

Garden Game: Shifting Cultivation, Indigenous Hunting and Wildlife Ecology in Western Panama

Derek A. Smith¹

Participatory research documented the hunting yields of 59 households in five neighboring indigenous villages in western Panama. These households captured 2,580 kg of game over 8 months, with 47% of the harvest coming from agricultural areas. The quantity of game captured in anthropogenic habitats is influenced by the hunting strategies employed. Only 25% of game captured during hunting trips was captured in agricultural areas, as opposed to 93% while “awaiting” and 65% using traps. Reliance on different strategies is in turn dependent on age, gender, and access to firearms. I argue that garden hunting is not a response to game depletion, but rather a productive activity that is complementary to broader cultural and economic patterns, and that simultaneously protects crops from animal predation. The creation of heterogeneous habitat mosaics through shifting cultivation has played a key role in the relationship between people and wildlife in the humid neotropics, leading to adjustments in both animal foraging patterns and indigenous hunting practices.

KEY WORDS: indigenous hunting; shifting cultivation; cultural landscapes; neotropical wildlife; Buglé; Panama.

INTRODUCTION

Almost three decades ago, Olga Linares (1976) called attention to the importance of “garden hunting” in the humid neotropics. Her archaeological analysis of faunal remains led her to conclude that certain terrestrial mammals that forage in anthropogenic habitats were likely more abundant near human settlements, and provided a reliable, convenient

¹Department of Geography and Environmental Studies, Carleton University, Ottawa, Canada; e-mail: dereka_smith@carleton.ca.

protein resource for prehistoric horticulturists. Since then, numerous field researchers have noted that game animals raid the fields of shifting cultivators and that indigenous hunters capture game in agricultural areas. Nevertheless, despite its widespread practice, garden hunting has received little systematic study. Knowing the type and quantity of game caught in anthropogenic habitats under different conditions can help explain why and when indigenous hunters rely more heavily on garden game and the implications this may have for other species found only in mature forest. This paper presents research on hunting as practiced by the Buglé of western Panama, with a focus on the type and quantity of game captured in anthropogenic versus mature forest habitat, the factors conditioning the importance of garden hunting, and the role of agricultural areas in neotropical wildlife conservation. Two hypotheses directing the research were: (a) that garden areas are a significant source of game among the Buglé, and (b) that there are significant differences in the type of game captured in agricultural areas which are related to the foraging patterns of different game species.

THEORETICAL CONTEXT

Concern about the loss of biodiversity has fueled a vigorous debate about the relationships between indigenous peoples and wildlife in the humid neotropics (Alcorn, 1993; Alvard *et al.*, 1997; Herlihy, 1997; Johnson, 1989; Peres and Zimmerman, 2001; Redford, 1990; Redford and Stearman, 1993). Localized depletion of certain game species has been documented in a variety of settings, as indicated by declining yields over time, the need to travel farther to find game, or lower game densities in hunted versus similar, un hunted areas (Baksh, 1995; Good, 1995; Mittermeier, 1991; Orejuela, 1992; Peres, 2000a, b; Stearman, 1995). Over time, hunting can result in depauperated "empty forests" leading to changes in the floristic composition of forests through impacts on seed dispersal and other processes (Andresen, 2000; Bodmer, 1991; Dirzo and Miranda, 1991; Redford, 1992). However, the degree of game depletion is highly variable. Hunting yields are conditioned by numerous factors, including settlement patterns, the availability of different technologies, proximity to markets, time constraints, and food taboos and other cultural proscriptions (Balée, 1985; Bergman, 1980; Godoy *et al.*, 1995; Grenand, 1992; Gross, 1975; Hames, 1979; McDonald, 1977; Nietschmann, 1972; Reichel-Dolmatoff, 1996; Ross, 1978; Vickers, 1980, 1991; Yost and Kelley, 1983). The type and quantity of game captured at a particular site and the impacts of different harvest rates are also conditioned by the varying abundance of different species across space and over time, which in turn is highly dependent on the distribution of different types

of habitat—including anthropogenic habitat (Bodmer, 1995; Eisenberg and Thorington, 1973; Nietschmann, 1972; Peres, 1994; van Shaik *et al.*, 1993).

A number of scholars have attempted to measure the impact of indigenous hunting by comparing harvest rates with estimates of maximum sustainable yields (Alvard *et al.*, 1997; Leeuwenberg and Robinson, 2000; Mena *et al.*, 2000; Townsend, 2000). Sustainable yields are based on rates of reproduction, which are in turn calculated using an estimate of each species' population density at carrying capacity (Robinson and Redford, 1991). While it remains an excellent approach, this model suffers from a large degree of uncertainty. One of the most significant problems to be resolved is the questionable accuracy of the average population density estimates that are used to determine sustainable yields. Species' densities can vary tremendously from place to place in relation to soil fertility, forest structure, and interspecific competition (Beck-King and von Helversen, 1999; Emmons, 1984; Robinson and Redford, 1986), and are often subject to significant measurement error (Cant, 1977; Glanz, 1982; Hill *et al.*, 1997). Furthermore, estimates are typically obtained from remote forest locations where human influences on natural processes are slight, while indigenous hunting usually takes place in regions characterized by heterogeneous environments that include both undisturbed and anthropogenic habitats associated with shifting cultivation. Models that evaluate the sustainability of indigenous hunting that are based on ecological dynamics of forest areas unaffected by humans may consequently generate misleading results.

Habitat modification through shifting cultivation plays a pivotal role in the relationship between indigenous peoples and wildlife. Rotational agriculture creates habitat mosaics that include gardens, fallows in various stages of succession, undisturbed vegetation, and a variety of ecotones. While forest clearance destroys habitat for many species, at relatively low human population densities, the creation of cultural landscapes that include a mix of anthropogenic and natural habitats can provide benefits to others. A wide variety of game animals forage in agricultural fields and fallows, sometimes causing significant crop losses (Balée, 1985; Balée and Gély, 1989; Berlin and Berlin, 1983; Borge and Castillo, 1997; Carneiro, 1983; Gordon, 1982; Hames, 1980; Posey, 1984; Smole, 1989; Ventocilla, 1992). In fact, in some areas, indigenous farmers plant crops in special areas or deliberately manage fallows to increase the abundance of fruit trees that attract game (Balée and Gély, 1989; Nations and Nigh, 1980) so it is not surprising that indigenous hunting in gardens and fallows has been reported frequently (Balée, 1985; Carneiro, 1970; Gordon, 1982; Hames, 1980; Herlihy, 1986; Medellín-Morales, 1990; Naughton-Treves, 2002; Nietschmann, 1972; Posey, 1985; Ross, 1978; Ruddle, 1974; Smole, 1989; Steinberg, 1998; Vickers, 1991).

This paper address the relative importance of gardens and fallows as a source of game, and what role these anthropogenic habitats might play in wildlife ecology and conservation management. Some have suggested that reliance on smaller game species such as those that are found in garden areas represents a response to the depletion of larger, more vulnerable game animals in the surrounding forest (Chicchón, 1995; Ross, 1978; Stearman, 1995), the exact opposite of Linares' (1976) thesis that prehistoric hunters specialized in the capture of "commensal" species, largely disregarding forest game. While it may be tempting to assume that indigenous hunters shift their attention to more resilient species found in agricultural areas only after game in the forest has been depleted, there are insufficient quantitative data comparing harvests from anthropogenic and primary forest habitat to support this argument, let alone studies that focus on the type and quantity of game in these different environments over time.

STUDY AREA AND METHODS

The research presented here took place in the northern portion of the Province of Veraguas, in western Panama. The region is one of the more remote parts of the country and retains large tracts of biologically diverse broadleaf, evergreen rain forest,² in part because it was rapidly depopulated soon after the Spaniards first arrived on the isthmus in the early 16th century (Castillero, 1995). Today it is home to the Buglé, who have been slowly expanding their range from neighboring areas to the west, as well as more recent Ngöbe arrivals and the descendants of mestizo families who arrived as refugees fleeing armed conflict around the turn of the 20th century. The population of the Buglé, who are the main focus of this study because of their greater involvement in hunting, has been estimated at from less than 2,000 to over 18,000 (República de Panamá, 2001; Young, 1995). They are one of the least understood cultural groups in Central America and until recently have usually been identified as a subgroup of the Ngöbe, despite the fact that the two have mutually unintelligible languages (Herrera and González, 1964). Despite centuries of disruption and change, the Buglé continue to speak their native language, depend on traditional agricultural practices, and maintain an intimate relationship with their natural surroundings.

