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ZOOARCHAEOLOGICAL HABITAT ANALYSIS OF ANCIENT MAYA LANDSCAPE CHANGES

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ABSTRACT.—Consensus has not yet been reached regarding the role of human-caused environmental change in the history of Classic Maya civilization. On one side of the debate, researchers argue that growing populations and agricultural expansion resulted in environmental over-exploitation that contributed to societal collapse. Researchers on the other side of the debate propose more gradual environmental change resulting from intentional and sustainable landscape management practices. In this study, we use zooarchaeological data from 23 archaeological sites in 11 inland drainage systems to evaluate the hypothesis of reduction of forest cover due to anthropogenic activities across the temporal and spatial span of the ancient Maya world. Habitat fidelity statistics derived from zooarchaeological data are presented as a proxy for the abundance of various habitat types across the landscape. The results of this analysis do not support a model of extensive land clearance and instead suggest considerable chronological and regional stability in the presence of animals from both mature and secondary forest habitats. Despite relative stability, some chronological variation in land cover was observed, but the variation does not fit expected patterns of increased forest disturbance during periods of greatest population expansion. These findings indicate a complex relationship between the ancient Maya and the forested landscape.

Key words: zooarchaeology, animal habitat, landscape change, Maya collapse, Late Classic Maya.

RESUMEN.—Aun no se han logrado consensos con respecto a la función de los cambios ambientales causados por los humanos en la historia de la civilización Clásica Maya. Por un lado del debate, algunos investigadores sostienen que la creciente población y la expansión de la agricultura causaron la sobrexplotación que contribuyó al colapso social. Investigadores de la otra postura del debate proponen un cambio ambiental gradual resultante de las prácticas de manejo sustentable e intencionales del paisaje. En este estudio, usamos datos zooarqueológicos de 23 sitios arqueológicos para evaluar la hipótesis de la reducción de la cubierta forestal debido a actividades antropogénicas a través del lapso temporal y espacial del mundo maya antiguo. Las estadísticas de la fidelidad al hábitat derivadas de los datos zooarqueológicos se presentan como una aproximación a la abundancia de diferentes tipos de hábitats en el paisaje. Los resultados de este análisis no apoyan un modelo de liquidación extensiva de la tierra, en vez de esto, indican una estabilidad cronológica y regional

considerable en la presencia de animales tanto de hábitats primarios y secundarios de los bosques. A pesar de la estabilidad relativa, se observaron algunas variaciones cronológicas en la cubierta terrestre, pero la variación no se ajusta a los modelos esperados de un incremento en la perturbación forestal durante los períodos de mayor expansión poblacional. Estos hallazgos sugieren una relación compleja entre los antiguos mayas y el paisaje boscoso.

RÉSUMÉ.—Il n'y a pas encore eu de consensus au sujet du changement environnemental causé par le facteur humain dans l'histoire de la civilisation classique Maya. D'un côté du débat, les chercheurs soutiennent que les populations croissantes et le développement agricole ont entraîné une surexploitation de l'environnement, qui à son tour a dégénéré en effondrement social. De l'autre côté du débat les chercheurs proposent un changement environnemental plus graduel résultant de pratiques intentionnelles et soutenues en matière de direction de l'aménagement du terrain. Dans cette étude, nous utilisons des données zoo-archéologiques en provenance de 23 sites archéologiques afin d'évaluer l'hypothèse de réduction de la couverture forestière causée par les activités anthropogéniques à travers le laps temporel et spatial de l'ancien monde Maya. Les statistiques de fidélité de l'habitat provenant des données zoo-archéologiques sont présentées en tant que données représentatives de l'abondance des divers genres d'habitat tout au long du terrain. Les résultats de cette analyse ne soutiennent pas de modèle de déblaiement de terrain considérable, mais mettent plutôt en évidence l'importance de l'équilibre chronologique et régional quant à l'existence d'animaux appartenant à la fois à l'habitat forestier primaire et secondaire. Malgré la stabilité relative, une certaine variation chronologique dans la superficie du sol fut observée, mais cette variation ne concorde pas avec les schémas prédictibles de bouleversements croissants de la forêt pendant les périodes d'accroissement le plus important de la population. Ces trouvailles suggèrent une relation de complexité entre le Maya ancien et le terrain forestier.

INTRODUCTION

Explanatory models of the growth and decline of the ancient Maya civilization often include heated debate about the role of changing environmental conditions resulting from human land use. On one side of the debate are models that emphasize the key role of human-caused environmental failure. These models propose that rising populations, urban growth, and the increasing demands of the Maya political elite encouraged unsustainable expansion of extensive agriculture resulting in primarily monocropped, open, agricultural fields and a consequent reduction of mature or secondary forested land (Culbert 1988; Deevey et al. 1979; Sanders 1979; Santley et al. 1986; Webster 2002; Wiseman 1985). In these models, environmental mismanagement was exacerbated by global climate change and extended periods of drought that led to an increased impact of cultural activities (Brenner et al. 2002; Gill 2000; Haug et al. 2003; Hodell et al. 1995; Leyden 2002).

The other side of the debate emphasizes biotic stability or low-impact landscape management. These models suggest that the process of landscape modification was a gradual one of intentional succession manipulation and

intensive agricultural production (such as terraces and raised fields, and high diversity household gardens) that resulted in a managed mosaic landscape of field and forest (Dunning and Beach 1994; Dunning and Beach 2000; Dunning et al. 1998a; Fedick 1996; Ford 1996; Ford et al. 2001; Gomez-Pompa et al. 1987; Gomez-Pompa and Kaus 1999; Netting 1993; Peters 2000). Climate change is discussed in these models in terms of local responses to the impact of drought and climate unpredictability (Rosenmeier et al. 2002b; Shaw 2003) and the enhanced ability of the managed landscape in ameliorating the effects of these changes (Allen et al. 2003; Faust 2001).

Paleoenvironmental evidence does not consistently support one view or the other. A large body of research, primarily from paleolimnological studies, provides clear evidence of environmental changes such as soil erosion and deforestation in some areas of the ancient Maya world (Abrams et al. 1996; Binford et al. 1987; Brenner 1983; Brenner et al. 2002; Deevey et al. 1979; Leyden 2002; Rice 1996), whereas in other areas paleoenvironmental research suggests biotic stability following initial land clearance in the Preclassic period (Anselmetti et al. 2007; Beach and Dunning 1995; Beach and Dunning 1997; Beach et al. 2006; Dunning et al. 1997; Dunning et al. 1998b). In addition, specific paleoenvironmental research on animal remains recovered from Maya archaeological sites does not support models of extreme forest reduction or either extinction or extirpation of animal populations, although they do indicate some human impact on both environments and animals (Emery 2004; Emery et al. 2000; Wright 2006). This variability in research results leads one to question the validity of broad interpretations of human impacts on the Maya landscape, and encourages a careful consideration of the implications of the well-documented regional and temporal differences in climate, vegetation, and population density across the region.

In this paper, we apply habitat fidelity analyses to original and published zooarchaeological data from 23 sites distributed across 11 inland drainages in the Maya cultural region to infer the prehistoric distribution of habitat types. The study sites range in time from the Middle Preclassic to Late Postclassic (Table 1), and include sites located in the northern and southern Maya lowlands and the Guatemalan highlands (Figure 1). The dataset includes sites and regions where prior paleoenvironmental evidence has suggested variable anthropogenic impacts on the local environment. We discuss the results in light of the divergent arguments for human impact on the ancient environment.

