ANALISYS OF FRAGMENTATION EFFECT ON DEER POPULATION DENSITY IN RELATION TO QUALITY HABITAT FOR LARGE CARNIVORES IN THE BIOSPHERE RESERVE OF CALAKMUL, SOUTHEAST MEXICO

M. C. Sanchez Alonso
9922005

Third Year Double Unit Project

First Supervisor: Phil Shaw
Second Supervisor: Jonathan Steer

Hand in date: 08/07/02
Word Count:

Table of Contents

Page No

Abstract ………………………………..…………………………………….. 1

1. Aims and Objectives ………………………………………………. 2

2. Introduction ……………………...……… 3

***2.1 Pumas* ………………………………………………………………..** 4

***2.2 Jaguars* ………………………………………………………………** 9

***2.3 Behavioral patterns of cervid species* ……………………………...** 11

3. Study site ……………………………………………………………….. 12

3.1 Vegetation structure ……………………………………………………… 16

3.2 Caobas Site ……………………………………………………………..… 17

***3.3 Costa Maya Site* ……………………………………………………..** 17

4. Methodology ……………………………………………………………. 19

4.1 Data Collection ………………………………………………………… 21

***4.2 Environmental Variables* ………………………………………...** 21

***4.3 Something to consider* ………………………………………………** 22

***4.4 Analysis* ……………………………………………………………...** 22

5. Results …………………………………………………………………..

***5.1 Comparison of relative population density of deer* ………………...** 23

***5.2 Extrapolating the results* …………………………………………....** 23

6. Discussion ………………………………………………………………

6.1 Fragmentation effect, habitat degradation and carnivore populations 26

***6.2 Prey depletion* ……………………………………………………….** 27

***6.3 Human and predators competition* ………………………………....** 28

***6.4 Socially-induced depression* ………………………………………...** 30

7. Conclusion ……………………………………………………………… 31

***7.1 Solutions* ……………………………………………………………..** 32

8. Acknowledgements ……………………………………………………….. 34

References .…………..…………………………………………………… 35

Appendix 1 ..……………………………………………………………. 40

Appendix 2 ……………………………………………………………………. 41

Appendix 3 ……………………………………………………………………. 42

Appendix 4 ……………………………………………………….……… 43

Abstract

In this study we analyze the effect of fragmentation occurring in a large remaining tropical area in the state of Campeche, Southeast Mexico. The possible consequences to the population of large carnivores such as the jaguar (*Panthera onca)* and the puma *(Puma concolor)* which co-exist in this area are analyzed by assessing and comparing the population of one of their common prey: deer. The relative population density of the three different species of cervids found in this neotropical region is used to estimate habitat quality for the existing jaguar and puma populations. Two independent sites in the Mayan Jungle, southeast Mexico were surveyed: one outside the Biosphere Reserve of Calakmul and the other within the nucleus zone of the reserve. The existence of legal protection and the level of human disturbance are the main characteristics, which differentiate the two sites. Throughout our study it was found that the cervid population was significantly lower in the non-protected site. This can decrease the populations of jaguars and pumas, as prey availability is the main density dependant factor affecting their population.

1. Aims and objectives

The objectives of this report are clearly described as follow:

- To compare the abundance of cervids in the two studied areas in order to note any differences in the relative population density.

- To evaluate the causes, if any, of the different distribution of deer populations in both sites.

- To evaluate prey availability and habitat quality for large carnivores inhabiting the area surveyed.

2. Introduction

Human-induced changes in forested landscapes have direct implications for animal populations due to the introduction of new factors in the area (e.g., monocultures, selective logging) and for their usually high rates of occurrence (e.g. clearing for industrial purposes) (Lawton, 1997). The geographical distribution of many mammalian carnivores, specially the largest species, have declined drastically over the last 500 years due primarily to a combination of human-related activities: first, suitable forest habitat is destroyed and second, habitat quality is often diminished. Biologists today find natural ecosystems shrinking rapidly and many wildlife species seriously threatened. The magnitude of these effects depends largely on the type and extent of human activity and the species under consideration.

The main factors creating and increasing fragmentation effect are agriculture, urbanisation, forest logging and land degradation, which nowadays are dominating much of the landscape. This landscape conversion has not been randomly made. Forest remnants that exist today are often in steep, inaccessible and less productive areas. The consequences of habitat change are often irreversible in the changing geographic distributions of numerous species, and the effects of forest fragmentation are well documented for many vertebrate species. Human-caused habitat alteration has accelerated recently and the general consensus is that increasing rates of habitat degradation, loss and fragmentation, coupled with the ecological effects of isolation and patch dynamics, are largely responsible for increasing the rate of species decline and endangerment (Laurance & Bierregaard, 1997).

This study compares two different sites in order to observe and analyze the effect of fragmentation of suitable habitat on deer population density in relation to habitat quality for large carnivores like *Panthera onca* and *Puma concolor*. The first site, CAOBAS, is characterized by its rapidly increasing population and the consequently disappearance of potential habitat. There is a massive hunting activity even in the areas where the hunting is not permitted and corn plantation surrounding the villages that increases correlating the population growth. This particular area is situated outside the Biosphere Reserve of Calakmul, thus lacking legal protection. The second site, COSTA MAYA, is situated in the nucleus zone of the reserve, where the disturbance and hunting is prohibited in theory and minimal in practice. This reserve was formed in 1987 in order to preserve the biggest pristine jungle area left in Mexico, using endangered and/ or umbrella species like the jaguar, to achieve it.

2.1 Pumas

Pumas have a very broad latitudinal range encompassing a diverse array of habitats (Fig. 1), from arid desert to tropical rainforest to cold coniferous forest, from sea level up to 5,800 m in the Andes (*Redford and Eisenberg 1992*). While several studies have shown that habitat with dense understory vegetation is preferred (*Seidensticker et al. 1973, Logan and Irwin 1985, Laing 1988*), pumas can live in very open habitats with only a minimum of vegetative cover (*Lindzey 1987, Seidensticker 1991b*). They have been occasionally reported from areas of intensive agricultural cultivation, although such animals are likely to be transient (*Tischendorf and Henderson 1993*). Pumas are opportunistic predators (Emmons, 1987) dependant on a high scale on the presence and abundance of deer as the main prey species of their diet (Table 1).

The puma's historical distribution included every major habitat type in the Americas up to the boreal forests of the far north, but pumas have been essentially eliminated from eastern North America. Severe reduction of native ungulate populations through hunting and forest clearance during the nineteenth century, coupled with direct persecution of the puma, are the probable causes (*Wright 1959*). Deer have since multiplied and spread, and the puma is now found in areas colonised by deer which were outside its historical range, such as the Great Basin Desert in the western U.S. (*Berger and Wehausen 1991*). Ackerman *et al*. (*1986*) suggested that the energy requirements of females with young are such that viable populations cannot exist in areas devoid of deer-size ungulates. For example, they predicted that a resident female (based on studies in southern Utah) would kill a white-tailed deer every 16 days, and that the interval would shrink to nine days when her kittens were three months old, and to three days when the kittens were nearly mature at 15 months. It is interesting that the puma occurs in a variety of habitats and takes both large and small prey, similarly to the leopard in the Old World, while the jaguar, like the tiger, is closely tied to well-watered forested environments and is capable of taking very large prey.

