indep events	# photos
Mammals										
Bat	1	1			1	1	1	1	7	8
Central American Agouti	8	9	16	21	68	214	65	269	32	75
Collared Peccary	6	6	4	15	14	70	17	42	9	22
Domestic Dog					55	147			5	6
Gray Four-eyed Opossum					9	23			2	2
Gray Fox	189	345	120	203	207	331	72	147	59	103
Horse									4	7
Human	864	1849	417	1965	2519	7831	640	9588	680	5555
Jaguar	65	101	32	58	27	107	44	129	101	274
Jaguarundi	1	1			9	26			1	6
Margay	3	3			9	46	7	18	3	8
Mexican Porcupine			1	1						
Nine-banded Armadillo	2	2	12	21	9	32	9	20		
Northern Raccoon	1	1			3	5	1	3	2	6
Northern Tamandua	1	1							1	5
Ocelot	20	33	35	76	59	199	70	196	28	60
Opossum	8	30	27	40	136	314	87	221	9	24
Paca	29	34	19	32	31	84	24	73	26	65
Puma	15	49	17	31	54	191	36	99	63	169
Red Brocket	13	28	27	59	21	88	8	22	26	105
Rodent	1	1	1	1	10	19	3	3		
Squirrel	3	3	3	7	1	3	2	5	3	9
Striped Hog-nosed Skunk	3	5	3	9	25	49	4	17		
Tayra	2	3	2	2	11	23	7	18	1	2
Unknown Cat			1	1			1	1		
White-lipped Peccary			4	4	1	1			32	107
White-nosed Coati	5	6	6	4	10	28	10	19	9	26
White-tailed Deer	121	692	134	411	72	247	172	694	146	327

Table 3 continues on the next page….

Table 3 continued from previous page

Hill Bank	2009		2010		2011		2012		2013	
Species (common name)	# indep events	# photos	# indep events	# photos	# indep events	# photos	# indep events	# photos	# indep events	# photos
Birds										
Agami Heron					1	1				
Baird's Tapir	35	107	22	61	14	62	49	262	38	254
Bare-Throated Tiger-Heron							2	6	1	5
Black-bellied Whistling Duck	12	1								
Black-throated Bobwhite	4	3								
Blue-crowned Motmot							2	3		
Brown Jay							1	3		
Collared Forest-falcon	2	7								
Common Black-hawk									1	3
Common Paraque	8	10	1	3	9	17			43	200
Crested Guan							17	62		
Dove	1	1	7	12	22	62	12	32	7	17
Eastern Meadowlark					1	1				
Gray-necked Wood-rail	7	8	15	22	2	5	11	23	3	13
Great Black-hawk	1	1								
Great Curassow	83	134	54	124	110	366	61	221	124	607
Great Tinamou	2	3	7	14			4	17	11	34
Grey-necked Wood Rail					1	3				
Hawk									6	24
Heron									1	1
Limpkin	1	1	1	1	1	5	12	40		
Ocellated Turkey	175	565	128	380	137	487	80	335	51	132
Plain Chachalaca	11	13	1	1	1	2	9	13		
Seedeater							1	2		
Slaty-breasted tinamou							7	18		
Spectacled Owl			1	2						
Song Bird					2	6	3	5	7	11
Tinamou (unknown)	2	2			32	98				
Turkey Vulture			1	3						
Unknown Bird	6	15	12	31	7	15	4	8	11	29
Wood Stork							1	1	1	1
Yellow-crowned Night-heron	12	15								
Other										
Butterfly			1	3			2	2	1	3
Frog			1	3						
Green Iguana					1	3				
Insect			2	10						
Lizard							1	2		
Snake									1	1
Unknown	5	7	16	21	22	31	8	9	12	15
Total	**1,728**	**4,096**	**1,151**	**3,652**	**3,724**	**11,243**	**1,567**	**12,649**	**1,568**	**8,321**
Grand total (events)	**9,738**									
Grand total (photos)	**39,961**									

Table 4: Summary of all photo data from Gallon Jug/Yalbac lands from first survey in 2013. Number of independent events consists of a photographic event of each distinct animal within a 30 minute time period regardless of the number of photographs. The number of photographs just adds up all photos of these animals even if the same individual was lingering around the camera station

Gallon Jug/Yalbac	2013	
Species (common name)	# indep events	# photos
Mammals		
Baird's Tapir	12	48
Bat	3	3
Central American Agouti	143	513
Collared Peccary	29	167
Cow	22	148
Coyote	1	1
Deppe's Squirrel	1	3
Domestic Cat	7	9
Domestic Dog	6	12
Gray Four-eyed Opossum	1	3
Gray Fox	319	621
Horse	29	73
Human	1912	11171
Jaguar	82	253
Jaguarundi	6	21
Margay	4	11
Nine-banded Armadillo	3	3
Northern Raccoon	3	5
Ocelot	248	714
Opossum	21	43
Paca	35	77
Puma	130	425
Red Brocket	37	131
Spiny Pocket Mouse	2	6
Striped Hog-nosed Skunk	3	5
Tayra	4	12
White-lipped Peccary	85	150
White-nosed Coati	14	38
White-tailed Deer	222	780
Yucatan Squirrel	3	7

Table 3 continues to columns on the right.