RECONSTRUCTING MAYA HABITATS FROM ARCHAEOLOGICAL ANIMAL REMAINS

The Question of Maya Environmental Use.—Archaeological sites identified as Maya are found in southern Mexico, Guatemala, Belize and the northernmost portions of Honduras and El Salvador. This region has a long history of human occupation (dating to at least 5000–3000 B.C.), but shared cultural traits that archaeologists identify as Maya do not appear until approximately 2000 B.C. Starting in the Middle Preclassic (ca. 1000–250 B.C.) and running through the Classic period (A.D. 250–850), and in some areas until the arrival of the Spanish in the early 1500s, the Maya world was heavily populated. In many areas, the

TABLE 1.—Generalized chronology used in comparative analyses of site data. Period beginning and ending dates vary somewhat between sites in the Maya area, but comparisons in this paper are based on a generalized chronology for the region. Specific site chronologies are available in the published literature for each site.

Period	Dates
Preclassic	2000 BC-AD 250
Early Classic	AD 250–600
Late Classic	AD 600–850
Terminal Classic	AD 850–1000
Postclassic	AD 1000–1500
Colonial	AD 1519–1697

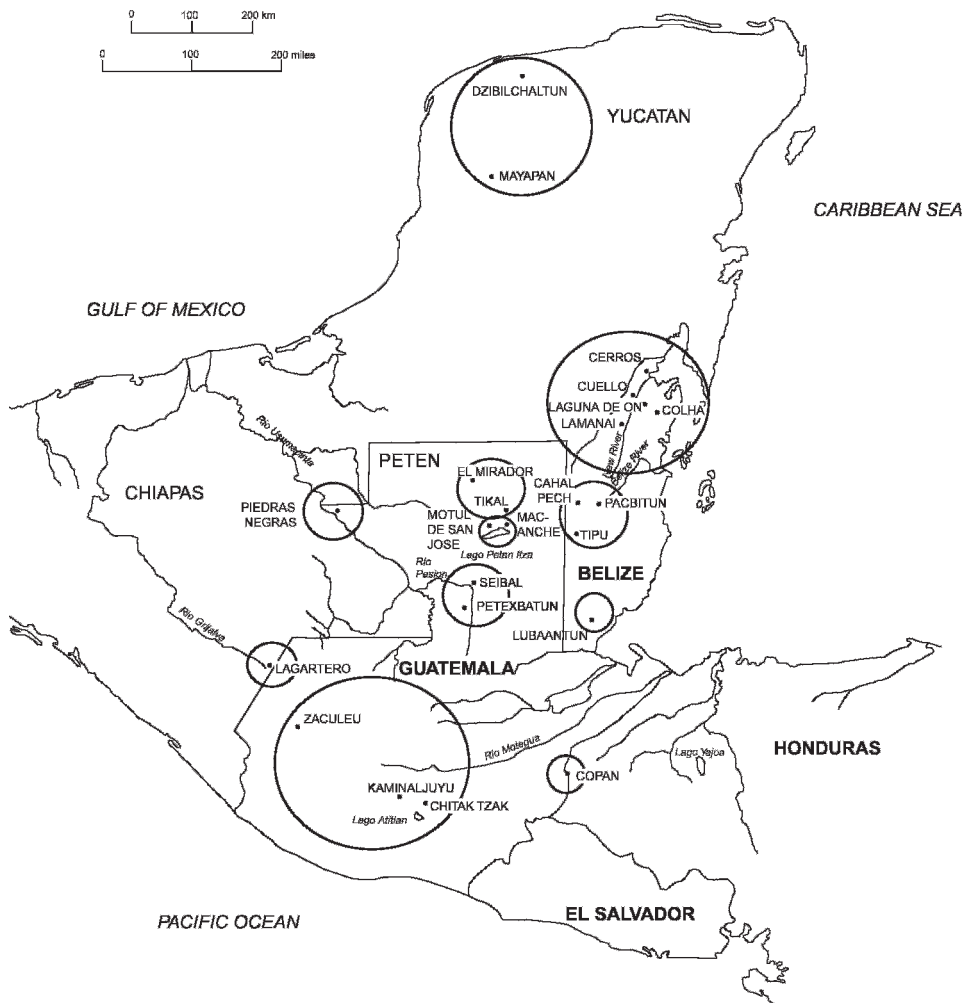


FIGURE 1.—Map of the Maya world with study sites and other neighboring sites labeled and regions circled (map by Emery).

Maya landscape was characterized by densely settled core sites containing the residential units of the politico-religious elite and surrounded by farmed agricultural lands and the residences of the agricultural and support populations. In models emphasizing adverse Maya impact on the ancient environment, a basic correlation is proposed between the large Classic period Maya populations and the paleoenvironmental data for forest disturbance. As populations grew, it is logically hypothesized that agricultural production also rose, resulting in expansion of agricultural fields at the expense of canopy forest. In many reconstructions, this shift from forested lands to fields resulted in soil erosion and the loss of soil fertility, resulting finally in the inability of the land to support the demands of large populations (Abrams et al. 1996; Culbert 1988; Deevey et al. 1979; Santley et al. 1986; Wiseman 1985).

The exact reconstruction of the extent to which the lands surrounding the Maya cities were populated, however, and the extent to which they included open agricultural fields, secondary forests (disturbed or managed), or closed forests, is controversial. In particular, reconstructions of ancient land cover conditions from paleolimnological studies can be problematic because the lake core data may only reflect the land cover conditions within the catchment areas of the sampled water body, an area that may not correspond to the areas of human settlement and agricultural expansion. Therefore, it is important to find proxy data directly from archaeological deposits that can speak to the question of land cover surrounding centers of prehistoric human habitation. One such avenue is through archaeological animal remains.

Habitat Analyses from Archaeological Animal Remains.—The derivation of environmental descriptions from the relative frequency of retrieved archaeological animal remains has a long history in the zooarchaeological sciences. Interpreted appropriately, there is a close link between the animal remains recovered in archaeological deposits, the habitats preferred and most frequently inhabited by these species, and the general environmental conditions implied by the presence of these habitats. In other words, abundances of animal remains can be used as a proxy for the habitats for which they are fidelic. This is true despite the bias imposed by human choice, use, and deposition of the animals culled from natural populations, since, in the final equation, resource availability will always have a direct impact on the resources used by an ancient people.

At a very simplified level the reduction of mature forest hypothesized for the end of the Classic Maya period would have decreased local populations of closed canopy forest-dependent “indicator” animal species such as jaguars (*Panthera onca*), while increasing habitat for crop invaders and edge-loving species such as white-tailed deer (*Odocoileus virginianus*). These changes will also alter the proportions of species with less exclusive fidelity to certain habitats, such as the smaller brocket deer that inhabits both secondary and closed canopy forest. The fidelity index calculated here attempts to take into account the proportion of time spent by each animal species in each representative environment. To derive basic fidelity values, we use current ecological research from the greater neotropical regions beyond the limited data of the Maya world. The basic fidelity values were then verified by tropical forest ecologists with experience in the area.