The study area consists of the lands used by the five neighboring villages found in the Río Caloveborita watershed, with a total of 99 households and 612 people at the time of field research (Fig. 1). The size of the zone

²For more information on the fauna of the region see Eisenberg, 1989; Emmons, 1990; Leigh *et al.*, 1982; McDade *et al.*, 1994; Savage and Villa, 1986.

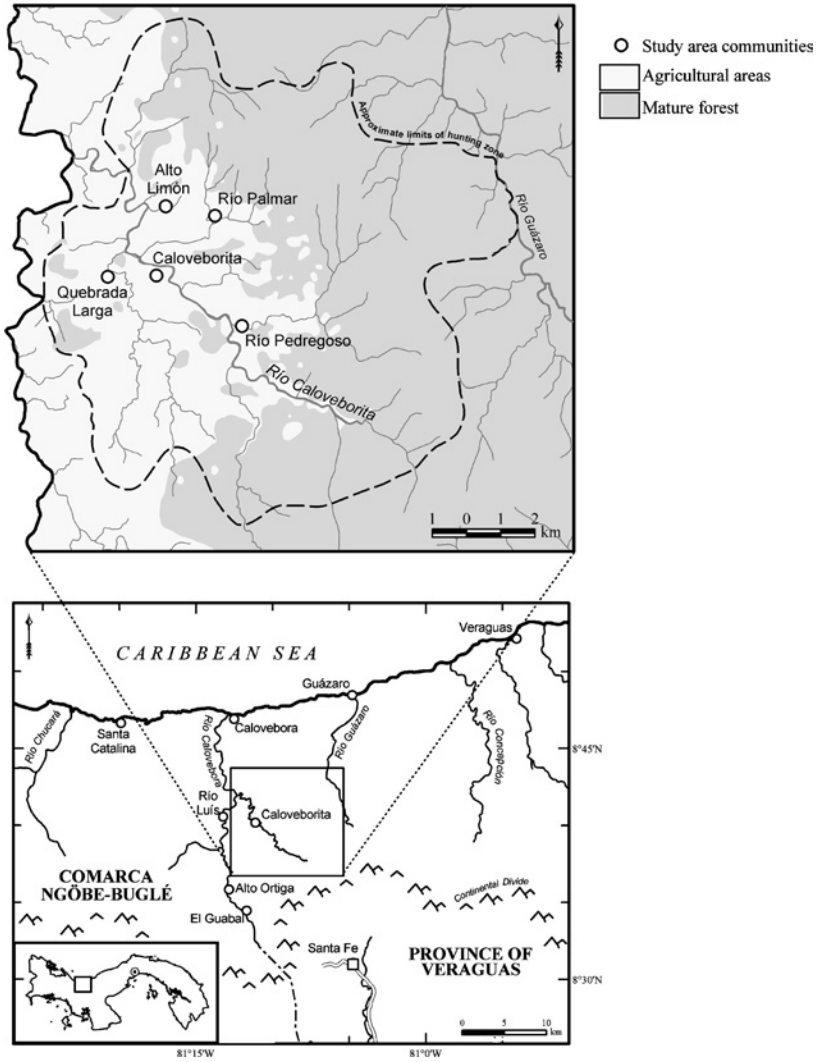


Fig. 1. Location of the study area.

used by hunters at the time of fieldwork was approximately 131 km², 61 km² consisting of mature forest and the remainder of gardens, fallows, small pastures, and village lands. Families in the Caloveborita region rely on shifting cultivation, and participate to varying degrees in animal husbandry, hunting, fishing, and gathering wild plant foods. Most households have at least two or three active gardens, as well as fallows in various stages of regrowth.

Because no true dry season exists, vegetation cleared for new farms is usually not burned, but rather left to decay in the field, and farms are initiated year-round. As in other rain forest regions inhabited by indigenous communities, larger expanses of agricultural land surround riverine settlements, and as one moves away from the villages toward unoccupied lands, islands of forest appear, and clearings gradually disappear. Local livelihoods are based on subsistence activities rather than market economies, but most men work on sugar plantations outside of the region for one to several weeks during the harvest season.

The research, which was formally endorsed by the indigenous federation representing the region, was carried out over a period of 12 months, from June 1999 to June 2000. Throughout this period, I undertook participant observation, conducted interviews, carried out field mapping, and accompanied villagers on hunting trips whenever possible. A subset of 59 of the 99 households in the Caloveborita region was selected for more intensive research on hunting activity.³ This part of the research involved local investigators who were trained to administer weekly questionnaires in their respective villages for a period of 8 months (Smith, 2003b). From October 1999 to May 2000 the local investigators visited each household every week to record data on the timing of hunting trips, the technologies and strategies used, and information about each prey item captured, including the type of habitat in which the animal was encountered. Given that the local investigators had little formal education and no previous research experience, I met with them individually every 2 weeks or so to review the completed questionnaires to ensure that information was being recorded thoroughly and accurately, and to provide further training as needed (Smith, 2003b). Even though respondents were visited every week, some of the animals that were captured may not have been recorded at the time of the interviews, particularly small prey items given that people place little importance on small game, especially the numerous small birds that are caught by children. However, cross-checks confirmed that all of the important game animals were being recorded, and there were no indications that there was any conscious underreporting among the 59 households that agreed to participate in the study. Weights for each prey item were later compiled using average body mass estimates (Dunning, 1993; Eisenberg, 1981; Robinson and Redford,

³Forty households were removed based on results of a questionnaire that identified families whose reliance on hunting is negligible. The Buglé are the most numerous cultural group and the most active hunters, and were the main focus of the research, although a few Ngöbe and mestizo households were included. Hunters occasionally left the study area for brief periods during the research, usually to work for wages outside of the region, but overall, the study population was fairly stable. Only one of the 59 households participating in the hunting activity research moved out of the region during the study period, after providing information for 4 months.

1986; Stiles and Skutch, 1989). Toward the end of the field research I undertook structured interviews with a sample of 33 Buglé and other residents about game preferences and agricultural pests.

BUGLÉ HUNTING STRATEGIES

Hunting among the Buglé is an important component of a dynamic, diversified subsistence strategy, and part of a way of life that is intimately connected with the natural environment. It is an occasional, predominantly male activity practiced exclusively for subsistence. The primary technologies used are firearms, the bow and arrow, hunting dogs, machetes, slingshots, and a variety of traps. Rifles are the weapon of choice, although their use is limited due to their cost and the expense of ammunition. In addition to hunting trips—expeditions specifically dedicated to tracking and pursuing animals—there are three other general categories of how game is procured: “awaiting” at specific locations known to attract game, the use of traps, and the opportunistic capture of game. Each of these hunting strategies is associated with different types and quantities of game, as well as differences in the proportion of game encountered in agricultural areas.

Buglé men go on hunting trips when they have free time, which is often limited by the demands of agricultural work or the need to engage in wage labor. Hunting trips usually consist of an expedition of a day or less in areas within 4 or 5 km from the village, although hunters occasionally go on extended overnight trips to more distant forest areas. Hunting trips are most often directed toward the forest, but animals are also captured in agricultural areas on the way. Most trips can be characterized as general searches, but directed trips also occur, for example those that target tapir (*Tapirus bairdii*), white-lipped peccaries (*Tayassu pecari*), or animals that have been eating a farmer’s crops. The only dietary taboos involving larger animals are those that apply to snakes, the northern tamandua (*Tamandua mexicana*), the silky anteater (*Cyclopedes didactylus*), and the northern naked-tailed armadillo (*Cabassous centralis*). Among animals considered edible, game preferences are conditioned by body mass, ease of preparation, taste, and cultural attitudes toward different animals. Animals are used almost exclusively for meat, rather than for decorative, medicinal, ceremonial, or other purposes.