Table 3 continues from columns on the left.

Gallon Jug/Yalbac	2013	
Species (common name)	# indep events	# photos
Birds		
Blue-crowned Motmot	2	6
Common Pauraque	5	9
Crested Guan	6	41
Dove	17	40
Gray-necked Wood-rail	17	32
Great Curassow	465	1997
Great Tinamou	8	18
Ocellated Turkey	1964	6630
Plain Chachalaca	8	14
Turkey Vulture	1	3
Unknown Bird	5	9
Other		
Frog	2	101
Snail	1	30
Snake	1	6
Turtle	1	3
Unknown	25	32
Totals	**5,915**	**24,424**

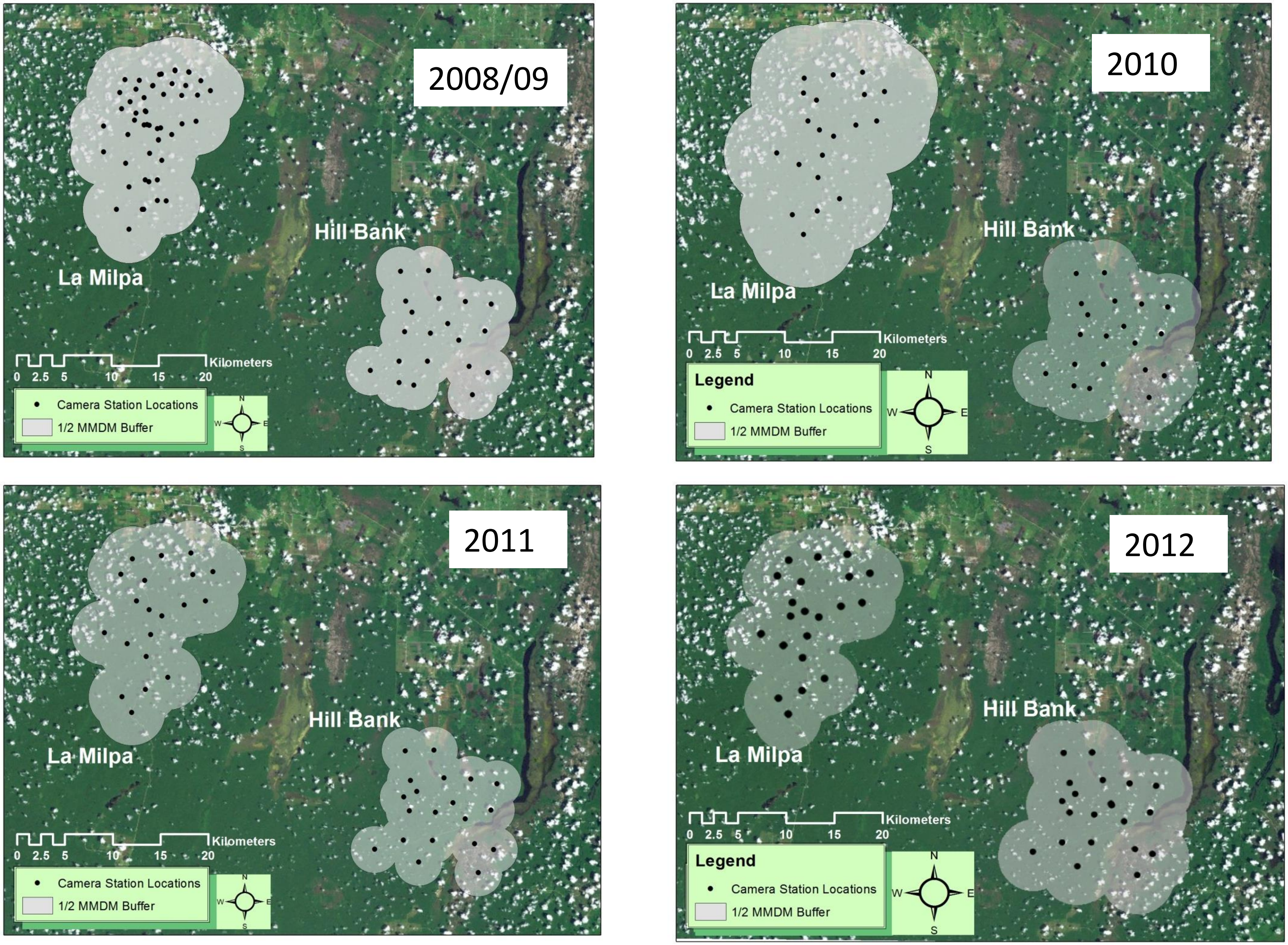

Figure 1. Locations of camera traps over 4 survey years in Rio Bravo Conservation and Management Area: La Milpa and Hill Bank sites. The buffers surrounding cameras traps are based on the ½ Mean (average) Maximum Distance Moved of all jaguars captured at more than one station within each site. This MMDM changes each year causing buffers (and hence areas surveyed) to change, sometimes dramatically, even when cameras are in the same locations. The ½ MMDM buffering technique has been criticized because the density estimates are highly influenced by this area surveyed. This had led to newer methods called Spatially Explicit Mark-Recapture (SECR) techniques.