Nevertheless, it must be emphasized that these assignments are broad, generalized, and somewhat subjective (discussed in more detail in the methods section of this paper). These fidelity values are then used to calculate sample-specific fidelity indices for each species or taxa recovered in the zooarchaeological samples of this study. The indices are combined to quantify changing proportions of animal species representative of different habitats for sites, periods, and regions. This proxy evidence allows a comparison of the proportionate representation of habitat types over time and space in the ancient Maya world.

These results are used to test the hypothesized reduction of forest cover due to anthropogenic activities. If the hypothesis of wide-spread deforestation and extensive agricultural and settlement expansion during the Late Classic period (ca. 600–850 A.D.) is valid, we expect to see the replacement of mature forest species by those with high fidelity for secondary forests, agricultural fields, and built environments (i.e. those occurring around human habitation areas) during this or the later Terminal Classic period. If agricultural expansion was not coincident with wide-spread deforestation (in the case of agricultural systems compatible with high diversity forest cover) during those same periods we would expect to see reduction in mature forest species, but less reduction in secondary forest species, and minimal increase in species fidelic to agricultural fields and built environments than the hypothesized extensive deforestation. Finally, if any land cover change was sufficient to have resulted in societal disruption on a large scale, it would also be consistent across the ancient Maya landscape and would be revealed in our study as extreme transitions from one habitat type to another particularly around the time of the Classic Maya collapse (~800–900 A.D.).

RESEARCH SAMPLES

This regional study presents habitat fidelity statistics derived from identifications of archaeological animal remains recovered from 23 Maya sites located in Mexico, Guatemala, Belize, and Honduras (Figure 1, Table 2). Zooarchaeological data were derived from published sources (Collins 2002; Kidder et al. 1946; Kozelsky 2005; Masson 1999; Pohl 1976; Pohl 1990a; Pohl 1995; Pollock and Ray 1957; Shaw 1991; Shaw 1999; Shaw and Mangan 1994; Stanchly 1995; Wing 1975; Wing and Scudder 1991; Woodbury and Trik 1954) and from our own published and unpublished research (Emery 1995; Emery 1997; Emery 2007; Emery and Baker 1992; Thornton and Emery 2007; Thornton and Emery in press). Because inland sites (with an abundance of terrestrial fauna and some freshwater aquatic fauna) and coastal sites (located within a day's walk from the coast and with assemblages dominated by invertebrates and marine fishes) are very different in terms of the impact of human activity, only assemblages from inland sites are considered.

The zooarchaeological samples include 32 chronologically defined sub-samples recovered from deposits dated to the Preclassic through Colonial periods (Table 1). Together the site samples provide comparative data from 11 inland drainage basins across the regions of most significant settlement during the Classic period. These drainages provide excellent background for the

TABLE 2.—List of sites analyzed with regional location and NISP values presented by time period. Specific data on taxa recovered and used in this analysis can be found in the published sources listed here.

Site name (region/ drainage in bold)	Time Period	Sample NISP ^a	Data source ^b
Highlands:			
Kaminaljuyu	Late Preclassic	78	Emery (1995); unpublished data; Kidder et al. (1946)
Grijalva:			
Lagartero	Late Classic	339	Kozelsky (2005)
Copan Valley:			
Copan	Early Classic	255	Collins (2002); Pohl (1995)
	Late Classic	402	
South Belize:			
Lubaantun	Late Classic	108	Wing (1975)
Pasión River:			
Aguateca	Late Classic	1894	Emery (1997); unpublished data
Altar de Sacrificios	Late Classic	67	Olsen (1972); Pohl (1976)
Arroyo de Piedras	Early Classic	70	Emery (1997); unpublished data
Bayak	Middle Preclassic	179	Emery (1997); unpublished data
Dos Pilas	Late Classic	244	Emery (1997); unpublished data
	Terminal Classic	362	
Punta de Chimino	Terminal Classic	687	Emery (1997); unpublished data
Seibal	Late Classic	576	Pohl (1976, 1990)
Tamarindito	Late Classic	155	Emery (1997); unpublished data
Petén Lakes:			
Macanche	Late Postclassic	160	Pohl (1976, 1990)
Motul de San Jose	Late Classic	473	Emery (2003); unpublished data
	Terminal Classic	64	
Trinidad de Nosotros	Late Classic	108	Thornton and Emery (2007); unpublished data
	Terminal Classic	144	
Usumacinta:			
Piedras Negras	Late Classic	838	Emery (2007); unpublished data
Interior Petén:			
El Mirador	Late Preclassic	114	Thornton and Emery (in press); unpublished data
	Late Classic	76	
Tikal	Early Classic	593	Moholy-Nagy (1994, 2003); Pohl (1976, 1990)
	Late Classic	2228	
Belize River Area:			
Cahal Pech	Middle Preclassic	112	Stanchly (1995)
Rio Hondo/New River:			
Colha	Middle Preclassic	448	Shaw (1991, 1999); Shaw and Mangan (1994)
	Late Preclassic	178	
	Terminal Preclassic	235	
Cuello	Middle Preclassic	1039	Wing and Scudder (1991)
	Late Preclassic	1247	
Laguna de On	Late Postclassic	200	Masson (1999)

TABLE 2.—Continued.

Site name (region/ drainage in bold)	Time Period	Sample NISP ^a	Data source ^b
Northern Lowlands:			
Dzibilchaltun	Terminal Classic	111	Wing and Steadman (1980)
Total =	23 sites, 32 samples	13,784	

Notes: a - sample NISP = number used in statistical analysis; b - this is not a complete list of all publications associated with each site/analysis.

research, since most have been evaluated using other methods of paleoenvironmental reconstruction, and the results have varied with some areas reporting high levels of land clearance and others reporting little or no impact. The regions with evidence for the most significant environmental degradation based on paleolimnological, archaeobotanical, and human biological evidence are the Petén Lakes drainage (Brenner et al. 1990; Islebe et al. 1996; Leyden 2002; Newell 2005; Rosenmeier et al. 2002a; Wiseman 1985), and the Copan Valley where it has been suggested that extreme deforestation led to societal collapse (Abrams et al. 1996; Whittington 1989; Whittington and Reed 1997). Regions where little adverse human impact has been suggested include the Pasión drainage (Beach 1998; Beach and Dunning 1995; Beach and Dunning 1997; Dunning and Beach 1994; Dunning et al. 1997; Dunning et al. 1998b; Emery 2004; Emery et al. 2000; Wright 2006), the Belize River area (Chase and Chase 1998; Fedick 1994; Healy 1983; Healy et al. 1983; Lohse and Findlay 2000), and the Rio Hondo/New River drainage of Northern Belize (Dunning et al. 1999; Lambert 1985; Pohl 1990b; Scarborough 1986; Turner and Harrison 1983).

METHODS

In this study, we define samples by chronological period, so although zooarchaeological remains have come from many different deposits at each site, we group site materials into chronologically defined samples (Table 1). Since the samples represent a variety of domestic and ritual contexts from various status groups, they provide a broad and undifferentiated view of animal use at each site. Samples have been variably recovered using no screening or screens of 1/4-inch mesh size, a character that cannot be controlled in this regional study. The lack of fine screen recovery methods (<1/4-inch mesh) at all sites increases the comparability of the samples, but also may bias the samples against small species and elements (James 1997; Shaffer and Sanchez 1994; Wake 2004). Since sample sizes in this study vary, only sub-samples larger than 50 specimens per time period are included to preserve statistical validity.