A second strategy for procuring game consists of “awaiting” animals at a fixed location, usually at night in a simple scaffold constructed in a tree. Awaiting almost always occurs in gardens where farmers have seen evidence that animals have been raiding their crops. At times hunters also

leave small piles of food in their field repeatedly over a few days so that an animal will be more likely to return. Hunters also occasionally await game in older fallows, for example where *tumá* trees (*Gustavia* sp.) are fruiting, as well as in primary forest, but this is much less common. A third general strategy for capturing game consists of using one of a variety of traps. The most common is a deadfall trap consisting of two short fences on either side of an animal trail, with a log weighted with stones suspended between them that falls on an animal when it trips a release. These traps are placed in both agricultural and mature forest areas where fresh tracks are discovered. Another trap consists of a long, low fence of palm leaves that can reach lengths of 100 m or more inserted into the forest floor. Narrow openings are made at intervals of about 2 m, and armed with snares placed at the opening a short distance above the ground. Large terrestrial birds—mainly the great currawong (*Crax rubra*) and great tinamou (*Tinamus major*)—are caught when they attempt to cross the fence through one of the openings. This trap is usually constructed in primary forest where they are most likely to catch susceptible prey, but relatively close to home so that caretakers can check their trap regularly. Additional traps that are used include snares tied to a spring mechanism and a conical net that is placed at the entrance of armadillo (*Dasyurus novemcinctus*) burrows.

Finally, the Buglé also catch game opportunistically. This “strategy” entails obtaining game while involved in another pursuit, such as clearing fields, weeding, collecting medicinal plants, or simply walking from one place to another. Farmers regularly carry weapons or bring dogs with them to their fields to take advantage of the possibility of encountering game unexpectedly, as is the case among other indigenous groups (Baksh, 1995). When mammals such as armadillos, agoutis (*Dasyprocta punctata*), or red brocket deer (*Mazama americana*) are discovered by dogs, work is interrupted to take up the chase. In addition, arboreal animals like sloths (*Bradypus variegatus* and *Choloepus hoffmanni*) and kinkajous (*Potos flavus*) are sometimes discovered when clearing trees for new farms. A great diversity of birds is captured by both adults and children with slingshots where they are found along trails, in agricultural fields, in isolated trees in pastures, and in gardens in the immediate vicinity of the home.

A primary reason why garden hunting is practiced in the Caloveborita region is the fact that many game species pose a serious threat to farm output. Not surprisingly, several of the most important species captured in agricultural areas are also among the most common agricultural pests identified in interviews with a sample of local farmers (Table I). Given the potential for significant losses, farmers employ a variety of practices to protect their fields from wildlife. Some build provisional shelters in their gardens

Table 1. Most Significant Vertebrate Crop Pests in the Caloveborita Region as Reported by Buglé and Other Local Farmers (*n* = 33)

Common name	Scientific name	Maize	Manioc	Yams	Peach palm	Rice	Dasheen	Bananas
Paca	<i>Agouti paca</i>	●	●	●	*			○
Great-tailed grackle	<i>Cassidix mexicanus</i>	●				○		
Blue ground-dove	<i>Claravis pretiosa</i>					●		
Central American agouti	<i>Dasyprocta punctata</i>	○		●	*			
Spiny rats, other rats	Echimyidae, Muridae	○	●	○	*		○	
Red brocket deer	<i>Mazama americana</i>		●		*			
White-nosed coati	<i>Nasua narica</i>	●	●					○
Blue-headed parrot	<i>Pionus menstruus</i>	●			●			
Collared aracari	<i>Pteroglossus torquatus</i>				●			○
Chestnut-mandibled toucan	<i>Ramphastos swainsonii</i>				●			○
Red-tailed squirrel	<i>Sciurus granatensis</i>	●			●	○		○
Collared peccary	<i>Tayassu tajacu</i>	●	●	●	*		●	
Blue-black grassquit	<i>Volatinia jacarina</i>					●		

Note. (●) primary pest; (○) secondary pest; (*) eats fallen fruit. Male and female farmers were asked to name the most significant animal pests that cause damage to each of the seven primary crops grown in the region. Primary pests are those reported by at least half of the respondents; secondary pests are those reported by over 20% of respondents. While not a precise quantitative method of assessing amounts of crop losses, the findings do indicate which animals are the most important pests. Although many species were often identified, there was considerable agreement between interviewees as to which animals are the most destructive. Only the most common pests are listed.

where they spend most of their time around harvest season. Others build scarecrows or burn small fires periodically in their fields to help keep animals away. Another important measure is awaiting game. Although Buglé hunters usually talk about awaiting in terms of a way of obtaining meat—and sometimes await animals in farms that do not belong to them—it is clear that in at least some cases a primary objective is to protect their gardens. This is evident, for example, when farmers await white-nosed coatis (*Nasua narica*) in maize fields to prevent the devastation that can be caused over a few days by a troop of several animals. The paca (*Agouti paca*), which eats maize, yams, and manioc, is one of the most commonly cited pests, and is a species that hunters often await at night in their gardens. Similarly, hunting trips may be organized specifically to kill animals that have been foraging in gardens, particularly collared peccaries (*Tayassu tajacu*) that have been raiding a field of tubers or a paca that has been eating maize. In some instances, distant farms are abandoned because farmers are not able to look after them properly, leaving them vulnerable to animal raids. Without the necessary vigilance, crops may be lost entirely to terrestrial mammals.

BUGLÉ GAME HARVESTS FROM ANTHROPOGENIC AND MATURE FOREST HABITATS

The 59 households participating in the hunting research caught 2,481 animals with a total yield of 2,580 kg over a period of 8 months (Table II). When extrapolated over an entire year, this represents an annual average of roughly 65 kg per household.⁴ The harvest includes 27 mammals, seven reptiles, and over 100 bird species, but just five mammals account for over half of the total harvest: pacas, agoutis, armadillos, collared peccaries, and howler monkeys (*Alouatta palliata*). Game captured during hunting trips accounted for 55% of the total harvest; 13% of the harvest was caught while awaiting; 12% was captured using traps; and the remaining 20% was caught opportunistically. Together, rifles and shotguns were used to catch almost half (49%) of the total harvest. The deadfall trap is the third most important technology, accounting for 8% of the total harvest. Variability in the amount of game captured within the community was significant, with the top 20 of 59 households accounting for about three-quarters of the total

⁴This average is not representative of all of the families in the study area. As noted earlier, a number of households were removed from the hunting study because none of the members are active hunters and rarely capture game. In addition, a few of the households that were included among the 59 households only captured a small quantity of game during the study period and might not be considered active hunting households. The average is thus in part an artifact of who is included and who is not.

Table II. Hunting Yields, Caloveborita Region, October 1999 to May 2000 (59 Households)

Rank	Scientific name	English name	Total (kg)	Number captured
1	<i>Agouti paca</i>	Paca	325	51
2	<i>Dasyprocta punctata</i>	Central American agouti	297	102
3	<i>Dasytus novemcinctus</i>	Nine-banded armadillo	294	110
4	<i>Tayassu tajacu</i>	Collared peccary	272	18
5	<i>Alouatta palliata</i>	Mantled howler monkey	190	33
6	<i>Tapirus bairdii</i>	Baird's tapir	150	1
7	<i>Bradypus variegatus</i>	Brown-throated three-toed sloth	119	39
8	<i>Choloepus hoffmanni</i>	Hoffmann's two-toed sloth	113	17
9	<i>Mazama americana</i>	Red brocket deer	104	4
10	<i>Sciurus granatensis</i>	Red-tailed squirrel	64	188
11	<i>Potos flavus</i>	Kinkajou	61	27
12	<i>Ateles geoffroyi</i>	Central American spider monkey	53	7
13	<i>Crax rubra</i>	Great curassow	52	14
14	<i>Rhinoclemys annulata</i>	Neotropical wood turtle	44	43
15	<i>Cebus capucinus</i>	White-faced capuchin monkey	41	14
16	<i>Puma concolor</i>	Puma	37	1
17	<i>Tinamus major</i>	Great tinamou	32	34
18	<i>Penelope purpurascens</i>	Crested guan	28	16
19	<i>Sylvilagus brasiliensis</i>	Forest rabbit	26	32
20	<i>Nasua narica</i>	White-nosed coati	25	9
21	<i>Ramphastos swainsonii</i>	Chestnut-mandibled toucan	24	39
22	<i>Basiliscus plumifrons</i>	Green basilisk	22	100
23	<i>Pteroglossus torquatus</i>	Collared aracari	18	84
24	<i>Panthera onca</i>	Jaguar	17	1
25	<i>Chelydra serpentina</i>	Common snapping turtle	15	3
26	<i>Bassaricyon gabbi</i>	Olingo	11	5
27	<i>Procyon lotor</i>	Northern raccoon	9	1
28	<i>Columba</i> spp.	Pigeons (3 species)	9	41
29	Echimyidae	Spiny rats (2 species)	8	19
30	<i>Iguana iguana</i>	Green iguana	8	3
	Other mammals (6 species)		21	43
	Other birds (over 100 species)		87	1,356
	Other reptiles (3 species)		3	26
	Total		2,580	2,481

harvest. There was no significant seasonality in hunting yields evident in the amount of game captured from month to month during the study period.