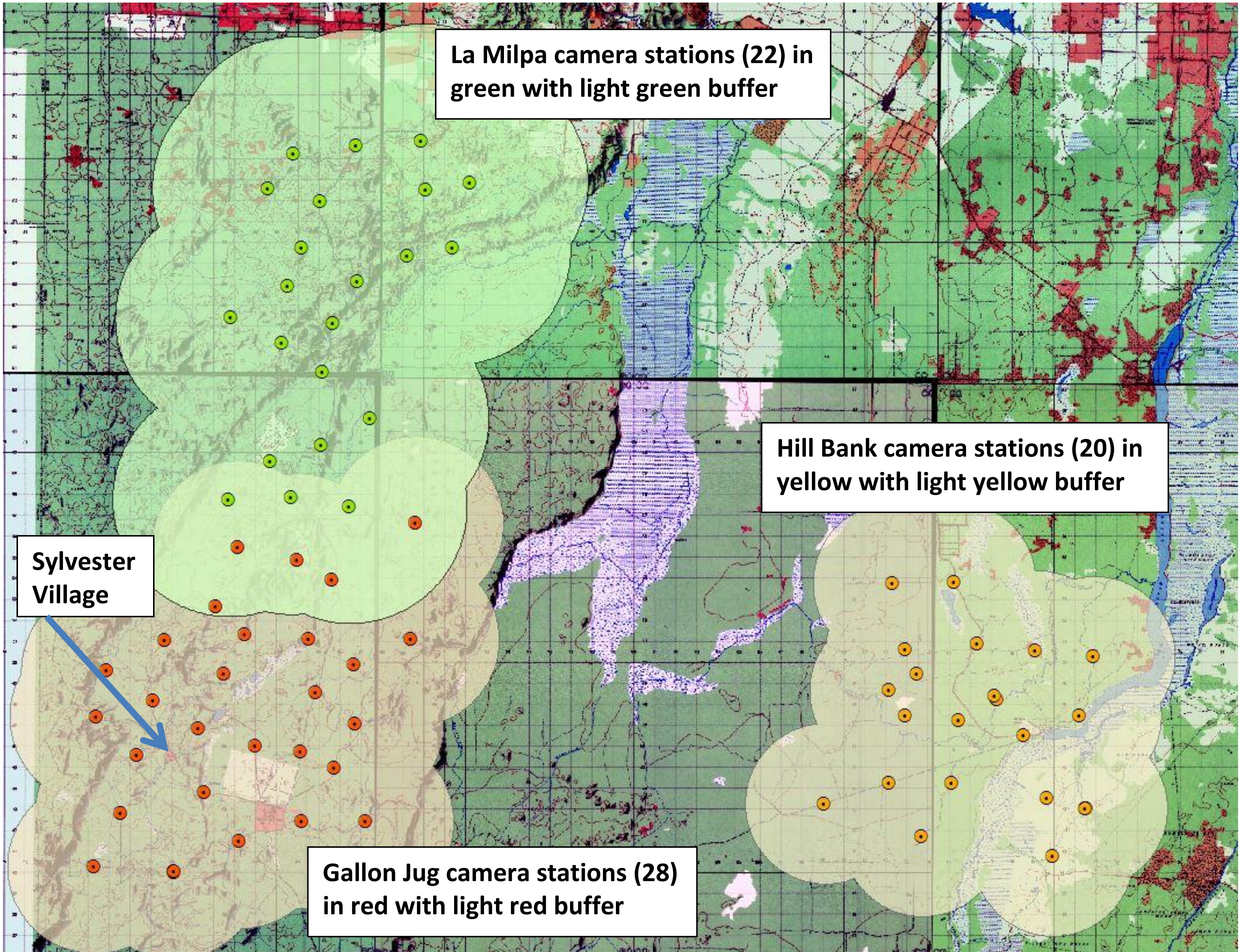

Figure 2. Locations of camera stations in 2013. We plan to put camera stations in these same locations in 2014 and hope to expand the number of stations to link Hill Bank to Gallon Jug/Yalbac.