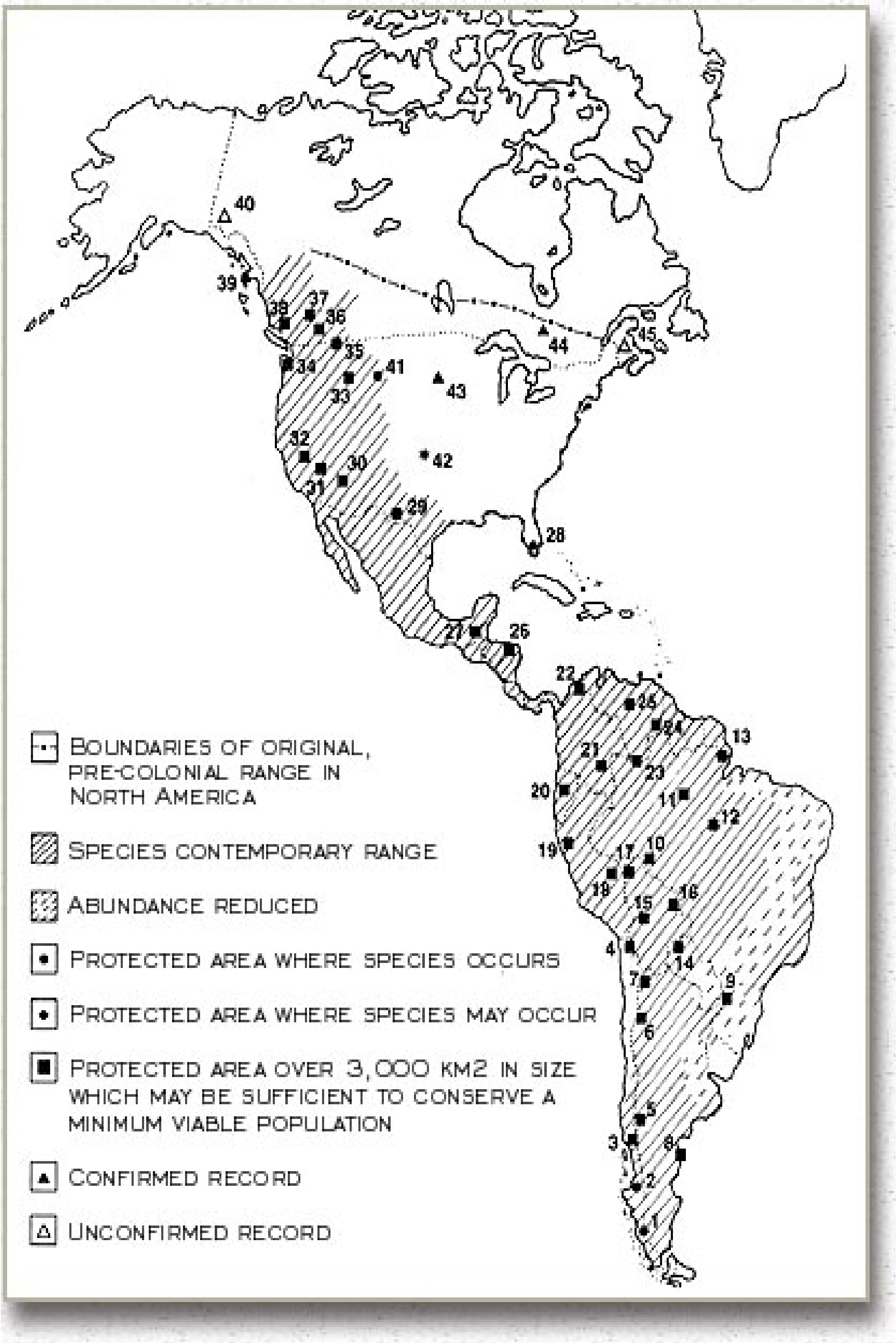


Figure 1. Past and present distribution of the puma *(Puma concolor)*

1. Los Glaciares II** (Argentina) + Torres del Paine II* (Chile) complex;
2. Laguna San Rafael II* complex;
3. Vicente Perez Rosales II complex;
4. Lauca II* complex (Chile);
5. Los Alerces II, Lanín II + Nahuel Huapi II complex;
6. San Guillermo IV* complex;
7. Los Andes I;
8. Península de Valdés VIII (Argentina);
9. Iguazú II** (Argentina) + Iguaçu II** (Brazil) complex;
10. Pacaas Novos II complex;
11. Amazonia II complex;
12. Araguaia II complex;
13. Lago Piratuba I (Brazil);
14. Defensores del Chaco II (Paraguay);
15. Isiboro Sécure II;
16. Noel Kempff Mercado II;
17. Manuripi Heath IV complex (Bolivia);
18. Manú II#;
19. Huascarán II# (Peru);
20. Ecuador parks: Sangay II**, Cayambe-Coca I, and Yasuní II complex;
21. Chiribiquete II;
22. Sierra Nevada de Santa Marta II* complex (Colombia);
23. Serranía de la Neblina II (Venezuela) + Pico da Neblina II (Brazil) complex;
24. Canaima II;
25. Aguaro-Guariquito II (Venezuela);
26. Río Platano II* (Honduras);
27. Calakmul V* (Mexico) + Maya IX* (Guatemala) complex;
28. Big Cypress II;
29. Big Bend II*;
30. Grand Canyon II** complex;
31. Death Valley III;
32. Yosemite II** complex;
33. Yellowstone II# complex;
34. Olympic II# (US);
35. Glacier II* (US) + Waterton Lakes II (Canada);
36. Jasper II complex;
37. Wells Gray II;
38. Tweedsmuir II;
39. puma shot on Wrangell Island in 1989;
40. puma sightings in the Kluane Lake region *(Tischendorf and Henderson 1993)* (Canada);
41. Black Hills National Forest/Custer State Park complex;
42. Ozark/Ouachita/Mark Twain National Forest complex;
43. young male puma captured in 1991 in agricultural region of south-west Minnesota;
44. puma shot near Lake Abitibi in 1992 *(Tischendorf and Henderson 1993)*;
45. tracks and scat found in east-central New Brunswick *(Cumberland 1993)*.

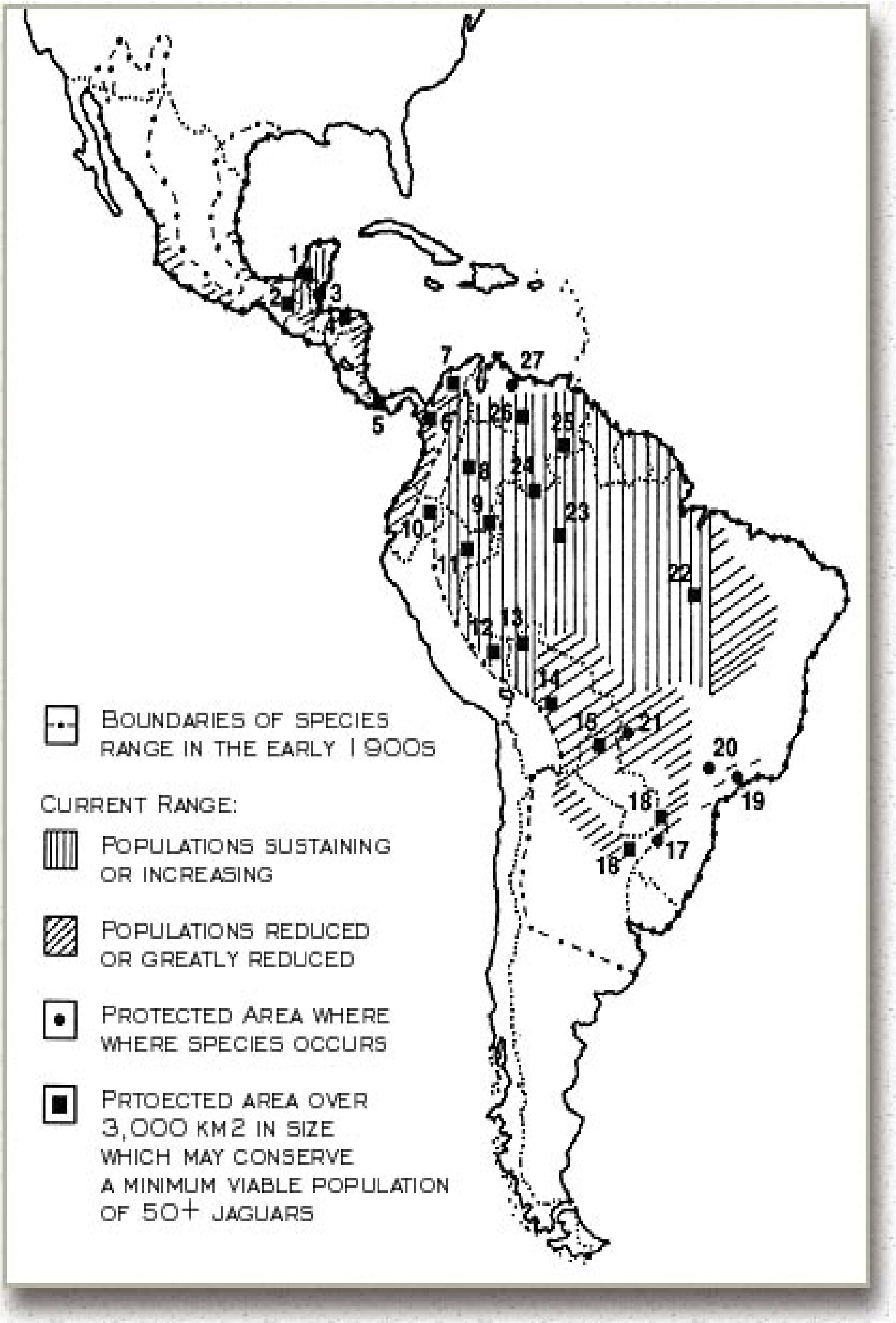


Figure 2. Past and present distribution of the Jaguar *(Panthera onca)*

1. Calakmul V* (Mexico) + Maya IX* (Guatemala);
2. Montes Azules II (Mexico);
3. Cockscomb Basin IV (Belize);
4. Rio Platano IX# (Honduras);
5. La Amistad (Talamanca) II# complex (Costa Rica & Panama);
6. Darién II# complex (Panama) + Los Katios II (Colombia);
7. Sierra Nevada de Santa Marta II* complex;
8. Sierra de la Macarena II complex;
9. Cahuinarí II complex (Colombia);
10. Yasuní II* (Ecuador);
11. Pacaya Samiria VIII;
12. Manú II# (Peru);
13. Manuripi Heath IV complex;
14. Isiboro Sécure II (Bolivia);
15. Defensores del Chaco II (Paraguay);
16. Iberá IV complex (Argentina);
17. Moconé Provincial Reserve (Argentina) + Turvo II (Brazil) complex;
18. Iguazú II** (Argentina) + Iguaçu II** (Brazil) complex;
19. Juréia-Itatins IV;
20. Alto Ribeira II complex;
21. Pantanal Matogrossense II;
22. Araguaia II complex;
23. Jau II complex (Brazil);
24. Pico da Neblina II (Brazil) + Serranía de la Neblina II (Venezuela) complex;
25. Canaima II;
26. Aguaro-Guariquito II;
27. Henri Pittier II (Venezuela).

2.2 Jaguars

Compared with the puma, the jaguar has a more limited distribution (Fig. 2), both geographically and in terms of habitat requirements. These requirements are dense cover, a water supply and sufficient prey (Mondolfi and Hoogesteijn, 1986). This cat is found in a variety of habitats, including humid tropical and subtropical forests, dry and very dry semideciduous forests, tropical dry thorny forests, dense thorny scrublands, premontane dry, humid and very humid forest, savanna, wet/swampy savannas, and semiarid thron scrubs. The species show a preference for terrain neighbouring rivers, streams, backwaters, swamps, mangroves, lagoons and riverine forests (Cabrera and Yeppes, 1960). Even when jaguars use open areas they always seek cover in nearby dense vegetation (Modoolfi and Hoogesteijn, 1986). These predators show a close association to water (Crawshaw and Quigley, 1991). Because of the habitat limitation requirements, jaguar populations are more likely to be isolated in smaller areas of suitable habitat and thus are more vulnerable.

The feeding habits of this large carnivore are mainly nocturnal in this particular region. As well as the puma, the jaguar is an opportunistic predator (Rabinowitz & Nottingham, 1986) which includes in its diet a diversity of species (Table.1). Among those, cervids occupy an important role on the jaguar's diet (Table 2).

In terms of numbers, based on density estimates (derived from footprints) of one jaguar per 26-32 km^2 in Mexico's Calakmul Biosphere Reserve, Aranda (*1996*) estimated a population of 125-180 jaguars for the 4,000 km^2 reserve, and 465-550 jaguars in an adjoining 15,000 km^2 of wilderness area in Petén, northern Guatemala - which has since been protected as the Maya Biosphere Reserve.

Table 1. Showing the prey found in a scat survey for *Panthera Onca* and *Puma concolor* in RBC, Aranda and Sanchez Cordero (1996).

TAXON	JAGUAR	PUMA
Collared peccary		
Tayassu tajacu	21	2
Deer	4	10
Mazama americana*		
Odocoileus virginianus		
Coatimundi		
Nasua narica	9	4
Armadillo		
Dasypus novemcinctus	6	1
Paca		
Agouti paca	2	1
Opossum		
Dydelphis sp.	0	1
Northern anteater		
Tamandua mexicana	1	0
Great curassow		
Crax rubra	3	0
Ocellated turkey		
Agriocharis ocellata	0	1
Unidentified bird	2	0
Unidentified snake	1	0
Unidentified turtle	1	0

Table 2. Showing the percentage prey present in the scats of *Panthera Onca* in RBC, Aranda (1991).

PREY TYPE	%TOTAL PREY
Large rodents	4.2
Edentates	4.2
Ungulates	58.2
Other large mammals	25
Total mammals	91.6
Chelonians	4.2
Snakes/lizards	4.2
Total reptiles	8.4

2.3 Behavioural patterns of cervid species

The cervid species in Calakmul are represented by Red brocket deer *Mazama americana,* White-tailed deer *Odocoileus virginianus* and Great brocket deer *Mazama pandora*. *M. americana* is mainly found in lowlands up to 2800m. It is fairly common and widespread in forested areas but their physiology's do not allow them to move through very dense vegetation. They are solitary species but are occasionally seen in pairs. They combine diurnal and nocturnal activities but are mainly seen at dusk or during the night. *Odocoileus virginianus* is as well widespread and fairly common. Its habitat comprises deciduous forest and grasslands. The species is active by day and night, but is more often seen at dawn or dusk and at night when it ventures into fields and open areas to feed. These species of deer are seen singly or in small groups. Little information is available on the biology of *M. pandora,* as this species of deer has just been discovered in the Calakmul reserve in 1998.

3. Study site

The Mayan Jungle and the Calakmul Biosphere Reserve (RBC)

The Mayan Jungle consists of one million hectares of tropical forest situated in the Yucatan Peninsula, County of Campeche, southeast Mexico. The whole area is relatively flat, varying from 100 to 300 m of height. The physical and biotic characteristics of the region are described in detail elsewhere (Gómez Pompa and Dirzo, 1995). The tropical climate that this region possess is classified as hot and humid, characterized by a strong seasonality in rainfall and an annual mean temperature of 24.9 C (García and March, 1990, cited in Gómez Pompa and Dirzo, 1995). Rainfall is concentrated from June to November, followed by a pronounced dry season from December to May. Average annual precipitation varies from 1,000 to 1,500 mm. This distinct wet season combined with the flatness of the area usually results in inundation of most of the land area. This phenomenon seems to alter the behavioral patterns of species inhabiting this neotropical region.