We incorporate primary zooarchaeological identifications from 11 sites that we have analyzed personally. These include Aguateca, Arroyo de Piedra, Bayak, Dos Pilas, Kaminaljuyu, El Mirador, Motul de San Jose, Piedras Negras, Punta de Chimino, Tamarindito, and Trinidad de Nosotros, all of which were identified by either Emery or Thornton using comparative collections from the Florida

Museum of Natural History (www.flmnh.ufl.edu/databases/zooarch/intro.htm) and standard zooarchaeological methods (Reitz and Wing 1999). Specific information on the methods of zooarchaeological identification for published samples included herein can be found in the publications associated with each zooarchaeological analysis.

Our analyses are based on the relative number of identified specimens (NISP), since this was the standard for quantification through the literature. This measure may over-represent species such as turtles and armadillos with extraordinarily large numbers of identifiable bones per individual, but this tendency is counteracted by the ubiquity of these species in all the assemblages. Other quantification methods derived from NISP tallies, such as the minimum number of individuals (MNI), are inappropriate for this analysis because they are more likely to be affected by sample size, which is small for many assemblages examined here (Cannon 2001; Grayson 1984).

In this zooarchaeological habitat fidelity analysis, we evaluate fidelity values calculated for each of four habitat types for all 93 terrestrial vertebrate animal species identified in the archaeological deposits at the sites under investigation (Table 3). Habitat types evaluated here include mature closed canopy forest (MF), secondary/disturbed forest (SEC), habitats with low or scattered arboreal vegetation including agricultural fields and savannahs (AGR), and residential or built habitats (RES). Riverine and wetland, habitats were also classified but are not included in this analysis of land cover change because our emphasis in this paper is on the terrestrial patterns. These are listed, however, in Table 3.

Fidelity classifications are based on current ecological data for neotropical species (e.g. Alvard et al. 1997; Cuarón 2000; Cullen et al. 2000; Eisenberg 1989; Emmons 1997; Escamilla et al. 2000; Howell and Webb 1995; Lee 2000; Medellín and Equihua 1998; Naughton-Treves et al. 2003; Nowak 1991; Reid 1997; Smith 2005). All mammal classifications were reviewed by Mel Sunquist, Ph.D., University of Florida, an expert in neotropical animal ecology, and Daniel Thornton and Roni Garcia, wildlife ecologists currently working in the tropical forests of northern Guatemala. Specimens that could not be identified to the level of at least taxonomic family were excluded, since they are not easily consigned to any particular habitat. Therefore, the subsamples included in this analysis comprise a total of 13,784 archaeological remains selected from a larger subset of identified remains. Species level identifications were used whenever possible, but in some cases the difficulty of identification required lumping at the family level (for e.g. *Tayassuidae* instead of *Tayassu pecari* and *Pecari tajacu*) despite very distinct habitat fidelities. In these cases, the values include all habitat types for which these animals are fidelic.

Although habitat fidelity measures are an effective means of evaluating patterns of landscape use over time, the determination of fidelity values is largely subjective and the assignments are broad and generalized. Difficulties in assignment are compounded by a lack of detailed ecological data regarding the distribution and behavior of many neotropical animals (Kricher 1997). As an example, the classification of white-tailed deer, one of the most common species, is debatable. On the basis of ecological information and ethnographic observations on Maya hunting in agricultural fields (from the literature and

Emery ethnographic observations, Pasión River region), we have classified this species as MF=0.1, SEC=0.45, AGR=0.45, reflecting its presence as noted by hunters in both secondary forest and open fields and its occasional presence in mature forest often along waterways (Cuarón 2000; Mendez 1984; Pohl 1977).

Once assigned, the derived fidelity values were used to create indices of relative habitat representation based on the number of specimens of each species present at an archaeological site. These are presented as relative values (MF, SEC, AGR) and as ratios of MF:SEC and SEC:AGR+RES to provide direct comparison between the relevant categories without effects of fidelity for other habitats not studied here (wetlands, riverine, etc.)

RESULTS

We begin by reviewing the relative frequency of representation of species fidelic to each land cover type to assess overall patterns (Figure 2a). The relative proportion of combined species fidelity values for MF, SEC, and AGR varies significantly between the sites investigated (Table 4). Regional variation, though overall lower than inter-site variation, remains statistically significant for species representing SEC and AGR. Importantly, MF does not vary significantly between regions. The proportion of species fidelic to MF is lower in all regions than those fidelic to SEC or AGR, particularly in the Copan Valley, south Belize and the Belize River area, and the northern lowlands. In most regions, SEC is higher than AGR (the exceptions being the interior Petén and the northern lowlands).

Mature forest, secondary forest, and agricultural/residential lands are next presented as ratios to better evaluate the variations in these important land cover categories. We present two ratios, mature forest:secondary forest (MF:SEC) to evaluate the proportion of forest types, and secondary forest:agricultural and residential lands (SEC:AGR+RES) to evaluate the proportion of disturbance habitats. In an overall perspective, the ratio of MF:SEC does not vary significantly at either the site or regional level (Table 4). The ratio MF:SEC is somewhat higher in the Pasión, Petén Lakes, and interior Petén regions than in the Copan valley, or the Belizean regions. Since mature closed canopy forest is limited in highland and arid regions, it is not surprising that the ratio MF:SEC is very low in the southern highlands or northern lowlands (Figure 2b). The ratio of SEC:AGR+RES is less consistent over all regions with significantly higher relative representation of secondary forest species over agricultural in the Grijalva basin, the Belize River area and the Rio Hondo/New River drainages. Much lower representation of secondary forest species relative to agricultural species is found in the highlands, Copan, and the interior Petén. These patterns correlate well with modern vegetation coverage. Some regions that are more forested today also appear to have been more forested in the past (including the Pasión and interior Petén, and to a lesser extent the Grijalva Basin). The Petén Lakes region is deforested today, but this is likely a result of modern settlement focused around Lake Petén Itza. Belizean sites, the site of Lagartero in the Grijalva basin and the northern lowlands had less mature forest cover but high proportions of secondary growth suggesting an open but highly diverse forest cover, similar to modern conditions. The southern highland fauna suggest more open conditions and more

TABLE 3.—Habitat fidelity values assigned to vertebrate taxa identified at the 23 study sites. Defined habitats include: mature/closed canopy forest (MF), secondary/disturbed forest (SEC), riverine/lacustrine and shoreline habitats (RIV), wetland/swamp and bajo habitats (WET), habitats with low or scattered arboreal vegetation (including agricultural fields and savannas) (AGR), and cleared habitats around human habitation areas (RES). For the purposes of this analysis only MF, SEC, AGR, and RES habitats are discussed.