Almost half (47%) of the total amount of game captured during the study period was encountered in agricultural areas (Table III). Of the 1,213 kg harvested from these areas, approximately 28% was encountered in active gardens, 28% in young fallow (up to ~5 years in age), 36% in tall fallow (> 5 years in age), 3% in pastures, and the remainder in the immediate vicinity of someone's house. The most important species caught in agricultural areas by weight are the paca (247 kg), followed by the armadillo (180 kg), and the collared peccary (166 kg). The harvest of just these

Table III. Hunting Yields in Agricultural Areas and Mature Forest, Caloveborita Region, October 1999 to May 2000 (59 Households)

	Total (kg)	Habitat			
		Mature forest		Agricultural areas	
		(kg)	(%)	(kg)	(%)
Mammals	2,237	1,197	53	1,040	47
Birds	252	145	57	108	43
Reptiles	91	25	28	65	72
Total	2,580	1,367	53	1,213	47

three species from agricultural areas accounts for 23% of the total harvest from both anthropogenic and primary forest habitats combined. The agouti (90 kg) also figures prominently in the harvest from agricultural areas, despite the fact that it is captured more frequently in mature forest areas.

In addition to absolute totals, it is useful to consider the proportion of the harvest obtained from the two broad habitat classes for individual species (Table IV). This gives a better indication of which species are more likely to be captured in agricultural rather than mature forest areas irrespective of the total harvest, providing clues about how the foraging patterns of game species may change in response to habitat modification. I have grouped the most important game taxa (total harvest >6.5 kg) into three categories based on the relative amounts captured in anthropogenic versus mature forest habitat. These are “garden game” taxa for which at least 75% of the harvest was obtained from agricultural areas, “deep forest game” species for which at least 75% of the harvest was obtained from primary forest, with “intermediate species” making up the remainder. By far the most important garden game species by weight is the paca. Just over three quarters of the harvest, 247 kg, was obtained from agricultural areas. The “deep forest game” species are the three primates found in the region (*Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus*), and three large birds—the crested guan (*Penelope purpurascens*), the great currawong, and the great tinamou. While some of the intermediate species could also be considered important garden game species, the contrast between the two ends of the spectrum highlights a fundamental distinction between game animals that forage and are captured in anthropogenic habitats and those that are sensitive to habitat disturbance and are caught primarily or exclusively in mature forest. These differences have important implications for understanding the human ecology of these regions and the ecological relationships between people and wildlife, as well as how to appropriately manage wildlife. It should be stressed, however, that the proportion of a

Table IV. Classification of Primary Game Species According to Proportion Captured in Agricultural Areas, Caloveborita Region, October 1999 to May 2000 (59 Households)

Scientific name	English name	Number captured	Total yield (kg)	Total from agricultural areas (kg)	% from agricultural areas
Garden game					
<i>Sylvilagus brasiliensis</i>	Forest rabbit	32	26	26	98
<i>Columba</i> spp.	Pigeons (3 species)	41	9	8	93
<i>Basiliscus plumifrons</i>	Green basilisk	100	22	20	90
<i>Ortalis cinereiceps</i>	Gray-headed chachalaca	17	7	6	86
Echimyidae	Spiny rats (2 species)	19	8	7	84
<i>Agouti paca</i>	Paca	51	32.5	24.7	76
Intermediate species					
<i>Sciurus granatensis</i>	Red-tailed squirrel	188	64	45	71
<i>Pteroglossus torquatus</i>	Collared aracari	84	18	12	69
<i>Bassaricyon gabbi</i>	Olingo	5	11	7	63
<i>Dasyopus novemcinctus</i>	Nine-banded armadillo	110	294	180	61
<i>Tayassu tajacu</i>	Collared peccary	18	272	166	61
<i>Nasua narica</i>	White-nosed coati	9	25	14	54
<i>Rhinoclemmys annulata</i>	Neotropical wood turtle	43	44	21	47
<i>Ramphastos vainsonii</i>	Chestnut-mandibled toucan	39	24	11	45
<i>Cholepeus hoffmanni</i>	Hoffmann's two-toed sloth	17	113	45	40
<i>Bradypus variegatus</i>	Brown-throated three-toed sloth	39	119	47	39
<i>Potos flavus</i>	Kinkajou	27	61	22	37
<i>Dasyprocta punctata</i>	Central American agouti	102	297	90	30
Deep forest game					
<i>Tinamus major</i>	Great tinamou	34	32	6	18
<i>Crax rubra</i>	Great curassow	14	52	8	16
<i>Cebus capucinus</i>	White-faced capuchin monkey	14	41	5	12
<i>Penelope purpurascens</i>	Crested guan	16	28	1	4
<i>Alouatta palliata</i>	Mantled howler monkey	33	190	0	0
<i>Ateles geoffroyi</i>	Central American spider monkey	7	53	0	0

Note. Does not include species where less than five individuals were captured.

species harvested in different types of habitat does not necessarily reflect its relative abundance in primary forest or agricultural areas. Estimating differential population densities in garden and forest areas would require transect surveys which were not done as part of this study.⁵

VARIABLES THAT CONDITION THE IMPORTANCE OF GARDEN HUNTING

Garden hunting yields are strongly related to the strategies hunters use. Awaiting occurs primarily in active gardens, and 93% of game caught while awaiting was captured in anthropogenic habitat (Table V). Traps are placed where people discover fresh animal tracks, and people tend to encounter them more frequently where they spend more of their time—in and on their way to their fields. Traps also need to be checked regularly so that captured prey do not spoil or get taken by predators, and so are placed fairly close to home rather than in distant forest areas. The deadfall trap is the most important trap used, and is more often placed in agricultural areas—Buglé hunters indicate that armadillos are particularly susceptible, and they account for about three-quarters of all game caught using this trap. Overall, 65% of game caught using traps was obtained in anthropogenic habitat. Opportunistic hunting also tends to occur close to home. While it is true that encounter rates are affected by variables such as the abundance of different species across space, wariness, and other variables, they are still largely dependent on where hunters spend their time. The Buglé, in the course of an average week, spend much more time near their home and in agricultural areas than in mature forest, and as a result, opportunistic hunting is more prevalent in agricultural and village areas. Accordingly, 66% of all game caught opportunistically was encountered in anthropogenic habitat.

In contrast, most hunting trips are directed toward primary forest, and 75% of game captured during these expeditions was encountered in this type of habitat. However while Buglé hunters are motivated to go on expeditions to more distant forest areas to capture species that are scarce close to home, such as monkeys, tapirs, or large birds, hunting trips are

⁵There are few studies that systematically compare the abundance of tropical forest animals in undisturbed versus secondary forest. One exception is Jorgenson (1993) who found that chachalacas (*Ortalis vetula*) were more than twice as abundant in gardens and young fallows than in old (>50 years) secondary forest in a semihumid region of Quintana Roo, Mexico. Another exception comes from the Ituri Forest in Central Africa, where researchers compared the relative abundance of game species in secondary growth and mature forests used by Efe hunters (Wilkie and Finn, 1990). Four mammal species were significantly more abundant in regrowth areas, despite the fact that these zones experience more intensive hunting pressure.