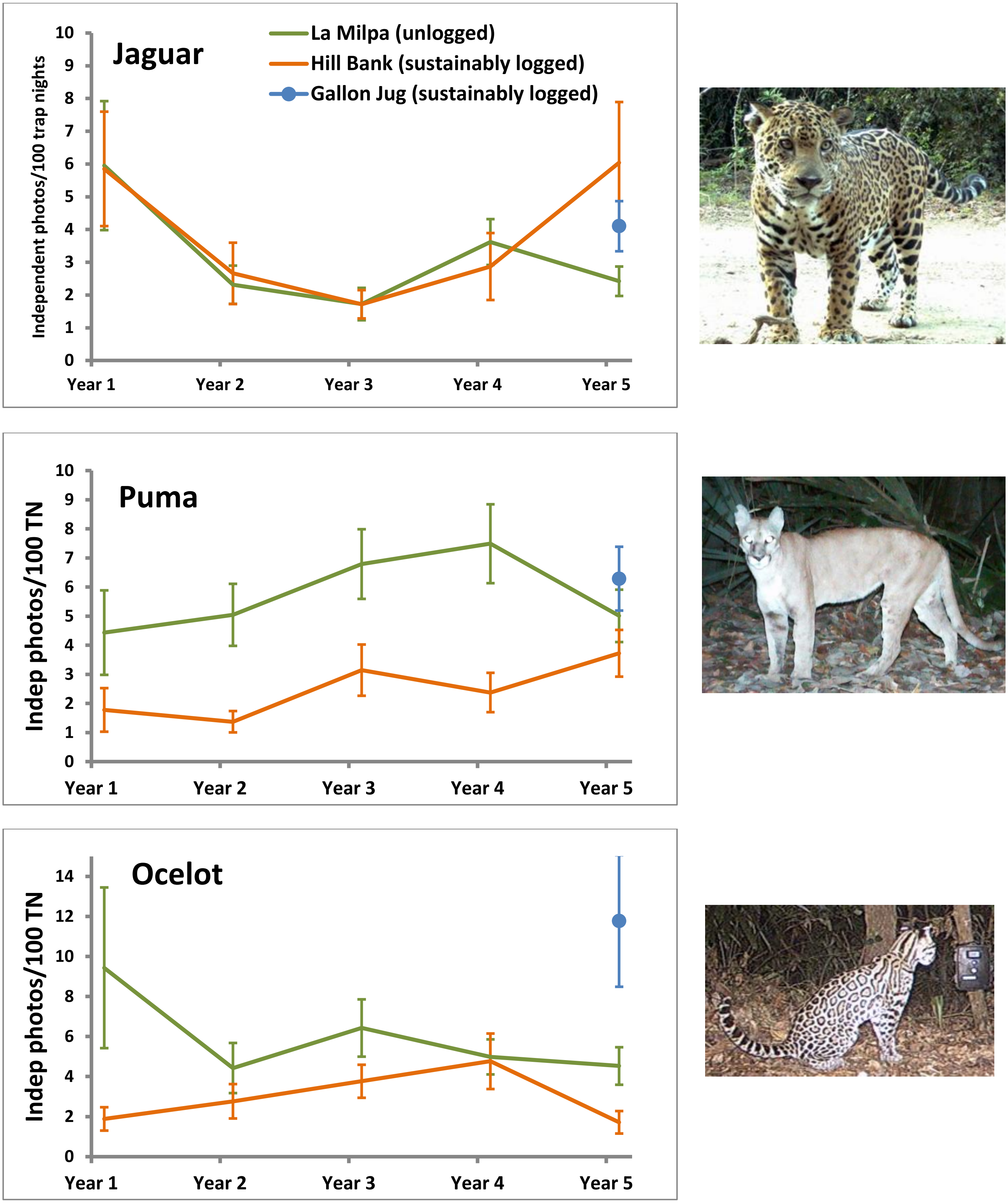

Figure 3. Photo trap rates for jaguars, pumas, and ocelots from 2008/9-2013. Trap rates are calculated as the # of independent events per 100 trap nights. Independent events are photo captures of distinct individuals (regardless of the # of photos) within a 30 minute time period. A trap rate of 5 would mean that 5 indep. events were recorded over 100 tap nights (with 25 cameras operational per night – that would mean 5 photo events in a 4 days). This metric is better used and an <u>activity index</u> rather than abundance index because one individual can dominate several traps. NOTE: Jaguars and pumas are on the same scale, ocelots are displayed on a slightly different scale to accommodate high traps rates in Gallon Jug and Year 1 of La Milpa.