Scientific name	Common name	MF	SEC	RIV	WET	AGR	RES
Mammals:							
<i>Didelphis marsupialis</i>	common opossum	0.1	0.5	0.2			0.2
<i>Marmosa</i> sp.	mouse opossum	0.5	0.5				
<i>Philander opossum</i>	gray four-eyed opossum	0.3	0.3	0.3		0.1	
<i>Tamandua mexicana</i>	northern tamandua	0.5	0.5				
<i>Dasypus novemcinctus</i>	armadillo	0.2	0.4			0.4	
<i>Cryptotis micrura</i>	shrew		0.5			0.5	
<i>Artibeus lituratus</i>	great fruit-eating bat	0.4	0.2	0.2		0.2	
<i>Desmodus rotundus</i>	vampire bat	0.33	0.33			0.33	
<i>Natalus stramineus</i>	Mexican funnel-eared bat	0.5	0.5				
<i>Alouatta pigra</i>	howler monkey	0.6	0.4				
<i>Ateles geoffroyi</i>	spider monkey	0.8	0.2				
<i>Sylvilagus</i> sp.	rabbit		0.5			0.5	
<i>Sciurus aureogaster</i>	Mexican gray squirrel	0.5	0.5				
<i>Orthogeomys hispidus</i>	pocket gopher		0.5			0.5	
<i>Coendou mexicana</i>	porcupine	0.6	0.4				
<i>Dasyprocta punctata</i>	Central American agouti	0.45	0.45			0.1	
<i>Agouti paca</i>	paca	0.25	0.25	0.2	0.2	0.1	
<i>Urocyon cinereoargenteus</i>	grey fox	0.2	0.4			0.4	
<i>Bassariscus sumichrasti</i>	cacomistle	0.5	0.5				
<i>Nasua narica</i>	coati	0.35	0.35			0.2	0.1
<i>Poto flavus</i>	kinkajou	0.5	0.5				
<i>Procyon lotor</i>	raccoon	0.1	0.15	0.25	0.25	0.1	0.15
<i>Eira barbara</i>	tayra	0.5	0.5				
<i>Galictes vittata</i>	grison	0.4	0.4	0.2			
<i>Mustela frenata</i>	long-tailed weasel	0.4	0.4			0.2	
<i>Conepatus semistriatus</i>	striped hog-nosed skunk		0.6			0.4	
<i>Memphitis</i> sp.	hooded/striped skunk		0.6	0.1	0.1	0.2	
<i>Spilogale</i> sp.	spotted skunk		0.5			0.5	
<i>Herpailurus yaguarondi</i>	jaguarundi	0.2	0.4			0.4	
<i>Leopardus pardalis</i>	ocelot	0.5	0.3	0.1	0.1		
<i>Leopardus wiedii</i>	margay	0.6	0.4				
<i>Puma concolor</i>	puma	0.4	0.4			0.2	
<i>Panthera onca</i>	jaguar	0.65	0.15	0.2			
<i>Tapirus bairdii</i>	Baird's tapir	0.2		0.4	0.4		
<i>Pecari tajacu</i>	collared peccary	0.33	0.33			0.33	
<i>Tayassu pecari</i>	white-lipped peccary	1					
Tayassuidae	peccary	0.6	0.2			0.2	
<i>Mazama americana</i>	red brocket deer	0.6	0.3		0.1		
<i>Odocoileus virginianus</i>	white-tailed deer	0.1	0.45			0.45	
Birds:							
<i>Cathartes aura</i>	turkey vulture		0.4			0.4	0.2
<i>Coragyps atratus</i>	black vulture		0.5			0.5	
<i>Buteogallus urubitinga</i>	great black hawk	0.4	0.6				
<i>Buteo brachyurus</i>	short-tailed hawk		0.5			0.5	
<i>Buteo magnirostris</i>	roadside hawk		0.5			0.5	
<i>Buteo nitidus</i>	gray hawk	0.4	0.5		0.1		

TABLE 3.—Continued.

Scientific name	Common name	MF	SEC	RIV	WET	AGR	RES
<i>Spizaetus ornatus</i>	ornate hawk eagle	0.7	0.3				
<i>Micrastur semitorquatus</i>	collared forest falcon	0.5	0.5				
<i>Crax rubra</i>	great curassow	0.8	0.2				
<i>Ortalis vetula</i>	chachalaca		0.5			0.5	
<i>Penelope purpurascens</i>	crested guan	1					
<i>Meleagris ocellata</i>	ocellated turkey	0.4	0.3		0.1	0.2	
<i>Colinus nigrogularis</i>	bobwhite quail		0.5		0.1	0.4	
<i>Cyrtonyx ocellatus</i>	ocellated quail	0.2	0.6			0.2	
<i>Dactylortyx</i> sp.	singing quail	0.2	0.6			0.2	
<i>Columbina talpacoti</i>	ruddy ground dove		0.5			0.5	
<i>Columbina/Leptotilia</i> sp.	ground dove		0.5			0.5	
<i>Leptotilia plumbeiceps</i>	gray-headed dove	0.5	0.5				
<i>Aratinga nana</i>	olive-throated parakeet	0.25	0.25	0.25		0.25	
<i>Amazona autumnalis</i>	red-lored parrot	0.33	0.33			0.33	
<i>Amazona farinosa</i>	mealy parrot	0.4	0.4			0.2	
<i>Ara macao</i>	scarlet macaw	1					
<i>Pionus senilis</i>	white-crowned parrot		1				
<i>Bubo virginianus</i>	great-horned owl		1				
<i>Glaucidium brasilianum</i>	ferruginous pygmy owl	0.5	0.5				
<i>Otus guatemalae</i>	Middle American screech owl	0.5	0.5				
<i>Nyctidromus albicollis</i>	common pauraque		1				
<i>Momotus mexicanus</i>	russet-crowned motmot	0.5	0.5				
<i>Momotus momota</i>	blue-crowned motmot	0.5	0.5				
<i>Choroceryle americana</i>	green kingfisher			0.5	0.5		
<i>Cotinga amabilis</i>	lovely cotinga	0.5	0.5				
<i>Cyanocorax morio</i>	brown jay	0.33	0.33			0.33	
<i>Cyanocorax sanblasiana</i>	san blas jay		0.5	0.5			
<i>Turdus</i> sp.	robin		1				
<i>Habia</i> sp.	tanager	0.5	0.5				
<i>Cardinalis cardinalis</i>	northern cardinal		0.6			0.4	
<i>Oryzoborus funereus</i>	thick-billed seed finch		1				
<i>Quiscalus mexicanus</i>	boat-tailed grackle		0.2	0.2	0.2	0.2	0.2
<i>Icterus</i> sp.	Oriole	0.5	0.5				
Amphibians/Reptiles:							
<i>Bufo marinus</i>	cane toad		0.2	0.2	0.2	0.2	0.2
<i>Rhinophrynus dorsalis</i>	Mexican burrowing toad	0.25	0.25			0.5	
<i>Rhinoclemys areolata</i>	furrowed wood turtle	0.2	0.2		0.2	0.4	
<i>Ctenosaura similis</i>	black spiny-tailed iguana		0.2			0.4	0.4
<i>Terrepene mexicana</i>	Yucatan box turtle		0.25		0.5	0.25	
<i>Iguana iguana</i>	green iguana		0.2	0.5	0.2		0.1
<i>Boa</i> sp.	boa	0.18	0.18	0.18	0.18	0.18	0.1
<i>Drymarchon corais</i>	indigo snake	0.33	0.33			0.33	
<i>Masticophis</i> sp.	racer snake		0.5			0.5	
<i>Spilotes pullatus</i>	rat snake	0.33	0.33			0.33	
<i>Agkistrodon bilineatus</i>	cantil	0.5	0.5				
<i>Bothrops asper</i>	terciopelo	0.1	0.4			0.5	
<i>Crotalus durissus</i>	rattlesnake					1	