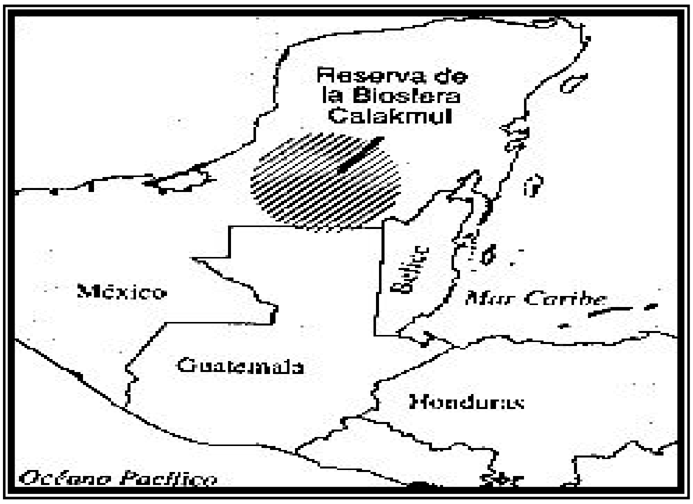


Figure 3. Showing the location of the Calakmul Biosphere Reserve (RBC), from Galindo-Leal (1999).

The Calakmul Biosphere Reserve (17º 09' to 19º 12'N and 89º 09' to 90º 08' W) is a fraction of this region and comprises 7231,85 ha. It is found in the Calakmul municipality in the state of Campeche, bordering Guatemala and Belize (Fig. 3). The reserve has two nucleus zones comprising approximately 248,000 ha and a buffer zone of 474,924 ha (Fig. 4). The Calakmul reserve is part of the most extensive remnants of tropical forests in Mexico and Central America. There are approximately 550 species of vertebrates and over 1600 species of vascular plants in the reserve; many of these species are considered at risk of extinction but are relatively well protected. There are large populations of many species considered endangered in

Mexico such as white-lipped peccaries (*Tayassu peccari*), tapir (*Tapirus bairdii*), ornate hawk (*Spizaetus ornatus*), and King vulture (*Sarcoramphus papa*).

Plant species composition has a high degree of heterogeneity associated with soil depth, soil type, and drainage. Major plant communities are rain forests, semideciduous forests, and dry forests (Gómez Pompa and Dirzo, 1995). These forests differ, among other structural characteristics, in tree height and deciduousness. Rain forests are found in 5% of the area of the reserve and dominated by trees like *Manilkara achras, Talisia olivaeformis, Brosimum alicastrum, Stemmadenia donell-smithi, Bursera simaruba,* and *Cedrela odorata*. Semideciduous forests are the dominant plant community and cover 50% of the reserve. Important plant species in this community are *Vitex gaumeri, Lonchocarpus* sp., *L. yucatanensis, Malmea depressa, Croton reflexifolius, Caesalpinia yucatanensis, C. violacea, Manilkara achras, Brosimum alicastrum, Lysiloma latisiliqua, Coccoloba cozumelensis, C. acapulcensis, Guettarda* spp., *Jatropha gaumeri, Bursera simaruba* and *Talisia olivaeformis*. Dry forests are characterized by the low height of trees (< 15 m) and because many plants shed their leaves in the dry season. Abundant tree species in this community are *Bucida bucera, Haematoxylum campechianum, Manilkara achras, Metopium browneii, Diospyros anisandra,* and *Cameraria latifolia.*

There are 52 towns in the vicinity of the reserve, with a total population of approximately 25,000 people. Major towns are Zoh-Laguna, Xpujil, Conhuas and Dzibalchén. There are no indigenous people in the reserve and vicinity. Most people are immigrants from states like Tabasco, Veracruz, Chiapas, and Michoacán. The reserve is sectioned in two by a Federal two-lane Highway (No. 186) and several dirt roads. The settlement of immigrants around and within the reserve (Fig. 4) and the particularity of area partition by "ejidos" (land is possessed by farmers and not by the government, even the reserve, which makes implementation of conservation law more difficult) are increasing conservation threats. Direct anthropogenic factors such as deforestation and development of natural systems for agriculture and other uses (Fig. 5) has the greatest impact to the species of this region, such as top predators like the jaguar and the puma. This development and losses of habitat consequently lead to habitat fragmentation, which can lead to alterations of suitable habitat and loss of potential space for these large carnivores. Population studies in this area suggest that numbers of jaguars, pumas and other species are decreasing rapidly due to the particular increase in human population (Fig. 6). In Mexico and Central America, Swank and Teer (1989) found that jaguar populations existed in only 33% of their former range and 75% of those populations were considered to exist in reduced numbers.

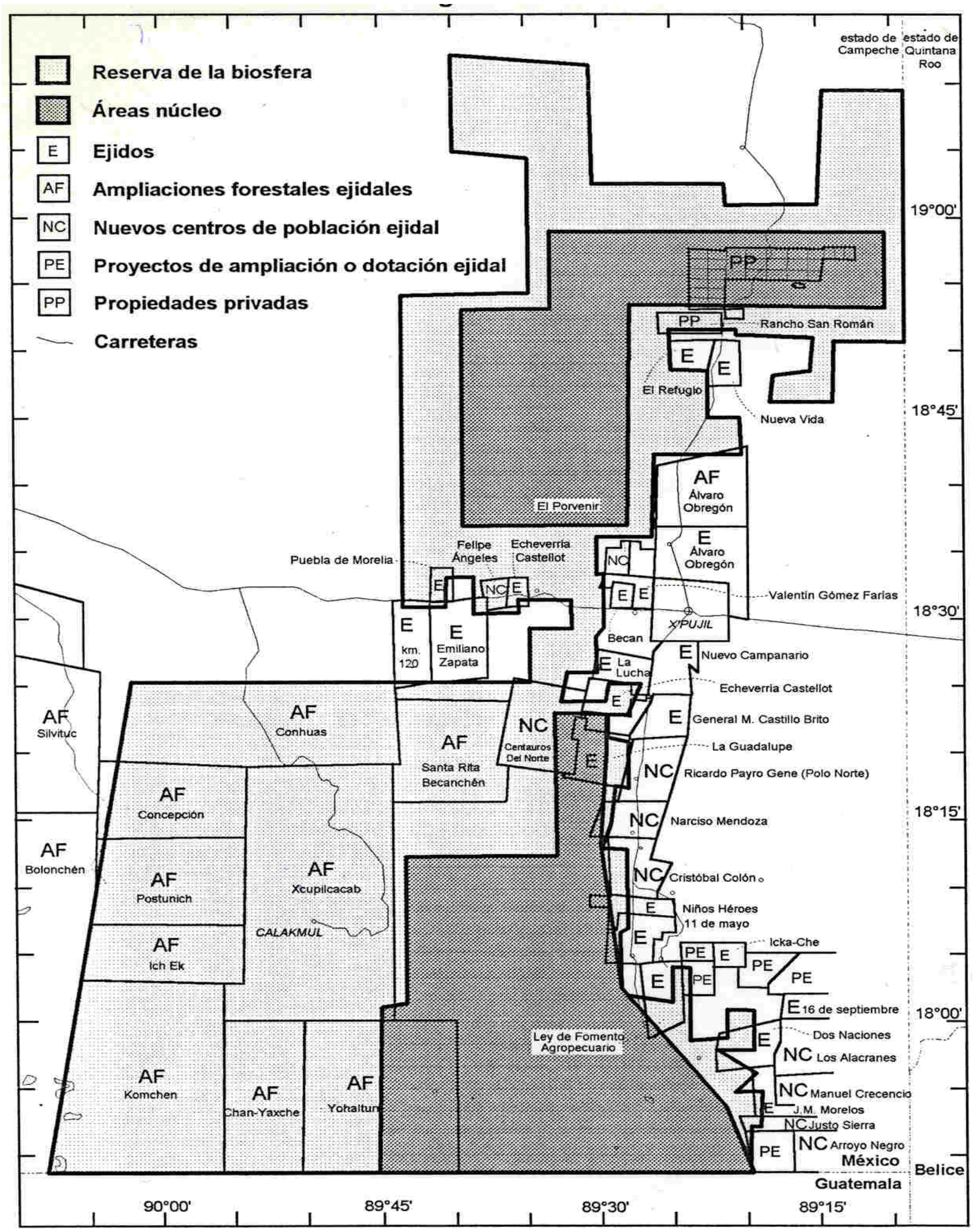


Figure 4. Showing the structure of the Reserve and the villages surrounding it.

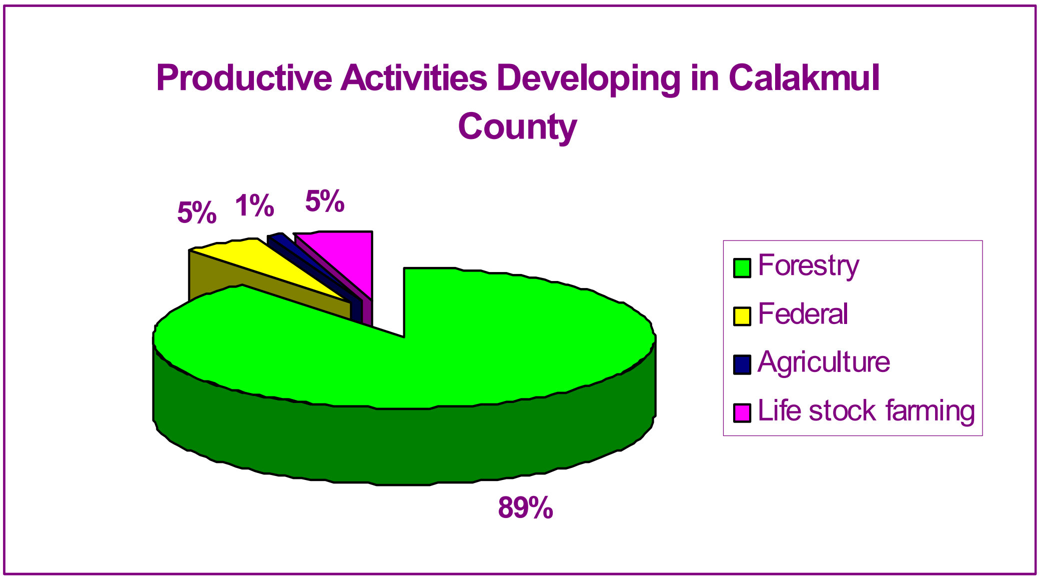


Figure 5. Productive activities in the county show the importance and significant percentage of forestry, the main factor responsible for habitat fragmentation. From Julia Carabias Lillo *et al*, 2000.