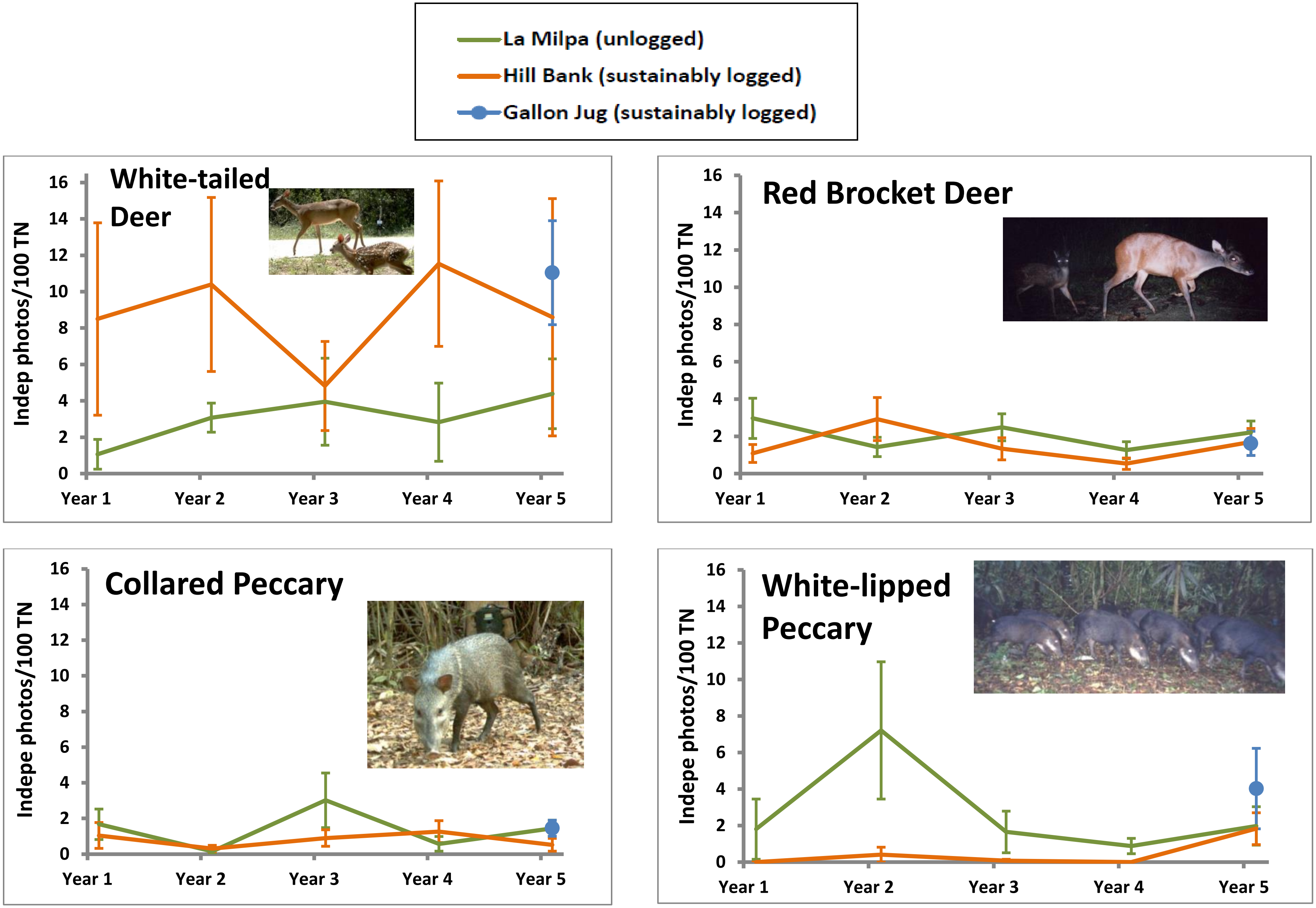

Figure 4. Photo trap rates for ungulate prey species 2008/9 until 2013. Trap rates are calculated as the # of independent events per 100 trap nights. Independent events are photo captures of distinct individuals (regardless of the number of photos) within a 30 minute time period. This metric is better used and an activity index rather than abundance index because one individual can dominate several traps. All graphs are on the same scale. White-tailed deer are most active at Hill Bank and Gallon Jug while WL peccaries more active at La Milpa except in year 5.