Table V. Proportion of Game Captured in Agricultural Areas and Mature Forest According to Hunting Strategy, Caloveborita Region, October 1999 to May 2000 (59 Households)

	Total (kg)	Habitat			
		Mature forest		Agricultural areas	
		(kg)	(%)	(kg)	(%)
Hunting trips	1,418	1,059	75	359	25
Awaiting	333	24	7	309	93
Traps	318	112	35	207	65
Opportunistic	511	172	34	338	66
Total	2,580				

only undertaken when men have free time, which is often limited by agricultural work or the need to engage in wage labor to obtain money for basic items like salt, sugar, tools, clothes, and school supplies for their children. Many if not most Buglé men work on sugarcane plantations outside of the region for one to several weeks during the harvest season from late January to early May, relieving pressure on wildlife resources in the Caloveborita region during this time. While less significant, game is also captured in anthropogenic habitat during hunting trips. As already indicated, game may be caught in gardens or fallows on the way to or from distant hunting grounds, and some trips are directed toward specific farms where animals have been raiding crops. In fact, 30% of game caught in agricultural areas was captured during a hunting trip, more than what was captured in anthropogenic habitat while awaiting, using traps, or opportunistically (Table VI).

It should be kept in mind, though, that hunting is not a purely economic activity determined by opportunity cost and the maximization of returns. Many Buglé men also go on hunting trips in mature forest areas because they enjoy it. While it is true that hunting is a critical source of food for many Buglé families, it is at the same time part of a tradition that is an integral part of their culture and identity. Men enjoy recounting stories about their hunting adventures, and it is evident that successful hunters enjoy a special respect among their peers. The “*daba dbimu*,” the mythical

Table VI. Proportion of Game Captured Using Different Hunting Strategies in Agricultural Areas and Mature Forest, Caloveborita Region, October 1999 to May 2000 (59 Households)

	Total (kg)	Hunting trips (%)	Awaiting (%)	Traps (%)	Opportunistic (%)
Agricultural areas	1,367	30	25	17	28
Mature forest	1,213	77	2	8	13
Total	2,580				

caretakers of forest animals, figure prominently in Buglé cosmology, and hunting represents one of the main links with their world. In addition, walking through the forest, observing the rhythms of the flora and fauna, collecting a handful or two of edible seeds or leaves, and sharing these experiences with young relatives all appear to have a value of their own that is appreciated by hunters. Hunting trips, then, can not be characterized as optimal foraging expeditions.

Nevertheless, while hunting trips do have intrinsic value, a decent return on the time invested is certainly desirable. According to local informants, the most important factor affecting hunting success is weaponry. Given the limited effectiveness of the bow and arrow in capturing arboreal and other game species, almost all hunting trips in primary forest today involve the use of a rifle or shotgun. Among adult males who do not go on hunting trips, the most commonly cited reason for not participating is lack of access to a firearm. Many of these people, however, still procure game with traps made from local materials or by awaiting in their gardens, which can be done successfully using a bow and arrow. Access to firearms thus plays a role in how much game is captured in agricultural areas.

The choice of hunting strategy, which affects the proportion of game caught in anthropogenic habitat, is not only related to access to firearms, however, but also to gender and age. For women, using traps is an alternative to going on hunting trips, which in general is not culturally acceptable except when accompanying their husbands—usually on longer, overnight expeditions on which their main tasks revolve around the preparation of meals. Women captured 21% of all game caught using traps during the study period, compared with their share of only 6% of the total harvest. Accordingly, of all game harvested by women, 65% was encountered in agricultural areas, significantly higher than the overall proportion of 47%. Likewise, most of the game captured by children is obtained closer to home along trails or in gardens, orchards, and other agricultural areas. Many elderly people told me that they no longer go on hunting trips because of their age, although they still capture game using other strategies. Consequently, research that focuses on individual hunters, as opposed to entire households, would likely underestimate the proportion of game obtained from agricultural areas.

DISCUSSION: GARDEN HUNTING, WILDLIFE ECOLOGY, AND CONSERVATION

The results of this study confirm both of the initial hypotheses, namely that agricultural areas are a significant source of game and that there are

significant differences in the type of game captured in anthropogenic versus mature forest habitat. Almost half of all game captured in the study area was encountered in anthropogenic habitats, showing that garden hunting plays a key role in the nutritional well-being of many Buglé families. The few studies that have documented game harvests from agricultural areas by indigenous communities elsewhere in the neotropics also show that significant proportions of the hunting yield come from anthropogenic habitats, although to a lesser degree. Balée and Gély (1989) report that roughly one quarter of all game brought home by the Ka'apor in northeastern Brazil is captured in garden areas, and a study among Wayapi villages in French Guiana and neighboring Brazil shows that secondary forests provide 28% of the mammal and bird harvest (Grenand, 1992). Among the Chimane in eastern Bolivia, the proportion of game captured in agricultural areas ranges up to about 40% (Chicchón, 1995). A study of Yucatec Maya hunting found that 70% of all game animals were killed in young secondary forest, gardens, and village areas (Jorgenson, 1993), although the proportion by weight was likely lower. Similarly, almost two thirds of all successful hunting outings among the Kuna of Cangandi, Panama were found to occur in gardens (Ventocilla, 1992).

The types of animals captured in agricultural areas in these other locations are for the most part very similar to those caught by the Buglé in their gardens and fallows—pacas, agoutis, armadillos, brocket deer, collared peccaries, toucans, doves, and parrots (Balée and Gély, 1989; Chicchón, 1995; Grenand, 1992; Jorgenson, 1993). Similarly, according to Linares (1976), the three most important species captured by prehistoric garden hunters were the agouti, the paca, and the collared peccary. So it appears that the heterogeneous cultural landscapes created by shifting cultivators that include gardens, orchards, fallows, and undisturbed vegetation provide highly suitable habitat for many animals, and that there is a common set of garden game species that are captured in neotropical rain forest regions inhabited by indigenous horticulturists. The results of this study show that several of these species are captured in significant quantities in agricultural areas close to home and seem to be withstanding current hunting pressure.

The absolute and relative contribution of agricultural areas as a source of game is conditioned by several interdependent human factors. One of the most important of these is the choice of hunting strategies; the difference between the amount of game caught in agricultural areas versus primary forest while awaiting (93%) and during hunting trips (25%) is most striking. The practice of awaiting game in rain forest regions has received at least passing mention by researchers (Descola, 1994; Herlihy, 1986; for a fuller description, see Ventocilla, 1992), but the type and quantity of game caught while awaiting in different habitats and under different conditions

has as yet received little attention. The same is true for the use of traps and opportunistic hunting. This study shows that reliance on different hunting strategies and consequently the proportion of game captured from anthropogenic habitat, are conditioned by access to firearms, gender, and age. The role of agricultural zones as a source of game is likely also affected by crop choice and other planting decisions that affect the number and type of animals that forage in these areas.

Garden Hunting and Game Depletion

Whether heavy reliance on garden hunting is an adaptive response to game depletion remains a difficult question to answer without diachronic studies that document game depletion over time, accompanied by a shift toward greater emphasis on hunting in agricultural areas. Nevertheless, the Buglé case suggests that this has not happened, or at least that the process is more complex. In the first place, agricultural areas are clearly important as a source of game in the absence of evidence of significant game depletion. The spatial patterns of game extraction do not show an absence of game around settlements, except perhaps in the case of the primate species which are captured toward the peripheries of the shared hunting zone and the tapir, of which only one individual was captured during the 8-month study period (Smith, 2003a). However, other deep forest species, such as the great curassow, the crested guan, and the great tinamou—large birds that are the same as or closely related to those that have been locally depleted by indigenous hunters elsewhere (Peres, 2000b; Silva and Strahl, 1991; Vickers, 1991)—continue to be caught relatively close to human settlements (Smith, 2003a). This is especially significant when we consider that they are among the most highly prized species and are pursued whenever they are encountered. Other highly preferred animals (such as the paca, which is ranked third in the Caloveborita region, despite its modest size) are also among the most frequently captured species, and it would be incorrect to say that Buglé hunters have had to shift their attention to less desirable species in response to an overall scarcity of more desirable species. Moreover, with the exception of infrequent overnight expeditions, Buglé men do not usually venture farther than 3 or 4 km from home to hunt and do not feel the need to plan longer trips further into the forest to make hunting worthwhile. A comparison of harvest rates and estimates of maximum sustainable yields for several species likewise provides supporting evidence that most species are being hunted sustainably (Smith, 2003a). While some depletion of deep forest species has occurred in the immediate vicinity of human settlement, the creation of large “empty forests” has not occurred.