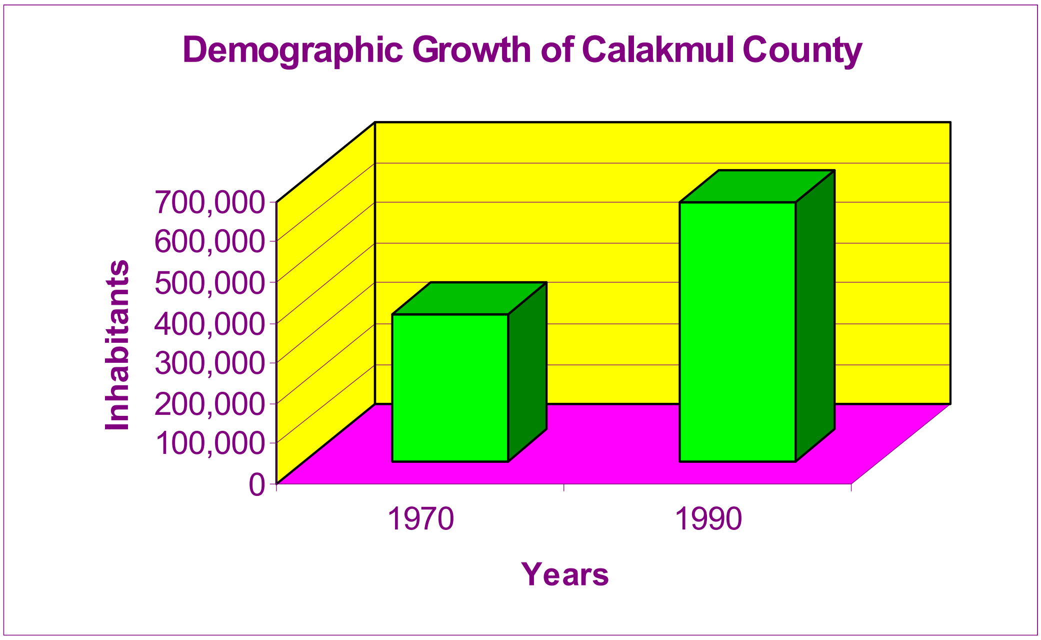


Figure 6. Showing the dramatic increase in a spatial time of 20 years, from Julia Carabias Lillo *et al*, 2000.

3.1 Vegetation structure

The whole area (i.e., including both study sites) is characterised by the same mosaic type of vegetation. The reserve is a big mixture of high canopy, medium canopy and low canopy cover where some significant patches of predominant type of canopy. However, the areas where the census was taken from, were similar in structure and composition.

Table 3. Number of registered taxa within type of vegetation RBC (Hernandez, 1992).

Vegetation type		Taxa	
	Family	Genus	Species
High canopy perennifolia or subperennifolia	61	121	145
Medium canopy subperennifolia	58	113	138
Low canopy subperennifolia	50	84	102
Aggregations of hidrofits	56	100	109

Table 4. Biologic forms on the different types of vegetation of RBC (Hernandez, 1992).

.

Vegetation type			Life	Forms		
	Trees	Scrub	Grasses	Epiphytes	Parasites	Bejucos
High canopy perennifolia or subperennifolia	42	15.8	11.7	10	2.8	115.8
Medium canopy subperennifolia	39.8	20	17	3.6	-	18.8
Low canopy subperennifolia	43	13.7	10.7	16.6	1	14
Aggregations of hydrofits	25.7	17.4	16.5	11	2.7	16.5

Table 5. Number of species per family in RBC (Hernandez, 1992).

Family	Spp No	Family	Spp No	Family	Spp No
Leguminosae	46	Orchidaceae	27	Rubiaceae	20
Compositae	16	Gramineae	14	Euphorbiaceae	13
Bignoniaceae	12	Sapindaceae	11	Bromeliaceae	11
Convolvulaceae	9	Paasifloraceae	9	Verbenaceae	9
Malpighiaceae	8	Moraceae	8	Tiliceae	8

3.2 Caobas Site (18º 15' N, 89º 03' W)

Our first study site is situated in the western part, outside the RBC in the State of Quintana Roo, south of the village of San José were human settlement, deforestation, agriculture, farming and hunting (either illegal and legal) occurs at a great scale (*see* appendix 2). This site comprises an area of approximately 60 km2 in the county of Caobas (Fig. 4). The main characteristics of this region, as many others surrounding the reserve is the high level of fragmentation and habitat loss which is still increasing. Competition for resources between humans and predator occur in two different forms. First, prey species are eliminated from the area by humans and secondly, livestock is taken by predators when the habitat quality is diminished in terms of prey availability.

3.3 Costa Maya Site (18º 14' N, 90º 37.5' W)

Our second study site is located in the southern part of the Calakmul Biosphere Reserve in the County of Campeche, west of the village of Narciso Mendoza (Fig. 4). It comprises an area of approximately 60 km^2 in a region named Costa Maya. This site is located in one of the core areas of the reserve, where the only human activity permitted is scientific research. Primary semideciduous forests that was impacted in past decades by gum collecting and some forestry covers the area. Illegal subsistence hunting is still relatively common in the areas closer to the Narciso Mendoza village.

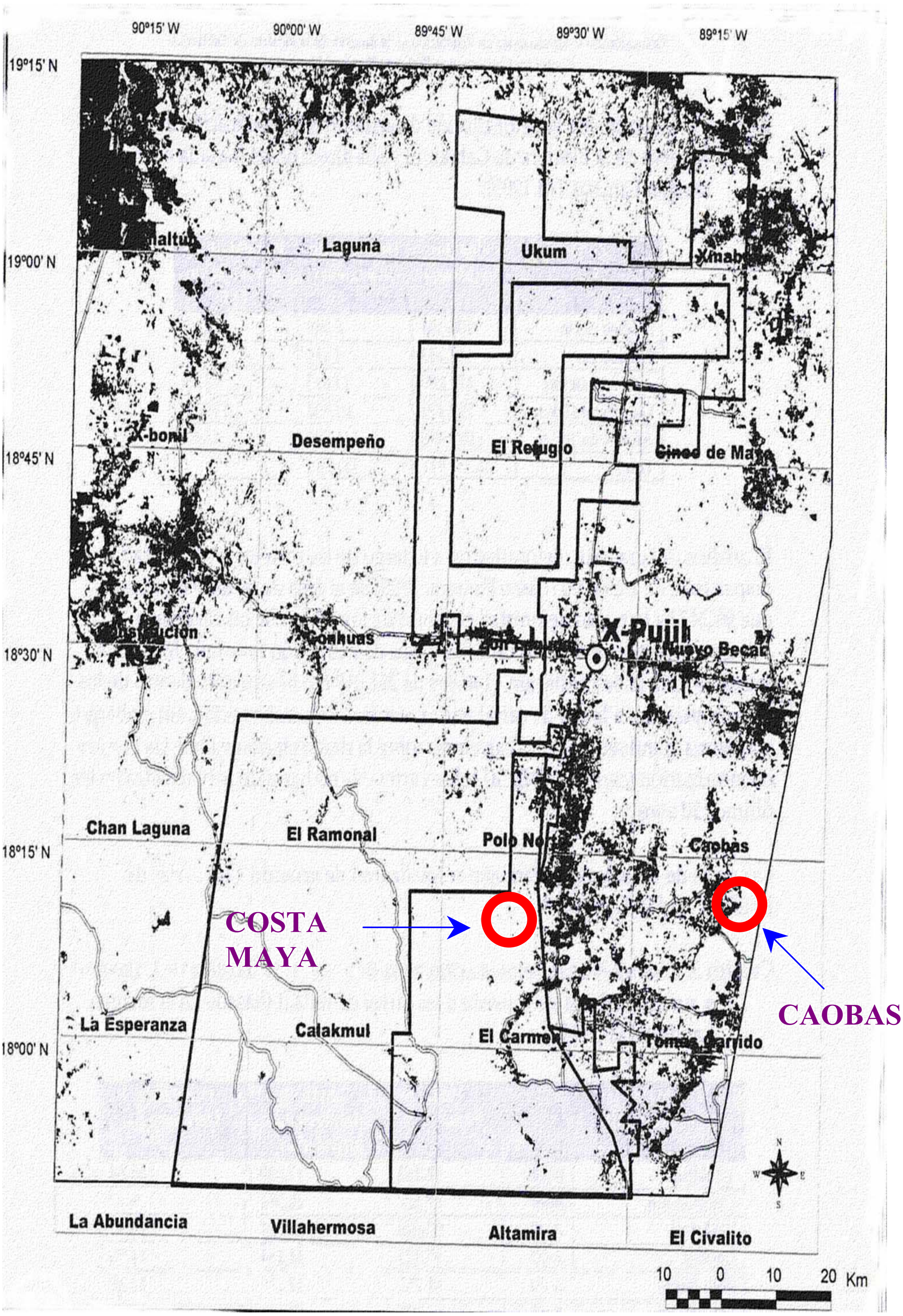


Figure 7. Deforestation map of the Mayan Jungle showing the exact locations of both study sites

4. Methodology

In ungulate-rich environments, calculating the numbers of appropriate-sized prey, given the carnivore assemblage present, might be a factor critical to accurately predicting potential carnivore density (Fuller, 1990). Nevertheless ungulate prey is easier to survey than are carnivores but it is expensive to get precise estimates, and methodologies can vary greatly. There are different methods of deer censuring (individual counts along transects, deer track counts, drive census, strip flushing census, Lincoln index, kill figures and infrared line scanning), different results being obtained depending on the methodology used (Downing *et al*, 1965; Fuller, 1990). We selected pellet count or dung density to achieve a relative abundance of deer presence in the sites. Studies of faecal pellet accumulation have been used successfully in the past to assess differential use of a variety of habitat types within a species population range (Collins and Urness, 1981). It is generally accepted that faecal pellet based methods of density evaluation can only give approximate deer densities for each area studied, rather than absolute population sizes. Any census method based on faecal accumulation requires a sampling method that is both reliable and representative of the area being censured.

The method is convenient for its being economical, time saving, effective and accurate. Where bush or woods are too thick to allow good visibility, pellet group counts may be the only feasible survey technique (Klinger *et all*, 1985). Due to the vegetation types of the area, we were obliged to use the pellet counting technique in order to calculate population densities in the sites.

Any census method based on fecal accumulation requires a sampling method that is both reliable and representative of the area being censured. Alteration of this methodology can be implemented to suit particular habitat types (Doney, 1991). Literature describes a number of different options (*see* Neff 1968). One important point is that increasing the amount of replication will increase the precision, so three replicates in each site were designed in both study sites, all with four sample units (transects). For the most efficient design, each route (transect) was surveyed only once. This method is inherently variable and requires a large sample size to obtain reasonable precision (Neff, 1968). Despite known limitations, pellet group counts remain the best method available for assessing relative deer numbers (Kirchhoff, 1990).

There are two assumptions in this method to take in consideration. The first one is that pellet groups are correctly identified and none are lost from the sampling plots (Eberhardt & Van Etten, 1956). The second one is that pellet group size and shape are suitable for a precise count. Groups of pellets with more than two and less that 26 days old were selected.

To be able to estimate the relative population density of deer from their pellets, it is necessary to establish the disappearance rate of the pellets and their quality in a study area. The faeces existence time may depend on many factors, both abiotic and biotic. The average time of pellet persistence on the forest floor vary but it is stipulated to be 26 days in summer or dry season (Aulak & Babinska-Werka, 1990). The disappearance rate is significantly affected by weather conditions: air temperature, amount of rainfall, number of rainy days, as well as the activity of coprophages. Due to the fact that the raining season was delayed during the study and not rain interfered with the disappearance of the pellets, we can accept this theory.