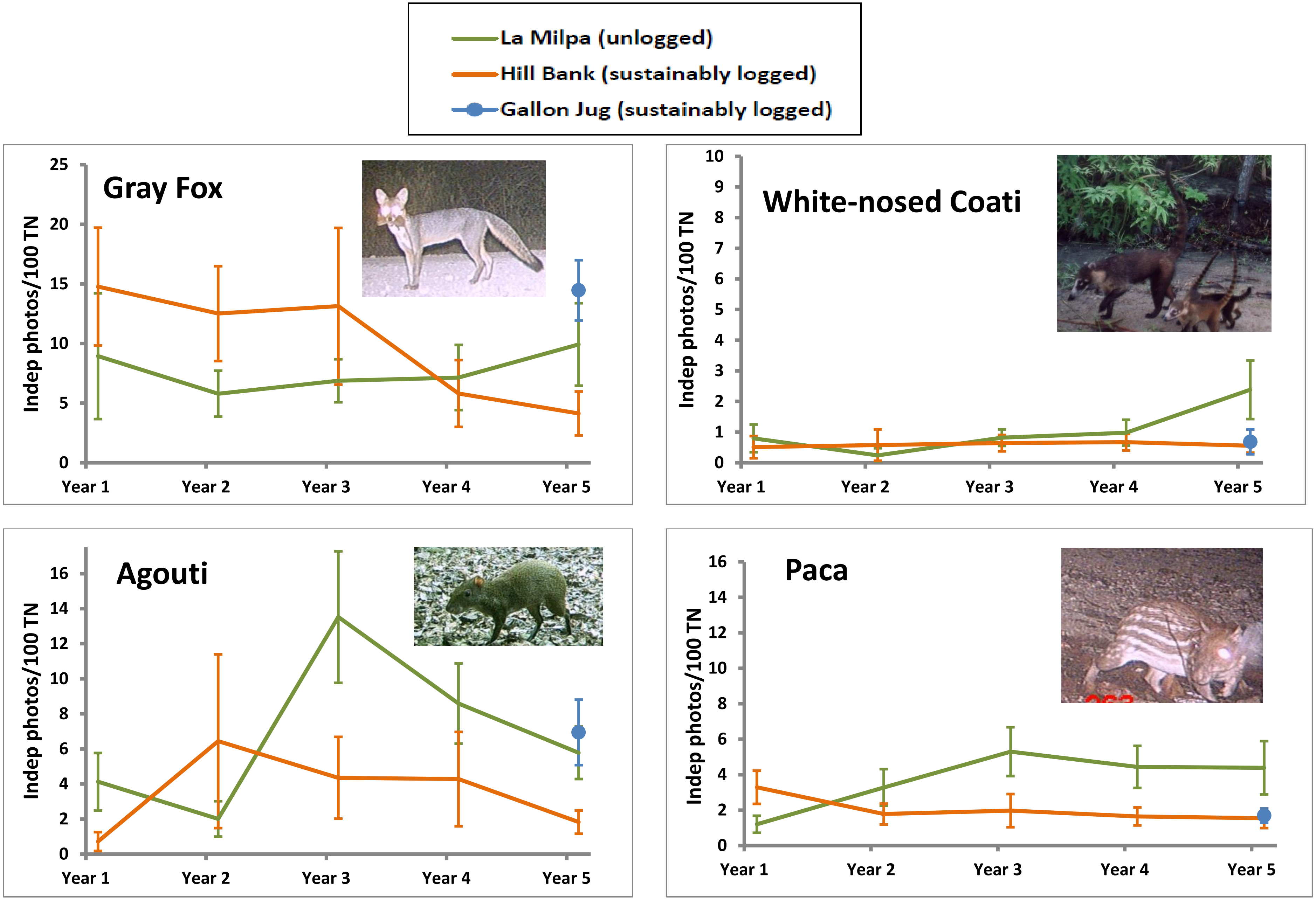

Figure 5. Photo trap rates for smaller carnivores (gray foxes and coatis) and for smaller prey (agoutis and pacas) from 2008/9 until 2013. Trap rates are calculated as the # of independent events per 100 trap nights. Independent events are photo captures of distinct individuals (regardless of the # of photos) within a 30 minute time period. This metric is better used and an activity index rather than abundance index because one individual can dominate several traps. Gray foxes are trapped substantially more than any other species (note y-axis scale). Agoutis and pacas are on the same scale.