In the Caloveborita region it appears that garden hunting is a worthwhile pursuit irrespective of how abundant game is in mature forest, with the added advantage that it helps protect crops from animal predation. It is also promoted by the fact that hunting in distant forest areas is limited by time constraints and access to firearms. For those who do have access to a rifle or shotgun, however, this does not necessarily discourage them from garden hunting because the species captured in anthropogenic habitats include large, highly prized animals such as the paca, collared peccary, and brocket deer. Garden hunting is thus complementary to broader cultural and economic patterns. However, this does not explain the underlying reasons why large quantities of game can be found in anthropogenic habitats, even in the absence of widespread wildlife management. While the Buglé occasionally spare fruit trees that attract game in new clearings, and some overplanting does occur to buffer crop losses caused by animal pests, the high proportion of game caught in gardens and fallows is not the result of wildlife management practices such as those that occur elsewhere among rural communities of the humid neotropics (Anderson, 1991; Balée and Gély, 1989; Nations and Nigh, 1980; Posey, 1984; Ventocilla *et al.*, 1995). It appears that efforts to enhance game resources near the home are simply not necessary—game species are attracted to anthropogenic habitats in significant numbers even without deliberate wildlife management. For an explanation, one must consider the relationships between shifting cultivation and wildlife ecology.

Ecological Characteristics of Garden Game

The importance of garden hunting is not merely a product of human choices—it clearly has something to do with the diet and behavior of the animals that are encountered by hunters in agricultural areas. All of the six garden game taxa captured by the Buglé are described by zoologists as either opportunistic foragers, tolerant of habitat disturbance, or as species that are commonly found in secondary forest, with the exception of the basilisk lizard which is first and foremost a semiaquatic reptile found along streams (Chapman and Ceballos, 1990; Delacour and Amadon, 1973; Reid, 1997; Ridgely and Gwynne, 1989; Seamon and Alder, 1999; Timm *et al.*, 1989). The forest rabbit (*Sylvilagus brasiliensis*), for example, is “fairly common and widely distributed in edges bordering evergreen forest, such as tree-fall gaps, roadsides, pastures, clearings, and brushy second growth” (Reid, 1997, p. 250) and is “more common in the successional plots and in clearings... than in primary forest” (Timm *et al.*, 1989, p. 108). The more important of the two spiny rats hunted by the Buglé, *Proechimys*

semispinosus, is a frugivorous habitat generalist with a broad diet that is common and often abundant in both evergreen forest and second growth (Reid, 1997; Seamon and Alder, 1999). It was also reported by a majority of interviewees in the Caloveborita region as a significant agricultural pest that eats manioc. The gray-headed chachalaca (*Ortalis cinereiceps*) “shuns forest, preferring tangles of vines and brush” (Delacour and Amadon, 1973, p. 96). The three *Columba* pigeons hunted in the Caloveborita region are all common near forest edges (Ridgely and Gwynne, 1989), and the paca is found in a variety of habitats, and can be “surprisingly common in small strips of riparian forest in agricultural zones” (Reid, 1997, p. 245).

In addition to taxa classified as garden game, many of the “intermediate” species are encountered frequently in agricultural areas. For example, 61% of armadillos were captured in gardens and fallows. The sheer quantity of armadillos encountered in agricultural areas reflects the fact that it occurs in many different types of habitat and eats a wide variety of foods, including insects, larvae, fruit, fungi, snails, slugs, earthworms, millipedes, centipedes, and small vertebrates (Kalmbach, 1943; Wetzel, 1983). The white-nosed coati has a similarly wide diet breadth and is also found in a variety of habitats (Kaufmann, 1983). The collared peccary is another adaptable species (Sowls, 1983), and one that according to Buglé and other local farmers is a major agricultural pest that can pose a serious threat to maize, yam, dasheen, and manioc yields. Over 60% of the collared peccary harvest documented in this study was encountered in gardens and fallows, and it was the third most important species captured in agricultural areas by weight. The red brocket deer forages on the leaves of many plants as well as fungi, flowers, and fruit, and although it may be more common in mature forest, it often forages in small clearings (Eisenberg, 1989; Reid, 1997). Only one tapir was captured during the study period, in primary forest, but a study in Costa Rica found that secondary forest was the most common habitat type used by this species, and that primary forest was used less than expected given the relative availability of these two types of vegetation (Foerster and Vaughan, 2002). It is important to note that some species may use different habitats to satisfy different needs (e.g., shelter, food, cover) and that the boundaries between vegetation types are permeable. Vegetation mosaics that include gardens, fallows, mature forest, and edge habitat are highly suitable for these and other species.

Other species that are caught frequently in village and agricultural areas are small animals that make use of large trees or small forest fragments within agricultural areas that are spared to help maintain trails or for house construction and other materials not found in anthropogenic biotopes. The red-tailed squirrel (*Sciurus granatensis*), for example, relies heavily on hard-shelled palm seeds, *gliheré* (*Dipteryx panamensis*) seeds, and the large fruits

of *tumá* and other trees that are left in clearings and along trails (Glanz *et al.*, 1982; Heaney, 1983). Farmers report that this squirrel also eats maize and peach palm fruit, and appears to be quite abundant in the Caloveborita region near human settlements—over 85% of these were encountered within 1 km of a house (Smith, 2003a). Other intermediate small game species captured frequently in garden areas were reported as significant pests by local interviewees, including the collared aracari (*Pteroglossus torquatus*) and the chestnut-mandibled toucan (*Ramphastos swainsonii*), both of which eat peach palm fruit and bananas.

In contrast to garden game species, deep forest game species are much more discriminating in their choice of foods and foraging areas. Howler monkeys, for example, eat only the young leaves of certain forest trees, and avoid foliage with low amounts of protein or high concentrations of tannins and other secondary compounds (Glander, 1983). The spider monkey (*Ateles geoffroyi*) exhibits “an extreme specialization for an arboreal way of life . . . [and] feeds with great selectivity at moderate to extreme heights in mature forests” (Eisenberg, 1983, p. 451). Unsurprisingly, neither of these species were caught by the Buglé in anthropogenic habitats. The white-faced capuchin (*Cebus capucinus*) has a more eclectic diet that includes the fruits of 100 or more plant species, leaves, flowers, and insects, but remains dependent on rain forest habitat (Baldwin and Baldwin, 1976; Freese, 1983; Hernández-Camacho and Cooper, 1976). The three other species classified as deep forest game are large birds that are also sensitive to habitat disturbance and are found almost exclusively in primary forest areas (Amadon, 1983; Delacour and Amadon, 1973; Ridgely and Gwynne, 1989).

Thus, garden game species (as well as some intermediate species) are adapted to disturbances, including both those that are caused by natural processes such as a tree fall, and those resulting from shifting cultivation which also opens the canopy facilitating the colonization of fast-growing, heliophitic plants, followed by various stages of successional regrowth. At low human population densities, indigenous shifting cultivation “mimics . . . the natural gap-phase dynamics of the forest” (Andrade and Rubio-Torgler, 1993, p. 551). The ecological importance of early successional stages is manifest in the fact that some rodent species were not able to persist on Barro Colorado Island, Panama as secondary forests matured (Glanz, 1982). Tolerance of secondary growth has been described as an essential survival tool for game species in Mexico (Leopold, 1959), and Ojasti (1991) likewise states that capybara (*Hydrochaeris hydrochaeris*) populations in South America have not decreased to the same degree as other species of similar size in part because they are less sensitive to deforestation, adapting easily to open habitat. Timm (1994) notes that shifting cultivation in a forested region of Costa Rica is associated with increases

in the diversity and abundance of certain marsupials, bats, and small-to-medium sized rodents, due in part to the presence of crops and increases in edge effects and ecotone habitat. Where secondary growth is abundant due to human disturbance, riparian birds are especially common, and certain woodpeckers, tanagers, orioles, pigeons and other birds are seen much more often in anthropogenic habitats than in mature forest (Gordon, 1982; Terborgh, 1975). One of the pioneers of neotropical ornithology in fact suggested over a half century ago that birds that nest in secondary growth in neotropical forest areas may have adjusted their breeding season to the clearing and burning cycles of shifting cultivators (Skutch, 1950).