A pellet group was defined as one or more fecal pellets based on the similar size, shape, colour and position relative to other pellets. All pellet groups were counted if the estimated center of the group fell within 0.5 m of the rope used to measure. Only fresh pellets were counted. We identified pellets that were old by observational cues, e.g., hole marks from decomposition made by microorganisms living in the soil. The main reason for this is to minimize counting droppings from the same individual(s) more than once, leading to an overestimate of deer densities. .

4.1 Data Collection

From 12th of July to 5th of August deer pellets were counted and recorded on both sites, Caobas and Costa Maya, during the raining season. On each site a 60 km^2 area was divided in 15 squares of which three were chosen randomly. On each chosen square, four parallel transect lines were established equidistant (100 m) from one another and orientated Northwards with the help of a compass. Each transect was 800 m long (Fig. 8) and any pellet group —minimum two pellets present to be considered as a group— was recorded. The number of pellets within the groups was recorded as well for density population means. Three people were involved equally in the observation and counting in both study sites.

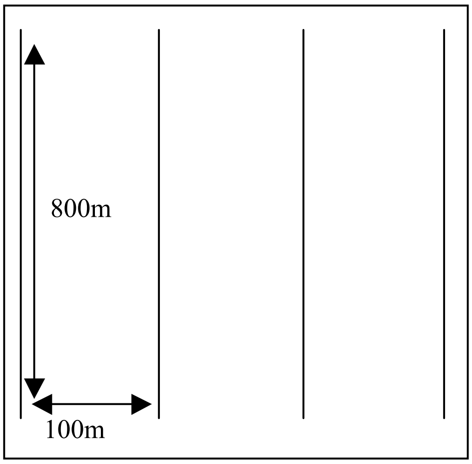


Figure 8. The methodology followed for pellet group counting; square-transects with a total number of four.

4.2 Environmental Variables

Temperature ranges did not vary significantly during the period of time of the study but weather was characterised by lack of rain. This phenomenon was unusual, as the study took place in the raining season.

Vegetation structure has been ignored in this study due to the similarities shared by the two study areas. In previous studies of deer in forested habitats, vegetation structure has not represented a significant factor to the preference of deer and therefore, altering the population density. Predation in the other hand, has shown statistically to be a limiting factor (Kirchhoff, 1990).

4.3 Something to consider

In the study site of Costa Maya, two of the random squares had 2 transects which were used in other survey activities (prey sighting). The path of these transects had been cleared of vegetation to facilitate the previous survey. The transects present were one meter wide, making the area more conspicuous to predators. This fact is likely to decrease the number of pellets found, as deer prefer to defecate in areas covered with vegetation canopy or sheltered by other means. We can therefore assume that more number of pellets would have been found if the transects were all made at the same time when the study took place.

4.4 Analysis

The sampling design, environmental conditions, variable pellet counts, and observer bias can affect the accuracy of pellet-group counts (*see* Neff 1968).

Frequency distributions of pellet groups have been described by the non-normal negative binomial distribution. In order to analyse deer pellet group data, using parametric statistics (e.g ANOVA and t-test) the data has to be transformed in order to obtain a normal distribution (Eberhardt & Van Etten, 1956):

$$Z = \log (x+1)$$

where x is the number of pellets per pellet group (*see* appendix 1).

5. Results

5.1 Comparison of relative population density of deer

A total of 98 pellet groups were sampled in July and August in 2001 in Caobas and Costa Maya. The number of recorded pellets in all three quadrats were added (Table 6 and 7). To determine whether deer relative abundance differentiates in both habitats, a t-test and 1-way analysis of variance (ANOVA) was applied. This analysis of variance is performed in the majority of deer pellet count studies (Green, 1979) where statistical significance is accepted at the 0.05 (95%). Analyses were performed on transformed data as recommended for negative binomial distributions (Anscombe, 1948). The results indicated a difference between the two study sites (t-test: P= 0.021; ANOVA: P= 0.014). Pellet group densities varied significantly on samples from both sites (Fig. 9). Deer relative abundance ranged from virtually none (zero-pellet groups found in 6 transects in Caobas) to very high (over pellet groups found in transects in Costa Maya). The results show that Costa Maya has the greatest number of pellet groups, where presence of cervids can be understood to be higher.

5.2 Extrapolating the results

If the results found in the samples used in this study can be extrapolated to the Reserve and even to the whole geographical area of the Mayan Jungle, fragmentation effect and habitat degradation are affecting negatively the population density of cervids as observed in Caobas. We could also assume that other species living in the same area are affected as well. The same will happen to any areas within the rainforest with similar characteristics as Caobas (in terms of human activities), where habitat fragmentation and degradation may be increasing.

Table 6. Showing the pellets found in the three replicates in Caobas site.

Caobas						
	Raw data			Transformed data Z=log(x+1)		
	Square 1	Square 2	Square 3	Square 1	Square 2	Square 3
Transect a	0	17	0	0.000	1.255	0.000
Transect b	0	39	0	0.000	1.602	0.000
Transect c	20	0	8	1.322	0.000	0.954
Transect d	3	0	43	0.602	0.000	1.643
Sum	23	56	51	1.924	2.857	2.598
Mean	5.75	14	12.75	0.481	0.714	0.649

Table 7. Showing the pellets found in the three replicates in Costa Maya site.

Costa Maya						
	Raw data			Transformed data Z=log(x+1)		
	Square 1	Square 2	Square 3	Square 1	Square 2	Square 3
Transect a	0	3	0	0.000	0.602	0.000
Transect b	10	478	400	1.041	2.680	2.603
Transect c	130	326	251	2.117	2.515	2.401
Transect d	6	87	22	0.845	1.944	1.362
Sum	146	894	673	4.004	7.741	6.366
Mean	36.5	223.5	168.25	1.001	1.935	1.592

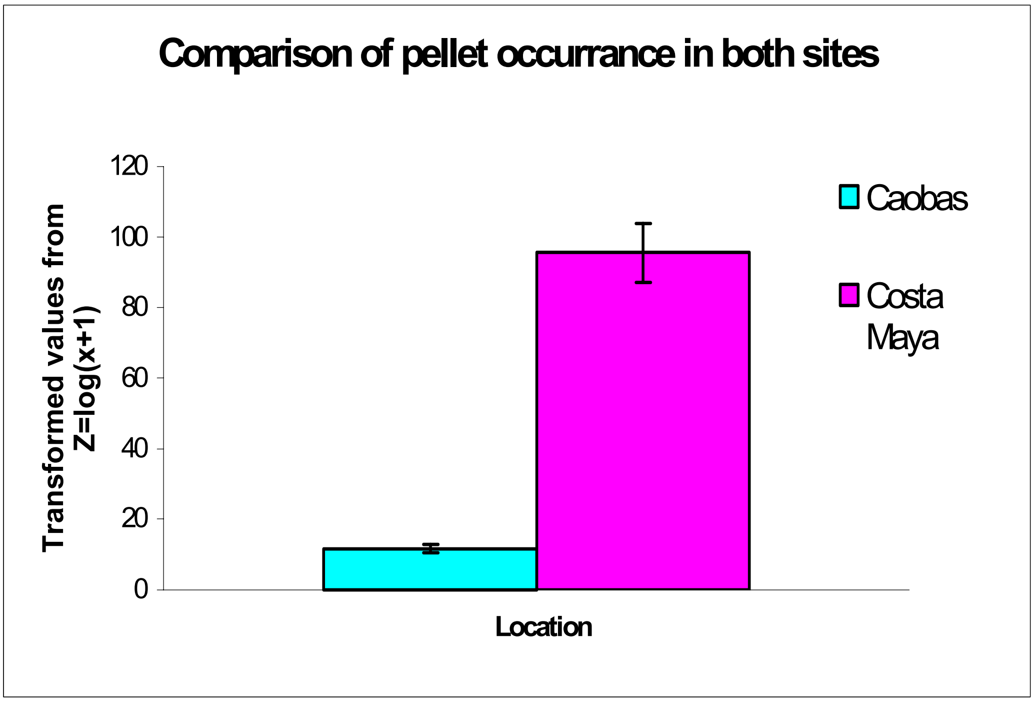


Figure 9. Showing the difference on pellet occurrence in both sites on transformed data. The higher number of pellets is found in Costa Maya site as expected by its location inside the reserve.

6. Discussion

6.1 Fragmentation effect, habitat degradation and carnivore populations

Many mammalian carnivores, especially the large ones, possess characteristics that make them particularly vulnerable to landscape changes. As predators, carnivores tend to live at relatively low densities, occupy large home ranges, are long lived, have low reproductive output and often disperse long distances as juveniles or sub-adults. However, all species do not respond in the same way to landscape changes. Habitat loss for some may be a gain for others: by increasing the amount of edge by fragmentation, it may degrade the quality of the remaining habitat for interior species and at the same time improve foraging conditions for generalist carnivores.

A variety of activities such as logging, livestock grazing, firewood collection and hunting and trapping of prey species which gradually degrades landscapes is a largely unmeasured phenomenon affecting carnivore populations because declines in habitat quality are associated with increases in home-range size, decreases in density and increases in energy expenditure associated with rearing young (Gittleman & Harvey, 1982).

The effects of fragmentation are subtler than those related to outright loss or habitat degradation (Table 8). It can rapidly increase isolation of the remaining smaller patches, but it also introduces a suite of other potential problems. At the individual level these changes may limit movement between habitat fragments, alters home range boundaries, modify habitat selection patterns, limit social interactions and increase predation rates. Because more productive habitats have been eliminated, many species are being forced into habitats of lower quality where survival probabilities are reduced. As more suitable habitat is lost population declines may exceed predictions because of the combined effects of isolation and loss of area. The consequences will depend on the size of the population, the amount of genetic variation contained within the population, the length of the isolation, the type of social system, the size of the area and quality of the habitat and other environmental variables.

IMPACT	SPECIES	
	Puma	Jaguar
Deforestation	HNI	HNI
Timber extraction	ML/NI	ML/NI
Dam construction	ML/NI	ML/NI
Mineral exploitation	ML/NI	ML/NI
Habitat alteration	ML/NI	HNI
Poaching (trade)	o	HNI
Predator control for livestock*	HNI	HNI
Human encroachment	HNI	HNI
* includes cattle, sheep and chicken		

HNI= High negative impact
ML/NI= Moderate/low negative impact

Table 8. Showing the impact of human activities to pumas and jaguars in the neotropics. From Oliviera (1994).

The same changes which may also isolate populations by reducing habitat connectivity, can lower dispersal success, alter reproductive and survival probabilities, increase the likelihood of inbreeding and result in local extinction or population declines. Small isolated populations are particularly vulnerable since they have a high probability of extinction due to demographic and environmental stochasticity (Fahrig, 1997). In addition to that, fragmentation can affect the dispersal ability of the animal creating a variety of scenarios. The appearance of young male jaguars (Heptner & Sludskii, 1992) and pumas (Beier, 1995) at locations many kilometers from the nearest known population confirms their dispersal abilities. More specifically, the jaguar is the most likely to be directly affected by habitat degradation *per se*, because of its dependency on canopy cover.

6.2 Prey depletion

The potential densities that populations of carnivores reach are more generally understood to be a reflection of resource abundance. Short and long term changes in prey abundance and availability, as well as geographic variation in food resources, are the major natural forces that influence the population viability of any carnivore in all demographic stages (e.g. breeder, transient juvenile, cub). With the smaller number of prey available per puma or jaguar a higher intra-specific and inter-specific competition is expected.