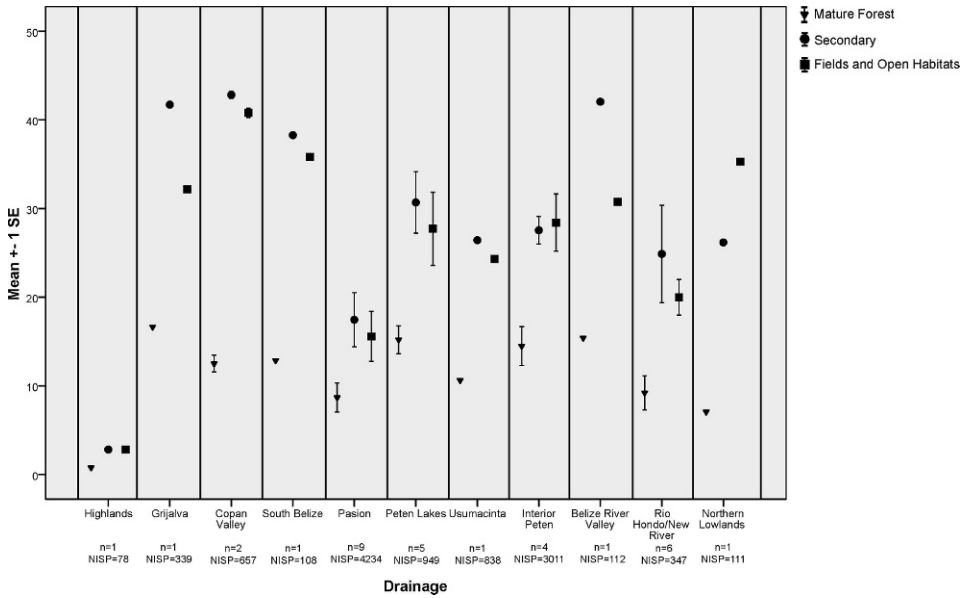


FIGURE 2a.—Variability in proportionate representation of remains of animals fidelic to mature forest, secondary forest, and agricultural lands. This chart provides mean and standard error from the mean for all site samples grouped by region (presented in approximate south to north order). These values reflect proportionate representation of species fidelic to these land cover types relative to all environmental types. Markers represent means, and bars represent one standard error of the mean. Note that triangles represent mature forest, circles represent secondary forest, and squares represent open habitats such as agricultural fields. Sample numbers (n) and sample NISP tallies for each region are listed along the x-axis.

agricultural lands. Given these relationships, and the predictive value of the fidelity measures, it is noteworthy that the Copan fauna suggest lack of both mature and secondary forest cover, and that the interior Petén data suggest high proportions of both mature forest and agricultural/residential species.

TABLE 4.—ANOVA values for all variables and ratios. Significant variation noted with *.

ANOVA (N=32)	Sites		Regions		Periods	
	F	Sig.	F	Sig.	F	Sig.
Mature Forest (MF)	4.287721	0.01*	1.847384	0.11	1.346418	0.27
Secondary (SEC)	7.621266	0.00*	2.863965	0.02*	1.304519	0.29
Agricultural/Open habitats with scattered trees (AGR)	4.033071	0.01*	3.943899	0.00*	1.879265	0.12
Residential (RES)	253.2796	5.46	347.3751	8.18	0.729223	0.63
Ratio of Mature to Secondary (MF:SEC)	1.061137	0.48	0.966231	0.49	0.65686	0.68
Ratio of Secondary to Agricultural and Residence (SEC:AGR+RES)	5.682716	0.00*	1.333735	0.27	3.021508	0.02*

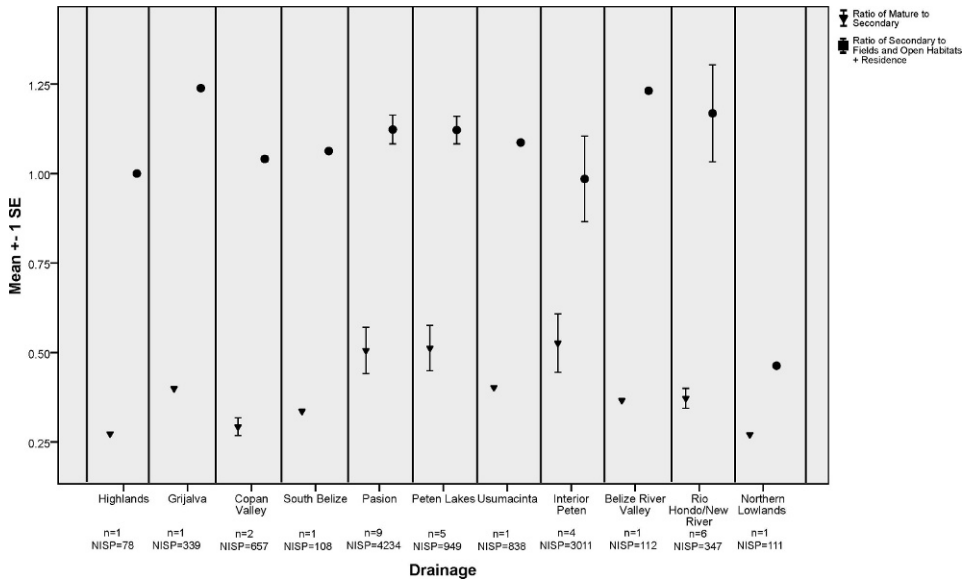


FIGURE 2b.—Variability in ratios of remains of animals fidelic to mature forest versus secondary forest, and secondary forests versus agricultural and residential lands. This chart provides mean and standard error from the mean for all site samples grouped by region (presented in approximate south to north order). Note that triangles represent the ratio of mature forest to secondary forests and squares represent the ratio of secondary forests to the combination of open habitats and residential areas. Markers represent means, and bars represent one standard error of the mean. Sample numbers (n) and NISP tallies for each region are presented along the x-axis.

To address chronological variation in land cover change at a broad regional scale, we calculated combined fidelity values for all samples dating to discrete time periods (Figure 3a). In this analysis, species representation of the various habitat types does not vary significantly over time periods (Table 4). At no time is MF a large component of the assemblages in comparison to SEC or AGR, but at no time does MF disappear or become less predominant in comparison to other land cover types.