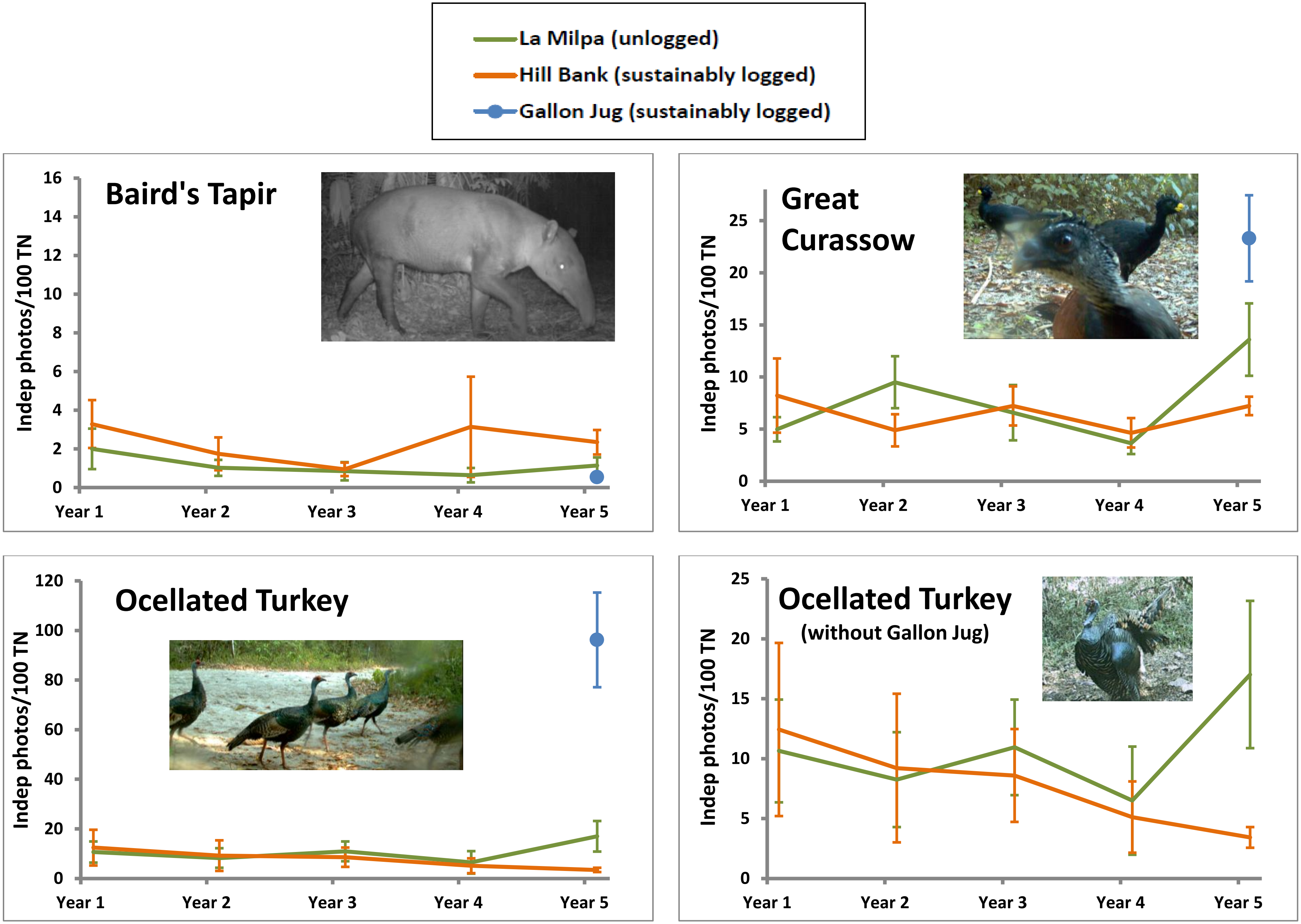

Figure 6. Photo trap rates for tapirs, curassows, and turkeys from 2008/9 until 2013. Turkeys are displayed both with and without Gallon Jug, because it was difficult to see the difference between La Milpa and Hill Bank when Gallon Jug was plotted. Trap rates are calculated as the # of independent events per 100 trap nights. Independent events are photo captures of distinct individuals (regardless of the number of photos) within a 30 minute time period. This metric is better used and an activity index rather than abundance index because one individual can dominate several traps.

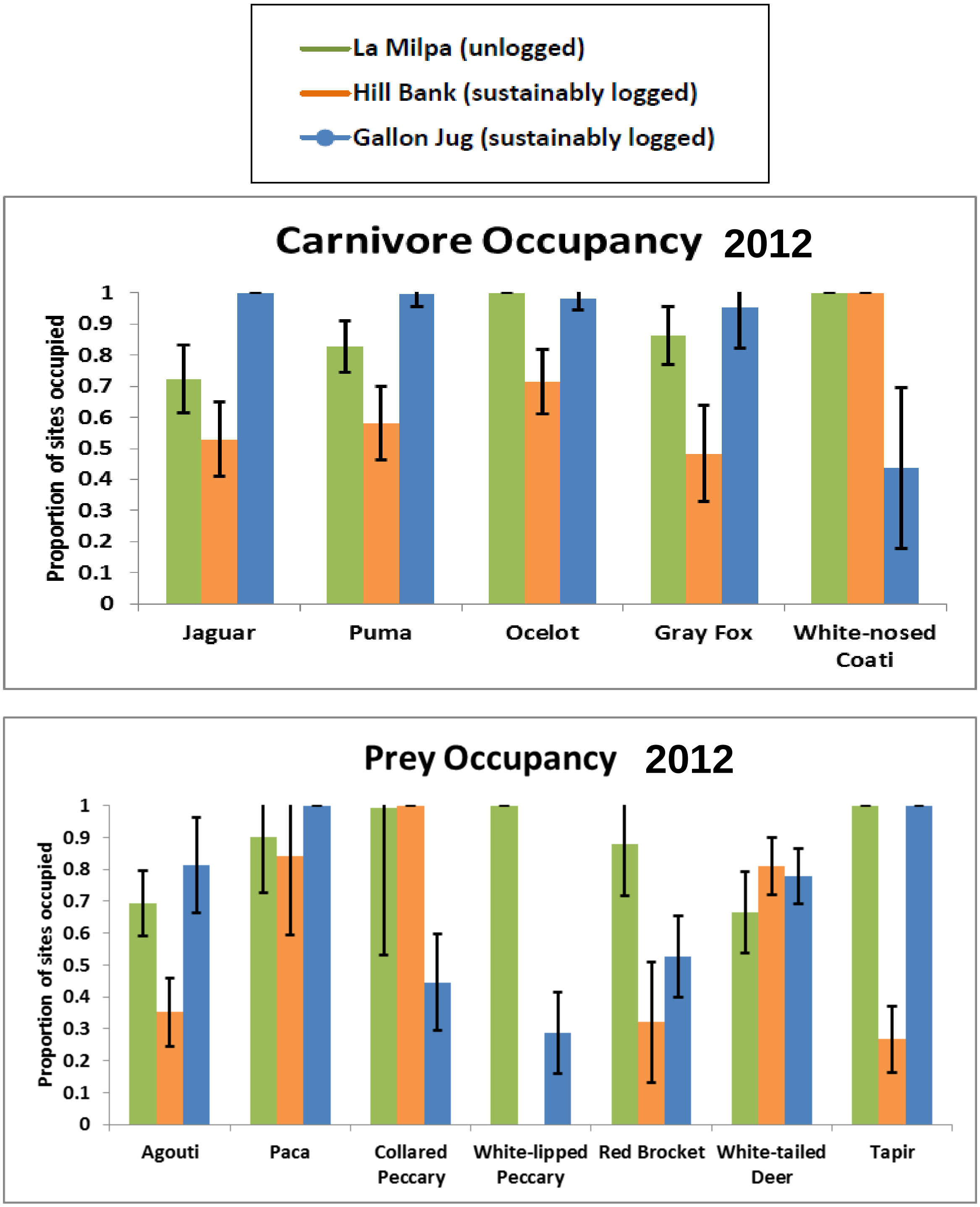

Figure 6. Occupancy analysis for 5 carnivore species (top panel) and 7 prey species (bottom panel) for 2012 (La Milpa and Hill Bank) and for 2013 (Gallon Jug). Occupancy goes from 0-1 and represents the number of camera stations where the species is present across each site. For example, jaguars were present at ~70%, ~50%, and 100% of the camera stations for La Milpa, Hill Bank, and Gallon Jug respectively. Occupancy modeling incorporates detection probability into the analyses.