The effect of prey depletion can be seen in studies of tigers where the carrying capacity for breeding females was reduced, as well as the cub survival and the population size. There are other studies, which confirm this theory such as

Seindernsticker *et al*, (1973) who proposed that the density of the breeding population of mountain lions (*Puma concolor*) was set by a vegetation topography/prey number-vulnerability complex phenomenon. Across a wide range of species, data indicate that carnivore densities are positively correlated with prey density. Snow leopard (*Panthera uncia*) densities may be highest where blue sheep (*Pseudois nayaur*) densities are highest (Oli, 1994). A more quantitative comparison of lion (*Panthera leo*) densities in two areas indicated higher numbers where year-round prey were more numerous (Hanby *et al*, 1995). These results strongly support the idea that food resources determine a large component of carnivore density. Therefore, we can consider food/prey availability to be a limiting factor that can be investigated comparatively and experimentally (Lack, 1954).

The consequences of the density-dependant relationship of food availability and population density in carnivores are changes in reproductive output: demographic parameters are likely to increase with its consequent increase in food and decrease with its consequent decrease in food availability. In addition to direct demographic changes in carnivore populations when prey availability changes, indirect changes in behaviour also occur that contribute to observed changes in carnivore densities. One of the most common behavioural changes is in the size of carnivore home ranges or territories. For example, individual pack territory size of gray wolf was negatively correlated with white-tailed deer (*Odocoileus virginianus*) density in Wisconsin (Wydeven *et al*, 1995). Another behavioural consequence of change in prey availability is an increase in the number of transient and dispersing individuals in a population. These transients and dispersers have lower reproductive output and often also have higher mortality rates.

The populations of jaguar and more specifically pumas inhabiting the fragmented study site of Caobas are under the risks mentioned above. If the situation of the site deteriorates further the consequences could be irreversible.

6.3 Human and predators competition

The feeding habits of pumas and jaguars suggest the possibility of competition with humans. The idea of competition becomes more realistic when one analyses the data on subsistence hunting of Indians and colonists in several areas of the neotropics (Fig 10). It is apparent form the diet content tables showed above and Fig. 10 that pumas and jaguars prefer the same species favored by humans. This suggests that humans can be competing with these two predators in areas of subsistence hunting, which in turn, would put additional pressure on these large cats in the areas of impact. The characteristic feeding habits of jaguars show greater pressure than pumas but both animals food habits overlap virtually completely with those of subsistence hunters (Jorgenson and Redford, 1993) which can lead to a population decline for both predators.

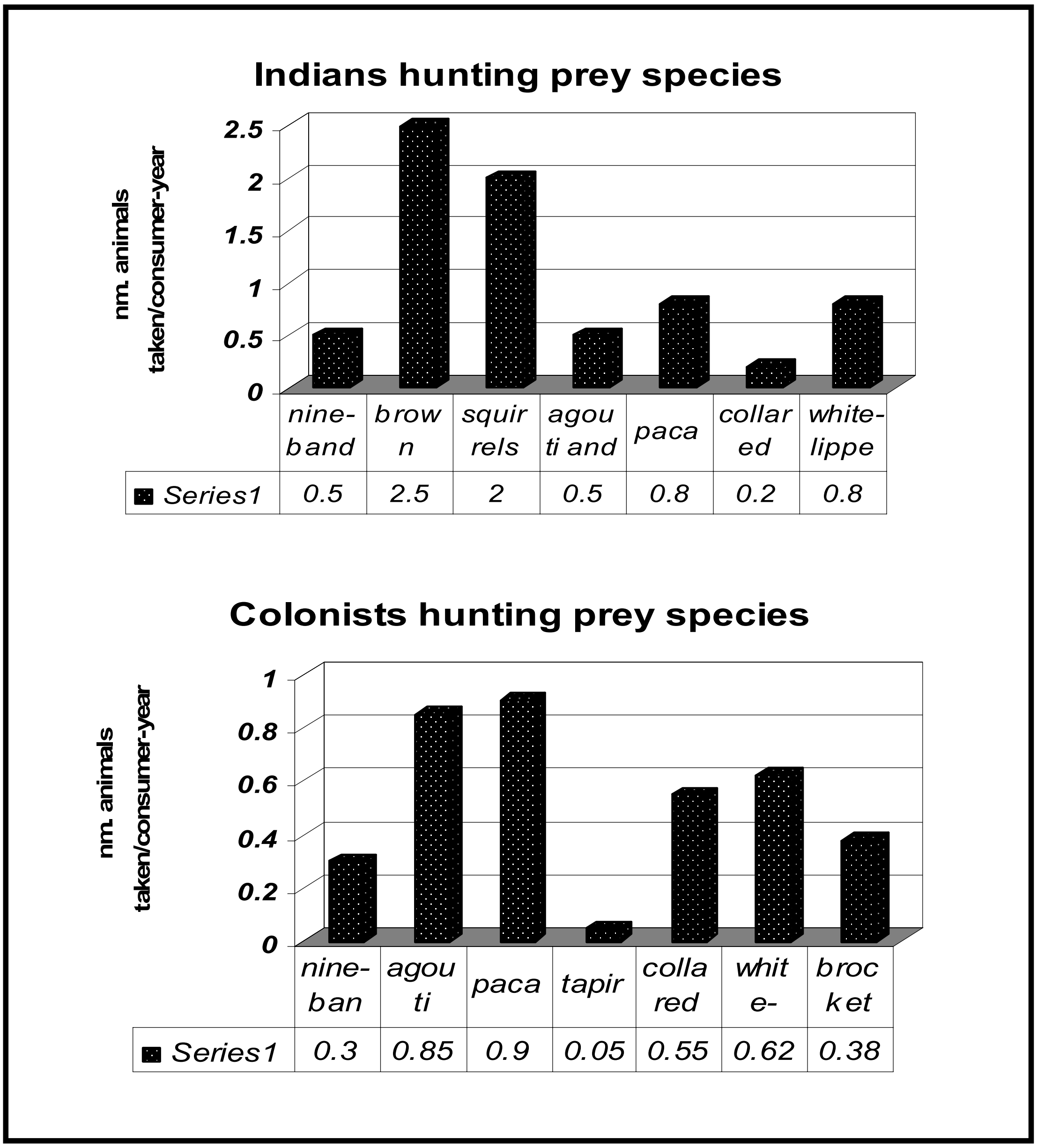


Figure 10. Harvest rate of the seven most relevant items in the diet of Indians and Colonists. The rate is expressed in terms of number of animals taken per consumer a year. Data taken form Redford and Robinson, 1987.

6.4 Socially-induced depression

A substantial part of the population of pumas and jaguars will not breed as a consequence of prey depletion. This can be seen as animals that die; or because they attempt to breed but they and/or their young all die; or because they are inhibited from breeding even though they survive but may breed in later years. Nevertheless, such non-breeders are physiologically capable of breeding if the more dominant or territorial (i.e. breeding individual) animals are removed. The consequences of individual dispersion to a secondary, less favorable habitat can worsen this situation dramatically as transients and dispersers have less reproductive success and are more vulnerable to death. This could be occurring in Caobas: even if the puma and jaguar populations were found to be satisfatorily high at the moment, this would be no guarantee that survival and reproductive success were optimal and that the population would not decline.

7. Conclusion

The empirical foundation for evaluating the effects of habitat change on carnivores is weak because of the problems involved on the study of such as small sample size, low densities, long generation time, or nocturnal habits. The practical approach can be achieved if the effect of the habitat change is observed on their main prey rather than the carnivore itself as seen in this study. The statistical confidence of many food and density-related demographic parameters often is wide, and additional important factors can influence carnivore density on a site-specific basis, or even at a species level. Thus, it is also important to understand the factors that confound the relationship between prey biomass and carnivore numbers. A comprehensive study of relations between predators and prey and the consequences of prey depletion to the populations of predators such as pumas and jaguars will have to include years of observations. It is clear, therefore that any conclusions reached in the present study can only be very tentative; nevertheless, it seems useful to consider some of the implications involved.

How carnivores respond to changing landscapes obviously depends on the timing and scale of alterations and the species inherent ability to adapt. Because hypercarnivores (strictly meat eaters) are sensitive to the distribution and abundance of prey any changes in these parameters —natural or anthropogenic— will potentially reduce carnivore populations via energetic constraints and alter spatial patterns. Predictions that the loss of key species like the jaguar could lead to a chain reaction causing the extinction of other taxa (faunal collapse) are severer in the tropics. For this reason, it is advisable to keep top predators, such as *Panthera onca* and *Puma concolor* as a vital part of the ecosystem in any conservation issues.

The difference in deer density between the Caobas and Costa Maya may be due to the fact that Caobas is an area with a high level of fragmentation and human disturbance while Costa Maya is an area within the reserve, benefiting from legal protection and an insignificant level of human disturbance. The individuals of pumas and jaguars present in Caobas are therefore more likely to be at risk than those in Costa Maya. aggravated by human-predator competition (Fig. 9) and the possible encounter with livestock, which often results in death for the predatory species by the farmers.

7.1 Solutions

To remedy the anthropogenic impact on these two species in the Mayan Jungle, the following conservation measures are suggested:

- To minimized impacts of competition between pumas and jaguars with humans
- To preserve protected habitats of sufficient size and productivity to support viable population sizes
- To establish the distribution of each species and the habitat available to its needs
- To implement legislation to protect the species and their prey that ensures long term conservation
- To reconcile conservation of pumas and jaguars with humans through the design of land use patterns compatible to both
- To create conservation education programs in all levels of the community in the role and importance of both predators, to show that protection is in their best interest
- To establish captive breeding programs as a precaution for future reintroductions (already taking place — Ada is the first female jaguar to be involved in a reintroduction program in Mexico)
- To include all these measures in an overall conservation strategy (Seal *et al,* 1987).

A proper program for jaguar or puma conservation has to be based in regional programs of ecological kind, which include the existence of large protected areas. Both predators can inhabit areas with a certain level of perturbation if canopy cover and natural prey are present and protected. Human activity in these areas can be minimised if selective deforestation, reduction of chewing gum extraction, harvesting on palm leaves and hunting on carnivore's prey is diminished. A major problem found in this area is the killing of farm animals by either jaguar or puma, situation that can be resolved if a management program for existent livestock is implemented. The management can include the supervision of livestock, increased security in dens and if necessary, the translocation of problematic predators to less fragmented regions. This measure has already taken place in Caobas site successfully.

Our findings suggest that the conventional model of nature reserves —discrete and isolated entities in a human dominated landscape— does not apply well to large carnivores due to the enormous home range needed for these species. In order to implement new conservation plans, an expansion of protected area within the reserve is needed to allow for viable populations of pumas or jaguars.

The structure of the Biosphere Reserve of Calakmul needs to be taken into account within the context of these conservation plans. The narrow natural corridor connecting the two almost isolated halves of the reserve has to be enlarged to improve population connectivity. At the same time, the disturbance around the edges of the Reserve has to be minimized either by expanding the protected territory or by allowing connectivity between habitat patches (Galindo-Leal, 1999). In this way, the existent status of the local jaguar and puma populations should improve. For thousands of years, the Mayan people inhabiting these forests worshipped both predators for their strength, a lesson of respect we could take into account when thinking of their present condition and uncertain future.