The fields and fallows of indigenous horticulturists also provide resources for forest animals that buffer periods of seasonal scarcity, which may result in more abundant and stable game populations. A study in Costa Rica, for example, indicates that many bird species adapted to tall forest habitat forage in secondary growth during periods when foods in the forest are scarce (Loiselle and Blake, 1992), suggesting that anthropogenic habitat can serve as a "keystone" resource. Although knowledge of how animals respond to food shortages in rain forests is incomplete, it is clear that such shortages can lead to population declines. Agoutis and pacas suffer seasonal food shortages during periods of reduced fruit fall and despite a shift to less optimal food items and the use of stored fat reserves, juveniles are more likely to perish during these lean times (Smythe *et al.*, 1982). Survival rates of the red-tailed squirrel show a similar pattern (Glanz *et al.*, 1982). Seasonal variation in food availability has also been shown to have an impact on population density of white-nosed coatis by affecting the timing of reproduction and age of first reproduction (Russell, 1982). The availability of forest fruit also varies across space as well as over time, which causes localized shortages affecting small species like spiny rats that have limited home ranges (Adler, 1998). The paca is also sensitive to microscale changes in food supply, and home ranges can shift rapidly in response to changes in fruit production (Beck-King and von Helversen, 1999). Thus, foraging opportunities in agricultural areas may be critical for animals in nearby forests during seasonal food shortages, or during infrequent but potentially devastating stochastic events that decrease food availability (e.g., extreme weather events). Importantly, the presence of a game species in an area and the frequency with which it forages in a particular farm or fallow are also conditioned by spatial patterns in the surrounding vegetation at a variety of scales (Daily *et al.*, 2003; Naughton-Treves, 2002; Naughton-Treves *et al.*, 2003). It is also worth noting that the interactions between habitat modification and wildlife foraging patterns are mutually influential, i.e., by foraging in gardens and fallows, animals likely have an impact on

the floristic composition of secondary regrowth through their role in seed dispersal, selective herbivory, and other processes.

Given that many species may benefit from the creation of anthropogenic habitats, it is possible that in some cases rain forests may not support as many mammal and bird species as cultural landscapes that include mosaics of gardens, fallows, and mature forest. Research on the dynamics of biodiversity at larger scales in regions where shifting cultivation occurs is rare, but one such study done in eastern Honduras shows how the diversity of diurnal raptors is most strongly correlated with landscape heterogeneity, rather than the presence or extent of any single habitat type (Anderson, 2001). However, it should be kept in mind that biodiversity as measured by species richness does not take into account the importance of rare or endemic species that may have a higher priority from a conservation perspective. For example, a comparison of bird diversity in mature forest and abandoned cacao plantations in Costa Rica indicates that overall, fewer species are found in mature forest but that four times as many forest specialists are found here, while many of the additional species found in anthropogenic habitats are common agricultural and woodland generalists with large ranges (Reitsma *et al.*, 2001).

The contrasting diets and habitat preferences of garden game and deep forest game underlie a fundamental difference in the types of interactions between indigenous peoples and wildlife in the rain forest setting. On the one hand, there are those animals that are absent from areas altered by humans, in many cases prized game species with low reproductive rates that are more vulnerable to overhunting. On the other are species that make use of anthropogenic habitats that surround the villages of indigenous horticulturists, and persist in the vicinity of villages despite the fact that they are hunted regularly. Foraging in anthropogenic habitats may not simply be the result of an inherent predisposition to do so. This behavior may in fact stem from adaptations that have enhanced survival and reproductive success. After all, humans have been modifying habitats in lower Central America through shifting cultivation at a significant scale since roughly 2,000 BC (Cooke, 1997). This may have been enough time for selective forces to act upon animals that are more prone to take advantage of foraging opportunities in anthropogenic habitats. However, although it is recognized that shifting cultivation and deliberate forest management have influenced the structure, floristic composition, and ecological dynamics of what were thought to be pristine rain forests (Alcorn, 1981; Balée, 1989; Denevan, 1992; Eduards, 1986; Gómez-Pompa *et al.*, 1987; Medellín-Morales, 1990; Posey, 1985, 1998), less attention has been given to the possibility that indigenous peoples have directly influenced wildlife ecology—although some researchers have gone as far

as to suggest that indigenous subsistence activities may have played a role in the evolution of some species (Gordon, 1982; Greenberg, 1992; Smole, 1989).

Conditions in the Buglé region of northern Veraguas are ideal for the coexistence of people and wildlife. Farmland is relatively abundant and small agricultural plots are widely dispersed and left fallow for up to 15 years or more, leading to a mix of gardens and secondary growth of varying ages. Landscape heterogeneity is further enhanced by the presence of small patches of primary forest in agricultural zones that are protected as reserves of valuable plant products. The transitional area between forest and village lands provides attractive foraging opportunities for a number of wildlife species found in the nearby forest, which is reflected in high harvest rates of garden game from agricultural areas. Moreover, in northern Veraguas there is no true dry season, and unlike most shifting cultivators, the Buglé do not burn the majority of their fields according to a well-defined seasonal schedule. Consequently, crops in different stages of growth are present at all times of the year, so that in theory at least, anthropogenic habitats can serve as important foraging areas for forest species during periods of dietary stress, regardless of when these may occur. The research presented here supports Linares' (1976) thesis that garden hunting has provided a reliable, convenient source of protein for indigenous horticulturists for centuries, and may have served as an important alternative to animal domestication. Through an evaluation of the ecological relationships between people and wildlife in neotropical rain forest regions where shifting cultivation is practiced, it becomes apparent that some degree of coevolution between indigenous practices and the foraging behaviour of certain game species has likely occurred.

CONCLUDING REMARKS

Romantic notions about the innate harmony between indigenous peoples and their natural surroundings have lost their appeal in large part because of evidence of game depletion (Alvard *et al.*, 1997; Johnson, 1989; Redford, 1990; Redford and Stearman, 1993). At the same time, images of indigenous hunters traveling farther and farther into the forest, leaving in their wake increasingly large zones devoid of game are also inaccurate, and undermine their struggles to retain access to their traditional lands and resources. As this study shows, indigenous peoples also capture significant quantities of game close to home in their farms and fallows. Almost half of all game captured in the Caloveborita region is obtained from agricultural areas, demonstrating that hunting in anthropogenic habitats can play a key role in the human ecology of indigenous peoples in the humid neotropics,

and should be considered to fully understand the relationships between people and wildlife in a rain forest setting.

Reliance on garden game is conditioned by access to firearms, time constraints, gender, and age. In addition to providing significant amounts of protein-rich food, garden hunting also has the added advantage of helping Buglé farmers protect their crops. It is thus a productive pursuit that is complementary to many other aspects of their culture and economy, and an activity that will likely to remain important irrespective of whether or not deep forest species are depleted. The heterogeneous mosaic of farms, fallows, and forest that surrounds human settlement is a suitable environment for many game species, helping them to persist in the vicinity of villages over long periods of time despite the fact that they are hunted regularly. Their abundance in these areas is likely enhanced through opportunities to forage in gardens and fallows, which may provide critical resources during periods when foods in the forest are scarce. Many of the species captured in agricultural areas, in fact, are reported by local farmers as significant agricultural pests.

The significance of garden hunting has important implications for wildlife management. In the first place, relatively high harvest rates may be sustainable in areas where a mix of anthropogenic and undisturbed habitats provides suitable conditions for what appears to be a common set of garden game species consisting primarily of terrestrial mammals. These heterogeneous zones might be considered what have been called “anthropogenic wild” areas where human activity is present, but does not jeopardize ecological health (Povilitis, 2002). At a larger scale, habitat modification through shifting cultivation is but one of many human activities (including the use of fire and other forms of plant management) that have been affecting the distribution and abundance of wildlife in the Americas for millennia, calling into question the notion that human activity invariably interferes with the preservation of “pristine” environments (Balée, 1995; Bennett, 1968; Denevan, 1992; Posey, 1998; Stahl, 1996). At low population densities, moderate and repeated disturbance by indigenous farmers can in fact enhance biodiversity, particularly at larger, regional scales (Smith and Wishnie, 2000; see also Peterson, 1981). Conservationists must also take into account that local people will likely reject measures that protect animals that are relatively abundant in their locales and that may be responsible for significant crop losses. The harvest of garden game may in fact alleviate pressure on more vulnerable species and help conserve faunal resources for future generations. Some of these deep forest species have been extirpated through much of their natural range and are of great concern at the global level, including the tapir, which is listed as endangered, and the great currasow, which is “near threatened” (IUCN, 2003).