Although the ratio of MF:SEC is fairly consistent, this ratio is somewhat higher during the Late Classic and Late Postclassic periods (Figure 3b). The ratio of SEC:AGR+RES is also highest during these periods. Of interest is the relative change in the two ratios over the period of highest human population and settlement impact, the Classic period. MF:SEC is low during the Terminal Preclassic and gradually rises through the Early Classic to a high level in the Late Classic, followed by a drop during the Terminal Classic. Tested with independent student t-tests, these differences are insignificant. The ratio of SEC:AGR+RES is quite low during the Early Classic, but is high in the Late Classic and at its lowest level during the Terminal Classic. This ratio varies significantly between the Late Classic and Terminal Classic (Independent Student t-test $t=2.265$, $p=0.038$). Both the ratio of MF:SEC and of SEC:AGR+RES

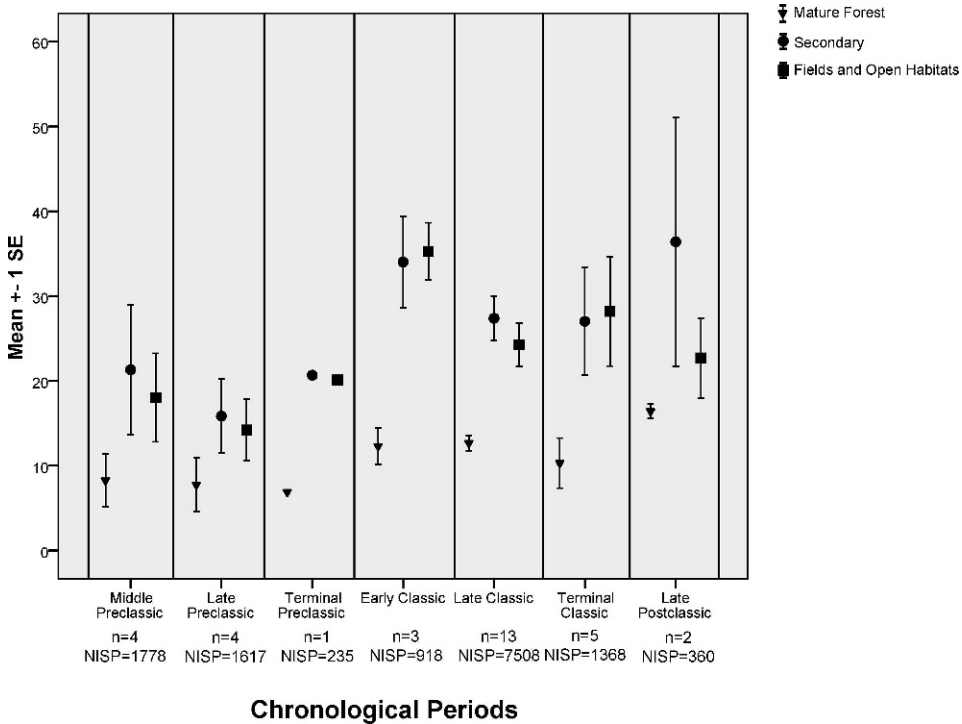


FIGURE 3a.—Variability of relative values of mature and secondary forests and agricultural lands in each time period. These values reflect proportionate representation of species fidelic to these land cover types relative to all environmental types. Note that triangles represent mature forest, circles represent secondary forest, and squares represent open habitats such as agricultural fields. Sample numbers (n) and NISP tallies are listed along the x-axis.

are highest during the Late Postclassic, but variability between samples during this period is also high so the difference cannot be evaluated statistically.

DISCUSSION

These analyses of ancient Maya habitats over time and space suggest considerable stability and regional consistency in the presence of animals from mature forests. We consider these to be intriguing proxy evidence for the stable presence of these forests during all time periods and through all regions of the Maya world.

The fidelity indices used here argue that mature forest was retained over sufficient proportions of the Maya area, and animals from these forests continued to be available during all time periods at least at the regional level. At particular sites, such as those in the Pasión region, fragments of mature forest could have persisted along waterways thus providing increased access to mature forest species in all time periods. In other regions, it is possible that mature forest was retained in areas less suitable for cultivation, even in heavily settled areas. It is also probable that mature forest species including jaguars, colorful birds,

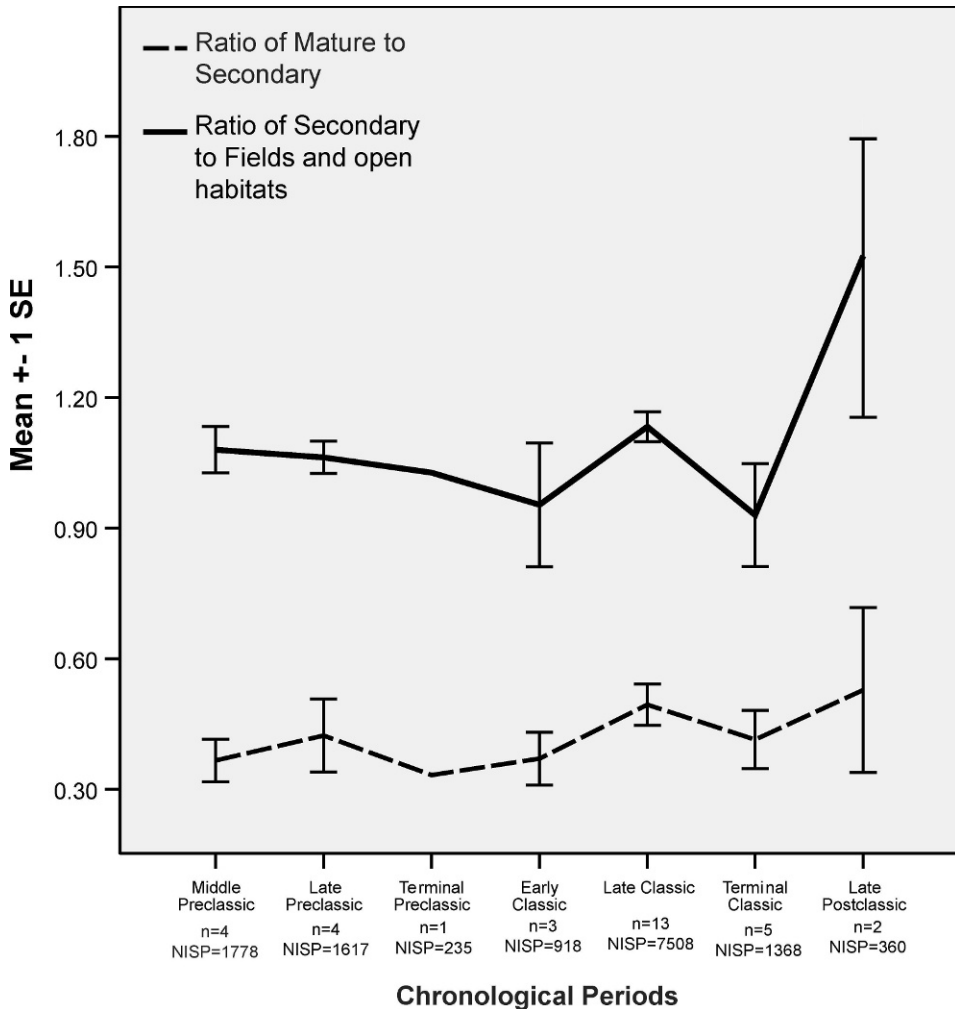


FIGURE 3b.—Variability in the ratios of forest types and disturbance type land cover over time. Note that the broken line represents the ratio of mature forest to secondary forests and the solid line represents the ratio of secondary forests to the combination of open habitats and residential areas. Error bars represent 1 standard error of the mean, points represent means of all samples per period. Sample numbers (n) and NISP tallies are presented along the x-axis.

monkeys, and other symbolically important species, were so highly prized that they could have been procured through trade or long-distance hunting expeditions even if mature forest habitat was not available within a region.