8. Acknowledgments

I thank Gerardo Ceballos and Cuauhtemoc Chavez, part of the team in the Ecological Institute of Mexico City —Universidad Nacional Autonoma de Mexico (UNAM)— for making this study possible and for helping me to cope in the true adventure in the rainforest of Calakmul. Also I am extremely grateful to Phil Shaw at UeL and Filippo Campagna for their supervision and amazing knowledge which contributed to this final report. Finally I would like to thank anyone who contributes to the conservation of carnivores in the neotropics and the animals themselves. The UNAM in Mexico City and "Unidos por la Conservacion" founded this project.

I dedicate this study to my father Jose Sanchez, who taught me and showed me the beauty, purity and magic of nature.

References

Ackerman, B. B., Lindzey, F. G., Hemker, T. P. (1986) *Predictive energetic model for cougars*, 333-352 *in* Miller, S. D., Everett, D. D. (eds.) *Cats of the world: biology, conservation and management,* National Wildlife Federation, Washington D.C.

Anscombe, F. J. (1948) The transformation of poisson binomial and negative binomial data, *Biometrika* **35**: 246-254

Aranda, M (1993) *Feeding habits of the jaguar in the Calakmul Biosphere Reserve, Campeche*, Asociacion Mexicana de Mastozologia Publicaciones, Mexico.

Aranda, M. (1996*)* Distribution and Abundance of *Panthera onca* in the state of Chiapas, Mexico, *Acta Zoologica Mexicana* **68**: 45-52.

Aranda, M. (1998) Densidad y estructura de una poblacion del jaguar (*Panthera onca*) en la Reserva de la Biosfera de Calakmul, Campeche, México*, Acta Zoológica Mexicana* **75**: 199-201.

Aranda, M., Sanchez Cordero, V. (1996) Prey Spectra of Jaguar (*Panthera onca*) and Puma (*Puma concolor*) in Tropical Forests of Mexico*, Study of Neotropical Fauna and the environment* **31** 65-67.

Aulak, W., Babinska-Werka, J. (1990) Estimation of roe deer density based on the abundance and rate of disappearance of their faeces from the forest*, Acta Theriologica* **35** (1-2): 111-120

Beier, P. (1995) Dispersal of juvenile cougars in fragmented habitat, *Journal of Wildlife Management* **59**: 228-237

Berger, J., Wehausen, J. D. (1991) Consequences of a mammalian predator-prey disequilibrium in the Great Basin Desert, *Conservation Biology* 5(**2**): 244-248

Cabrera, A., Yeppes, J. (1960*) Mamiferos Sud Americanos: vida, costumbres y descripcion*, Historial Natural Ediar, Compania Argentina de Editores, Argentina.

Carabias-Lillo, J., Provencio, E., De la Maza, E. De la Gala-Mendez, J. B. R. (2000*) Programa de manejo de la Reserva de la Biosfera Calakmul*, Instituto Nacional de Ecologia & SEMARNAP, Mexico

Ceballos, G. (1999) *Population size and conservation of jaguars (Pantera onca) in the Calakmul Biosphere Reserve, Campeche, Mexico,* Instituto de Ecologia, Mexico.

Collins W. B., Urness P. G., (1981) Habitat preferences of Mule Deer as rated by pellet group distributions, *Journal of Wildlife Management* 45, 4.

Crawshaw, P. G., Quigley, H. B. (1991) Jaguar spacing, activity and habitat use in a seasonal hooded environment in Brazil, *Journal o Zoology* **223**: 357-370.

Doney, J. (1991) A comparison of four methods of assessing dung density, *Deer* **10**(9): 558-560

Downing, R. L., More, W. H, Kight, J. (1965) Comparison of deer census techniques applied to a known population in a Georgia enclosure, Procedure Annual Conference Southeast, *Association of Game and Fish Community* **19**: 26-30

Eberhardt, L. L., Van Etten, R. C. (1956) Evaluation of the pellet group count as a deer census method, *Journal of Wildlife Management* **20**: 70-74

Edmonds, G. (1981*) Guidelines for national implementation of the conservation on international trade in endangered species of wild fauna and flora,* International Union for the Conservation of Nature and Natural Resources, Environmental Policy and law Paper No 17.

Emmons, L. H. (1987) Comparative feeding ecology of felids in a neotropical rainforest, *Behavioural Ecology Sociobiology* **20**: 271-273.

Escamilla, A. (1998) Habitat Mosaic, Wildlife Availability, and hunting in the tropical forest of Calakmul, Mexico, *Conservation Biology* **11**: 1592-1601.

Fahrig, L. (1997) Relative effects of habitat loss and fragmentation on population extinction, *Journal of Wildlife Management* **61**: 603-10

Ferreras, P. (2001) Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian Lynx (*Felis lynx pardinus*), *Biological Conservation* **100**: 125-136.

Fuller, K. S., Swift, B. (1985) *Latin American Wildlife Trade Laws* (2nd ed.) TRAFFIC (U.S.A) World Wildlife Found, Washington, D.C.

Fuller, T. K. (1990) Dynamics of a declining population of white-tailed deer population in north central Minnesota, *Wildlife Monographs* **110**: 1-39

Galindo-Leal (1999) *La gran region de Calakmul, Campeche: Prioridades biologicas de conservacion y propuesta de modifiacion de la Reserva de la Biosfera* (Borrador-Sintesis), Center for Conservation Biology, Stanford University & WWF, Mexico.

Gitlleman, J. L., Funk, S. M., Macdonald, D., Wayne, R. K. (2001) *Carnivore Conservation*, Cambridge University Press, UK.

Gittleman, J. L., Harvey, P. H. (1982) Carnivore home range size, metabolic needs and ecology, *Behavioural Ecology & Sociobiology* **10**: 57-63

Gomez-Pompa, A., Dirzo, R. (1995) *Areas naturales protegidas de México,* SEMARNAP, México D.F.

Green, R. H. (1979) *Sampling design and statistical methods for environmental biologists*, John Wiley & Sons, New York.

Hanby, J. P., Bygott, J. D., Packer, C. (1995) *Ecology, demography and behaviour in lions in two contrasting habitats: Ngorongoro Crater and the Serengeti plains*, University of Chicago Press, Chicago.

Hernandez, C. I. (1992) *Los factores ecologicos de la vegetacion del estado de Campeche*, C.N.A, Gerencia Regional del Sureste, Subgerencia de Estudios, Campeche, Mexico.

Heptner, V. G., Sludskii, A. A. (1992) *Mammals of the Soviet Union*, Vol II Carnivora (hyenas and cats), Smithsonian Institution Libraries and The National Science Foundation, Washington DC.

Iriarte, J. A., Franklin, W. L., Johnson, W. E., Redford, K. H. (1990) Biogeographic variation of food habits and body size of the American puma, *Oecologia* **85**: 185-190.

IUCN (1982a) *The UICN Red Data Book,* International Union for the Conservation of Nature and Natural Resources, Gland.

Jorgenson, J. P., Redford, K. H. (in press) *Humans and big cats as predators in the Neotropics,* Symposium Zoological Society, London

Kirchhoff, M. D. (1990) *Effects on forest fragmentation on deer in Southeast Alaska*, Alaska Department of Fish and Game Division of Wildlife Conservation Research Progress Report, Alaska.

Klinger, R. C., Kutilek, M. J., Shellhammer, H. S (1985) A comparison of deer survey techniques, *Ungulates* **91**: 487-491

Lack, D. (1954) *The natural regulation of animal numbers*, Oxford University Press, London.

Laing, S. P. (1988) *Cougar habitat selection and spatial use patterns in southern Utah,* M.S. thesis, University of Wyoming, USA.

Laurance, W. F., Bierregaard, R. O. (1997) *Tropical forest remnants: Ecology, management and conservation of fragmented communities*, University of Chicago Press, Chicago

Lawton, J. H., (1997) The science and no-science of conservation biology, *Oikos* **79**: 3-5

Lindzey, F. (1987) *Mountain lion* 656-668 *in* Novak, M., Baker, J., Obbard, M., Malloch, B. (eds.) *Wild furbearer management and conservation in North America,* Ministry of Natural Resources, Toronto.

Logan, K. A., Irwin, L. L. (1985) *Mountain lion habitats in the Big Horn Mountains, Wyoming,* Wildlife Society Bulleting **13**: 257-262.

Medellin, R., Ceballos, G. (1993*) Avance en el estudio de los mamiferos de Mexico*, Asociacion Mexicana de Mastozologia, Mexico.

Mondolfi, E., Hoogesteijn, R. (1986) *Notes on the biology and status of the jaguar in Venezuela*, 85-123 *in* Miller, S. D., Everet,D. D., eds. *Cats of the World: biology, conservation and management*, Natural Wildlife Federation, Washington, DC.

Neff, D., J., (1968) The Pellet group count technique for big game trend, census, and distribution: a review, *Journal of wildlife*, **32**: 597-614.

Nowell, K., Jackson, P (1996) *Wild cats: status survey and conservation Action Plan*, IUCN, Gland: IUNC

Oli, M. K. (1994) Snow lepards and blue sheep in Nepal: densities and predator: prey ratio*, Journal of Mammalogy* **75**: 998-1004

Oliveira, T. G. (1993) *Neotropical cats: Ecolgy and Conservation,* Universidade Federal do Maranhao, Brazil.

Rabinowitz, A. R., Nottingham, B. G (1986) Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America, *Journal of Zoology* **210**: 149-159

Reid, F. A. (1997) *A field guide to the mammals of Central America and Southeast Mexico*, Oxford University Press, Oxford.

Redford, K. H., Eisenberg, J. F. (1992) *Mammals of the Neotropics*, Vol. 2: The southern cone, University of Chicago Press, USA.

Redford, K. H., Robinson, J. G. (1987) The game of choice: patterns of Indians ans colonists hunting in the Neotropics, *Am. Anthropological* **89**: 650-667

Schimid-Holmes, S., Drickamer, L. C. (2001) Impact of forest patch characteristics on small mammal communities: a multivariate approach, *Biological Conservation* **99**: 293-305.

Seal, U. S., Jackson, P., Tilson, R. L. (1987) *A global tiger conservation plan* 487-489 *in* Tilson, R. L., Seal, U. S. (eds) *Tigers of the world: the biology, biopolitics, management and conservation of an endangered species*, Noyes Publications, Park Ridge, NJ.

Seidensticker, J. (1991b) *Pumas* 130-137 *in* Seidensticker, J., Lumpkin, S. (eds.) *Great cats,* Merehurst, London.

Seindernsticker, J. C., Hornocker, M. G., Wiles, W. V., Messick, J. P. (1973) Mountain lion social organisation in the Idaho primitive Area, *Wildlife Monographs* **35**: 1-60

Swank, W. G., Teer, J. G. (1989) Status of the Jaguar, *Oryx* **23**: 14-21.

Terbourgh, J. (1990*)* The role of felid predators in neotropical forest*, Vida Silvestre Neotropical* **2**: 3-5.

Terbourgh, J. (1992) Maintenance of diversity in tropical forests, *Biotropical* **24**: 283-292.

Tischendorf, J. W., Henderson, F. R. (1993) *The puma in the central mountains and plains*, Wildlife Society Meetings, USA.

Wendell, G., Teer, J. G. (1987) *Status of the Jaguar; a report to The National fish and Wildlife Foundation,* The World Conservation Union, Washington D. C.

Wright, B. S. (1959) *The ghost of North America: the story of the eastern panther,* Vantage, New York.