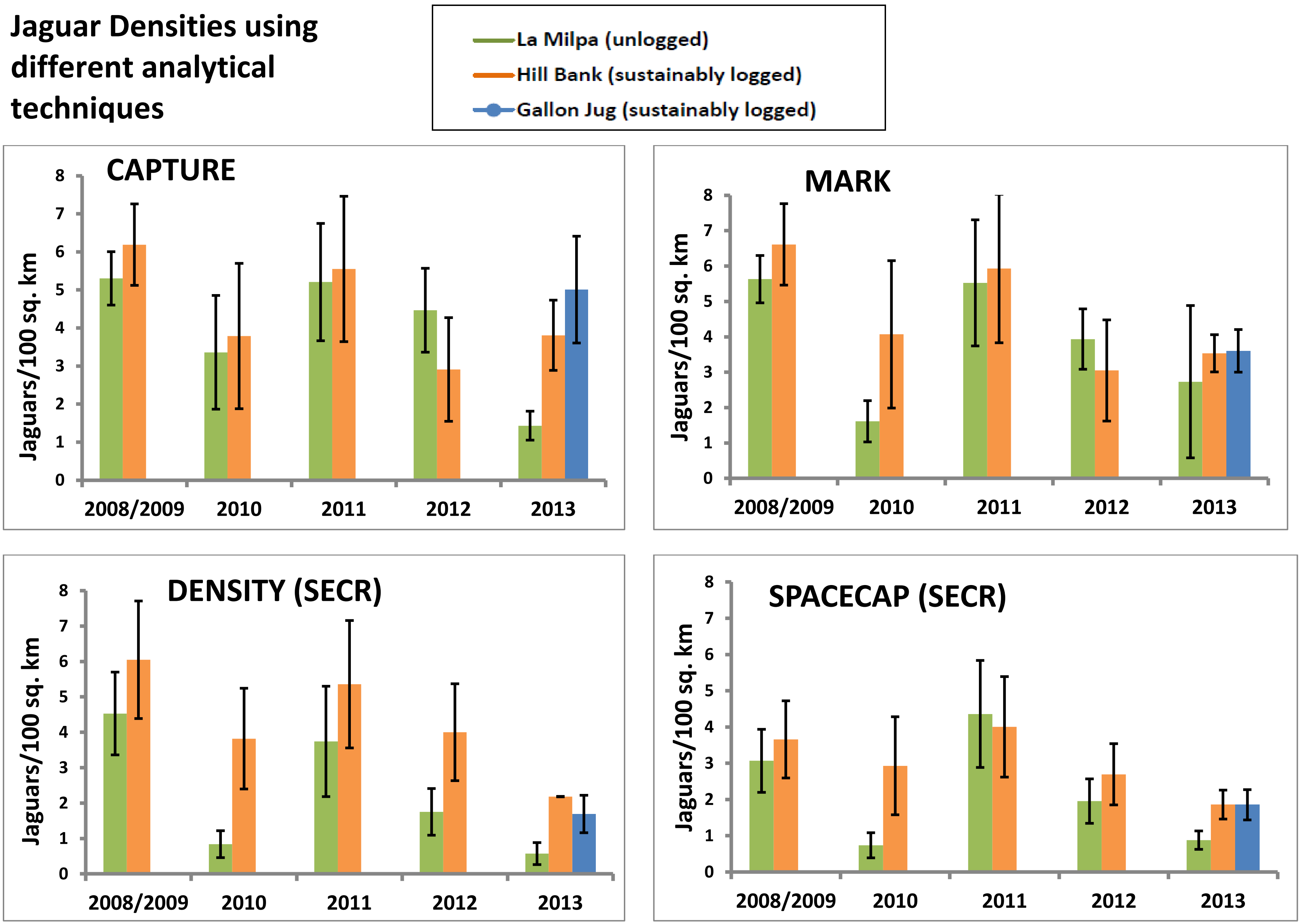

Figure 6. Mark-recapture analyses conducted in 4 ways to estimate jaguar densities. Programs CAPTURE and MARK use traditional ½ MMDM methods to estimate abundance. Some argue that these older methods overestimate abundance. Newer Spatially Explicit Capture-Recapture (SECR) models incorporate camera locations directly into the estimation process. In all cases it is clear that there is not much difference between the logged and unlogged sites as the confidence limits overlap. SECR models, especially SPACECAP, do tend to produce lower estimates.