Secondary forests, the most diverse and most stable of forest types, were, according to these results, the most common land cover throughout the ancient Maya world. The relationship of mature to secondary forest and secondary to agricultural and residential lands is of particular interest in this study. The category of “disturbed lands” is often conflated in environmental reconstruction models to include secondary forests, agricultural lands, and lands cleared for

settlement. In this study we have defined land cover types specifically on the basis of the animals that would be attracted to each type, not in terms of land utility. In modern Maya terminology for land use systems the three categories of "disturbed" lands are very different and there exists a virtual continuum of fully cleared through fully forested lands, each the product of intentional interaction between the Maya and the landscape (Atran 1993; Atran 2003; Campbell et al. 2006; Fedick and Ford 1990; Ford 1991; Gomez-Pompa et al. 1987). Secondary forests are in fact the habitat best suited for animal procurement since forest gaps and their edges are the favored habitat for many of the most important food species (Linares 1976; Neusius 1996; Robinson and Bennett 2004; Smith 2005; Stahl 2006). Even residential areas, primarily cleared of underbrush, include highly diverse home gardens and arboriculture, and attract their share of animals though fewer of these are considered important edible species. Important to this study therefore is the consistently high proportion of species fidelic to secondary forests to those from both mature forests and agricultural and residential lands in most regions and time periods. If, as is argued by many authors, including those in this volume, the ancient Maya specifically created and maintained secondary growth as 'forest gardens,' the high proportion of secondary growth species in the ancient Maya world is not unexpected.

Despite considerable regional and chronological stability in the relative proportions of species found in mature forest and secondary forest, our data indicate that some variation in land cover did take place over the history of the Maya occupation. These changes must be evaluated with reference to the settlement history of the Maya world. Densely settled centers characterized by monumental architecture and agricultural expansion appeared by the Late Preclassic. Population sizes and site complexity continued to increase throughout the Classic period, but in the lowland regions, show a slight decline between the Early and Late Classic transition in what is referred to as the Middle Classic "hiatus." Maya culture reached its apogee in the Late Classic period when settlement and population expansion, as well as political and social stratification, peaked at sites throughout the Maya lowlands. It is during this time period that settlements and agricultural fields were at their most expansive, and the number of non-agricultural, politico-religious elites was at its greatest. Political and economic reorganization and major shifts in settlement focus occurred during the "Classic Maya Collapse", which marks the transition between the Late and Terminal Classic periods. The Terminal Classic represents a time of cultural florescence in the northern lowlands as new cultural centers and trade systems appeared. These new cultural patterns continued throughout the Postclassic period until arrival of the Spanish in the 16th Century. (A complete review of Maya settlement history may be found in Henderson 1997).

Our results track an unexpected pattern of land cover change, given the history of population and settlement changes in the southern Maya lowlands at least. Population levels and political activity were high during the Late Preclassic and yet so, apparently, was the ratio of mature to secondary forest. Population sizes and political activity peaked again during the Late Classic, and both the ratio of mature to secondary forest and secondary forest to agricultural/residential lands appear to rise during this period.

Several possibilities might explain apparent incongruities of these patterns. As suggested by Ford (this volume), it is possible that during periods of highest population expansion, the ancient Maya were most effective at creating and maintaining the 'forest gardens,' so essential for their plant and animal resources. As Classic populations grew and settlements and agricultural fields expanded, it is possible that intentional efforts were made to maintain mature forest reserves and manage regions of secondary growth to ensure continued resource availability. This might not have been the case at all sites, but might have been a broad pattern over the regions as a whole.

Other scenarios are also worthy of discussion. As mentioned earlier, it is possible that the symbolic importance of high forest species for the ancient Maya meant that they went out of their way (and their territory) to acquire these fauna. It is particularly important that these species, and the white-tailed deer a species attracted to secondary growth, and one of the most common species in all Maya faunal assemblages, often represented status markers for the elite who, according to zooarchaeological evidence, maintained greater access to these resources (Emery 2002; Pohl 1985; Pohl 1994). Since many of the zooarchaeological assemblages from the Maya area were recovered from elite deposits, it is possible that the increases in mature forest fauna and in secondary forest fauna in the form of white-tailed deer, reflect increased use of these species by a steadily increasing number of elite during the periods of greatest political activity. Other zooarchaeological studies have shown that hunting was least sustainable and had greatest impact around the largest and most politically active sites (Emery 2007). Nonetheless, if these species were not available through at least long-distance forays or trade, none would have been recovered in the zooarchaeological record regardless of their importance to the elite or otherwise.

Finally, it is also important to consider the longer-term environmental impact of settlement and population expansions and contractions. Recent research in species response to habitat fragmentation indicates that animal populations decline and recover slowly from habitat alteration (Loyn 1987; Robinson 1999; Tillman et al. 1994). It is possible that rising use of mature and secondary forest species during the Late Preclassic, Late Classic, and Late Postclassic represent the rebound of fauna following hiatus periods during the Middle Preclassic, Early Classic, and Terminal Classic. Lower proportions of these species during the Terminal Preclassic and Terminal Classic, may represent the impact of settlement expansion from the preceding periods.

In conclusion, by calculating proportional habitat fidelity measures for different species found in zooarchaeological assemblages from various regions of the Maya world, we have created a relative measure of habitat representation that can be used as proxy evidence for evaluating land cover changes over time and space. In this study, we have found several suggestive pieces of evidence to indicate the intentional maintenance of secondary forest and possibly even mature forest at stable levels throughout ancient Maya occupation. We have not found significant evidence to support a model of extensive land clearance at any time.

Although we conducted a regional analysis, the observed site level variability indicates that settlement and land use strategies may have varied considerably

across the Maya cultural region. Further research should emphasize the qualitative details of each site's unique situation because the fidelity values used in this regional analysis are, by necessity, generalizations. Fidelity categories are not effective at capturing the difference between mature forests and gallery forests along river edges, a habitat known to harbor many species classified here simply as mature forest species, or between agricultural lands and natural areas of low growth, habitats with very similar animal groups but very different implications. These habitats vary at the site level and should be evaluated separately. As well, such generalized evaluations are not able to capture the effects of site-specific choices in animal management, such as domestic turkey and dog, and husbanded deer, peccary, and other species proposed by various authors on the basis of ethnographic evidence (e.g. Cooke et al. 2008; Hamblin 1985; Pohl and Feldman 1982). As future research recovers more large, well-dated zooarchaeological samples spanning the entire period of Maya occupation, it may be possible to address the question of environmental management versus mismanagement at this more detailed site level to improve our understanding of Maya land use.

Our research has thrown into question the relationship of Maya development and population growth on the one hand and loss of forest cover on the other. The link between environmental change and the 'Maya collapse' and other societal changes has been used in recent literature as a "lesson" in the importance of environmental conservation (e.g. Diamond 2004). This research and other such studies indicate that the uncritical adoption of the thesis of environmental mismanagement is not acceptable. It behooves us to be sure that the correct lesson is provided to the reading public – in this case perhaps that the relationship between the ancient Maya and their forests was complex and intentional, and that no single explanation for human impact on the Maya forest is appropriate since site-level histories are vital to our understanding.

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