Wydeven, A. P., Schultz, R. N., Thiel, R. P. (1995) *Monitoring of a recovering gray wolf population in Wisconsin, Ecology and Conservation of Wolves in a Changing World*, Canadian Circumpolar Institute, Alberta, Canada.

APPENDIX

Appendix 1

Figure 11. Showing the distribution of raw data previous to transformation.

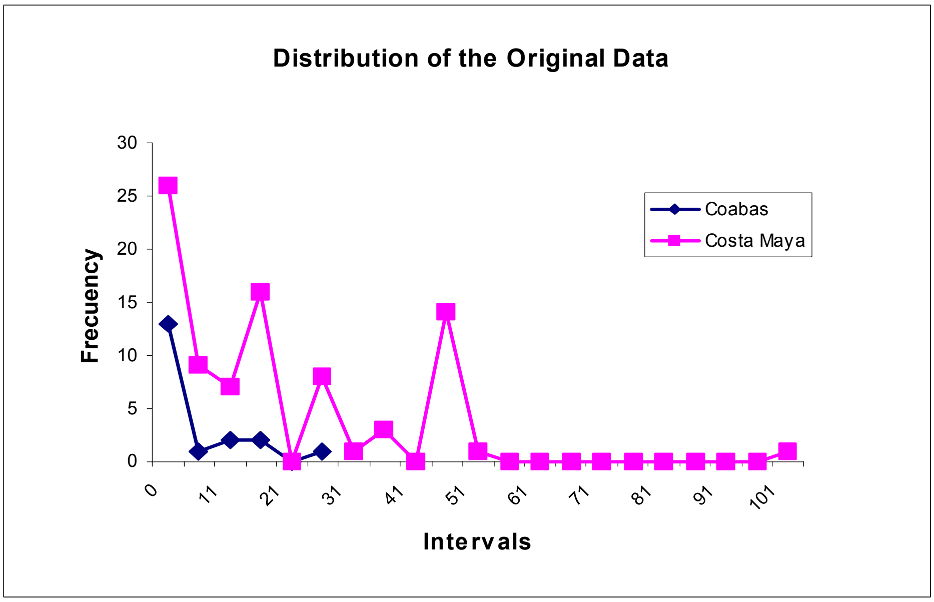
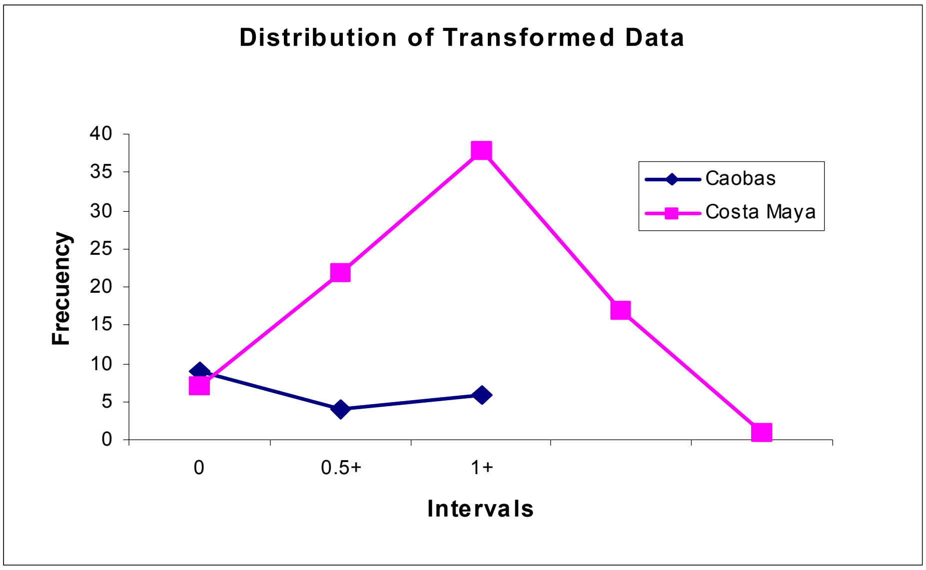


Figure 12. Showing the negative binomial distribution (raw data) transformed to a normal distribution.



Appendix 2

Data analysis results

F-Test Two-Sample for Variances

	Caobas	*Costa Maya*
Mean	0.967	7.955
Variance	1.597	70.919
Observations	12	12
Df	11	11
F	0.023	
P(F<=f) one-tail	1.7E-07	
F Critical one-tail	0.355	

t-Test: Two-Sample Assuming Unequal Variances

	Caobas	*Costa Maya*
Mean	0.967	7.955
Variance	1.597	70.919
Observations	12	12
Hypothesised Mean Difference	0	
Df	11	
t Stat	-2.843	
P(T<=t) one-tail	0.008	
t Critical one-tail	1.796	
P(T<=t) two-tail	0.016	
t Critical two-tail	2.201	

ANOVA: Single Factor

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	12.000	9.450	0.787	1.507
Column 2	12.000	93.177	7.765	79.909

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	292.095	1.000	292.095	7.175	0.014	4.301
Within Groups	895.568	22.000	40.708			
Total	1187.663	23.000				

Plate 1. Showing the fragmented landscape of Caobas County due to deforestation. Photo by the author

Plate 2. Showing Caobas Village within the County. This fragmented landscape is due to human settlement. Photo by the author.

Plate 3. Showing the effect of agriculture (mainly maize) on the landscape of Caobas. Photo by the author.

Appendix 4

Raw data:

DATE	LOCATION	TRANSECT	DISTANCE	NUMBER OF PELLETS
17/07/2001	Caobas	C3-1a		0
17/07/2001	Caobas	C3-2a		0
18/07/2001	Caobas	C3-3a	400m	20
18/07/2001	Caobas	C3-4a	350m	3
18/07/2001	Caobas	C5-1a	635m	15
18/07/2001	Caobas	C5-1a	700m	2
18/07/2001	Caobas	C5-2a	450m	20
18/07/2001	Caobas	C5-2a	620m	15
18/07/2001	Caobas	C5-2a	700m	2
18/07/2001	Caobas	C5-2a	800m	2
19/07/2001	Caobas	C5-3a		0
19/07/2001	Caobas	C5-4a		0
03/08/2001	Caobas	C8-1a		0
03/08/2001	Caobas	C8-2a		0
04/08/2001	Caobas	C8-3a	600m	3
04/08/2001	Caobas	C8-3a	695m	5
04/08/2001	Caobas	C8-4a	200m	3
04/08/2001	Caobas	C8-4a	360m	10
04/08/2001	Caobas	C8-4a	650m	30
26/07/2001	C. Maya	C13-1a		0
26/07/2001	C. Maya	C13-2a	250m	10
26/07/2001	C. Maya	C13-3a	30m	30
26/07/2001	C. Maya	C13-3a	125m	50
26/07/2001	C. Maya	C13-3a	510m	10
26/07/2001	C. Maya	C13-3a	510m	40
26/07/2001	C. Maya	C13-4a	375m	3
26/07/2001	C. Maya	C13-4a	550m	1
26/07/2001	C. Maya	C13-4a	750m	2
29/07/2001	C. Maya	C8-1a	350m	3
29/07/2001	C. Maya	C8-2a	85m	50
29/07/2001	C. Maya	C8-2a	85m	50
29/07/2001	C. Maya	C8-2a	100m	3
29/07/2001	C. Maya	C8-2a	110m	40
29/07/2001	C. Maya	C8-2a	115m	50
29/07/2001	C. Maya	C8-2a	115m	50
29/07/2001	C. Maya	C8-2a	120m	50
29/07/2001	C. Maya	C8-2a	120m	50
29/07/2001	C. Maya	C8-2a	405m	20
29/07/2001	C. Maya	C8-2a	430m	15
29/07/2001	C. Maya	C8-2a	500m	30
29/07/2001	C. Maya	C8-2a	500m	20
29/07/2001	C. Maya	C8-2a	510m	50
31/07/2001	C. Maya	C8-3a	8m	3
31/07/2001	C. Maya	C8-3a	10m	10
31/07/2001	C. Maya	C8-3a	80m	15
31/07/2001	C. Maya	C8-3a	140m	30
31/07/2001	C. Maya	C8-3a	170m	3
31/07/2001	C. Maya	C8-3a	230m	3
31/07/2001	C. Maya	C8-3a	240m	30

31/07/2001	C. Maya	C8-3a	245m	30
31/07/2001	C. Maya	C8-3a	260m	20
31/07/2001	C. Maya	C8-3a	265m	35
31/07/2001	C. Maya	C8-3a	290m	3
31/07/2001	C. Maya	C8-3a	415m	30
31/07/2001	C. Maya	C8-3a	425m	4
31/07/2001	C. Maya	C8-3a	520m	3
31/07/2001	C. Maya	C8-3a	670m	10
31/07/2001	C. Maya	C8-3a	700m	100
31/07/2001	C. Maya	C8-4a	25m	10
31/07/2001	C. Maya	C8-4a	75m	4
31/07/2001	C. Maya	C8-4a	150m	5
31/07/2001	C. Maya	C8-4a	675m	15
31/07/2001	C. Maya	C8-4a	675m	15
31/07/2001	C. Maya	C8-4a	675m	15
31/07/2001	C. Maya	C8-4a	675m	20
31/07/2001	C. Maya	C8-4a	695m	3
27/07/2001	C. Maya	C9-1a		0
27/07/2001	C. Maya	C9-2a	70m	50
27/07/2001	C. Maya	C9-2a	80m	50
27/07/2001	C. Maya	C9-2a	100m	10
27/07/2001	C. Maya	C9-2a	100m	10
27/07/2001	C. Maya	C9-2a	100m	5
27/07/2001	C. Maya	C9-2a	160m	3
27/07/2001	C. Maya	C9-2a	165m	20
27/07/2001	C. Maya	C9-2a	165m	50
27/07/2001	C. Maya	C9-2a	165m	40
27/07/2001	C. Maya	C9-2a	425m	3
27/07/2001	C. Maya	C9-2a	660m	3
27/07/2001	C. Maya	C9-2a	685m	50
27/07/2001	C. Maya	C9-2a	685m	15
27/07/2001	C. Maya	C9-2a	685m	15
27/07/2001	C. Maya	C9-2a	685m	20
27/07/2001	C. Maya	C9-2a	685m	50
27/07/2001	C. Maya	C9-2a	750m	4
27/07/2001	C. Maya	C9-2a	800m	2
27/07/2001	C. Maya	C9-3a	125m	5
27/07/2001	C. Maya	C9-3a	235m	30
27/07/2001	C. Maya	C9-3a	235m	20
27/07/2001	C. Maya	C9-3a	275m	20
27/07/2001	C. Maya	C9-3a	375m	20
27/07/2001	C. Maya	C9-3a	415m	20
27/07/2001	C. Maya	C9-3a	415m	20
27/07/2001	C. Maya	C9-3a	415m	20
27/07/2001	C. Maya	C9-3a	415m	20
27/07/2001	C. Maya	C9-3a	415m	20
27/07/2001	C. Maya	C9-3a	470m	30
27/07/2001	C. Maya	C9-3a	485m	20
27/07/2001	C. Maya	C9-3a	555m	3
27/07/2001	C. Maya	C9-3a	720m	3
28/07/2001	C. Maya	C9-4a	125m	1
28/07/2001	C. Maya	C9-4a	600m	3
28/07/2001	C. Maya	C9-4a	650m	6
28/07/2001	C. Maya	C9-4a	675m	2
28/07/2001	C. Maya	C9-4a	800m	10