The relationships between indigenous communities and wildlife through both habitat modification and hunting are complex, and understanding them is especially difficult in light of the rapid changes in indigenous belief systems and economic orientations that are occurring in response to greater interactions with other groups at regional, national, and international levels. Garden hunting, however, represents a common element of indigenous subsistence in neotropical rain forest regions, and offers the potential to be a core element in wildlife conservation management that balances use and conservation over the long term. Further research on the foraging patterns and abundance of garden game species in different environments and the development of methods to assess the sustainability of indigenous hunting that take into account the role of anthropogenic habitats in wildlife ecology can make important contributions toward this goal.

ACKNOWLEDGMENTS

I would like to express my gratitude to residents in the Caloveborita region for supporting the research, for their patient cooperation in the administration of questionnaires, and for sharing their knowledge during interviews. I would also like to thank the local investigators who participated in the data collection for their dedicated work. I am also grateful to David Cochran and three anonymous reviewers for valuable comments on earlier drafts of the manuscript. The National Science Foundation (Doctoral Dissertation Improvement Grant, NSF 19540/990818), the Chicago Zoological Society (Conservation and Research Grant), the Tinker Foundation (Tinker Foundation Field Research Grant), and the Pierre Stousse Memorial Fund, University of Kansas, provided generous financial support for the research.

REFERENCES

- Adler, G. H. (1998). Impacts of resource abundance on populations of a tropical forest rodent. *Ecology* 79: 242–254.
- Alcorn, J. B. (1981). Huastec noncrop resource management: Implications for prehistoric rain forest management. *Human Ecology* 9(4): 395–417.
- Alcorn, J. B. (1993). Indigenous peoples and conservation. *Conservation Biology* 7(2): 424–426.
- Alvard, M. S., Robinson, J. G., Redford, K. H., and Kaplan, H. (1997). The sustainability of subsistence hunting in the neotropics. *Conservation Biology* 11(4): 977–982.
- Amadon, D. (1983). *Crax rubra*. In Janzen, D. H. (ed.), *Costa Rican Natural History*, University of Chicago Press, Chicago, Illinois, pp. 569–570.
- Anderson, A. B. (1991). Forest management strategies by rural inhabitants in the amazon estuary. In Gómez-Pompa, A., Whitmore, T. C., and Handley, M. (eds.), *Rain Forest Management*, UNESCO and Parthenon Publishing Group, Paris, pp. 351–360.

- Anderson, D. L. (2001). Landscape heterogeneity and diurnal raptor diversity in Honduras: The role of indigenous shifting cultivation. *Biotropica* 33(3): 511–519.
- Andrade, G., and Rubio-Torgler, H. (1993). Sustainable use of the tropical rain forest: Evidence from the Avifauna in a shifting-cultivation habitat mosaic in the Colombian Amazon. *Conservation Biology* 8(2): 545–554.
- Andresen, E. (2000). Ecological roles of mammals: The case of seed dispersal. In Entwistle, A., and Dunstone, N. (eds.), *Priorities for the Conservation of Mammalian Diversity: Has the Panda Had its Day?*, Cambridge University Press, Cambridge, UK, pp. 11–25.
- Baksh, M. (1995). Changes in Machiguenga quality of life. In Sponsel, L. E. (ed.), *Indigenous Peoples and the Future of Amazonia: An Ecological Anthropology of an Endangered World*. Arizona Studies in Human Ecology, University of Arizona Press, Tuscon, Arizona, pp. 187–205.
- Baldwin, J. D., and Baldwin, J. I. (1976). Primate populations in Chiriquí, Panama. In Thorington, R. W. Jr., and Heltne, P. G. (eds.), *Neotropical Primates: Field Studies and Conservation. Proceedings of a Symposium on the Distribution and Abundance of Neotropical Primates*, National Academy of Sciences, Washington, DC, pp. 20–31.
- Balée, W. (1985). Ka'apor ritual hunting. *Human Ecology* 13(4): 485–510.
- Balée, W. (1989). The culture of Amazonian forests. In Posey, D. A., and Balée, W. (eds.), *Resource Management in Amazonia: Indigenous Folk Strategies*, New York Botanical Garden, New York, pp. 1–21.
- Balée, W. (1995). Historical ecology of Amazonia. In Sponsel, L. E. (ed.), *Indigenous Peoples and the Future of Amazonia: An Ecological Anthropology of an Endangered World*. Arizona Studies in Human Ecology, University of Arizona Press, Tuscon, pp. 97–110.
- Balée, W., and Gély, A. (1989). Managed forest succession in Amazonia: The Ka'apor case. In Posey, D. A., and Balée, W. (eds.), *Resource Management in Amazonia: Indigenous Folk Strategies*, New York Botanical Garden, New York, pp. 129–158.
- Beck-King, H., and von Helversen, O. (1999). Home range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: A study using alternative methods. *Biotropica* 31(4): 675–685.
- Bennett, C. F. (1968). Human influences on the zoogeography of Panama. University of California Press, Ibero-Americana, Berkeley, Vol. 51, pp. 1–112.
- Bergman, R. W. (1980). *Amazon Economics: The Simplicity of Shipibo Wealth*, Dellplain Latin American Studies, 6, University Microfilms International, Ann Arbor, Michigan.
- Berlin, B., and Berlin, E. A. (1983). Adaptation and ethnozoological classification: Theoretical implications of animal resources and diet of the Aguaruna and Huambisa. In Hames, R. B., and Vickers, W. T. (eds.), *Adaptive Responses of Native Amazonians*, Academic Press, New York, pp. 301–323.
- Bodmer, R. E. (1991). Strategies of seed dispersal and seed predation in Amazonian Ungulates. *Biotropica* 23(3): 255–261.
- Bodmer, R. E. (1995). Managing Amazonian wildlife: Biological correlates of game choice by detribalized hunters. *Ecological Applications* 5(4): 872–877.
- Borge, C., and Castillo, R. (1997). *Cultura y Conservación en la Talamanca Indígena*. San José, Costa Rica: Editorial Universidad Estatal a Distancia.
- Cant, J. G. H. (1977). A census of the agouti (*Dasyprocta punctata*) in seasonally dry forest at Tikal, Guatemala, with some comments on strip censusing. *Journal of Mammalogy* 58(4): 688–690.
- Carneiro, R. L. (1970). Hunting and hunting magic among the Amahuaca of the Peruvian Montaña. *Ethnology* 9(4): 331–341.
- Carneiro, R. L. (1983). The cultivation of Manioc among the Kuikuru of the Upper Xingú. In Hames, R. B., and Vickers, W. T. (eds.), *Adaptive Responses of Native Amazonians*, Academic Press, New York, pp. 65–111.
- Castillero Calvo, A. (1995). *Conquista, Evangelización y Resistencia: ¿Triunfo o Fracaso de la Política Indigenista?* Panama City, Editorial Mariano Arosemena and Instituto Nacional de Cultura.

- Chapman, J. A., and Ceballos, G. (1990). The cottontails. In Chapman, J. A., and Flux, J. E. C. (eds.), *Rabbits, Hares and Pikas: Status Survey and Conservation Action Plan*, IUCN, Gland, Switzerland, pp. 95–110.
- Chicchón, A. (1995). Faunal resource use by the Chimane of Eastern Bolivia: Policy notes on a biosphere reserve. In Sponsel, L. E. (ed.), *Indigenous Peoples and the Future of Amazonia: An Ecological Anthropology of an Endangered World*, Arizona Studies in Human Ecology, University of Arizona Press, Tuscon, Arizona, pp. 225–243.
- Cooke, R. G. (1997). The native peoples of Central America during pre-Columbian and Colonial Times. In Coates, A. G. (ed.), *Central America: A Natural and Cultural History*, Yale University Press, New Haven, pp. 137–176.
- Daily, G. C., Ceballos, G., Pacheco, J., Suzán, G., and Sánchez-Azofeifa, A. (2003). Countryside biogeography of neotropical mammals: Conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology* 17(6): 1814–1826.
- Delacour, J., and Amadon, D. (1973). *Curassows and Related Birds*, American Museum of Natural History, New York, NY.
- Denevan, W. M. (1992). The Pristine Myth: The landscape of the Americas in 1492. *Annals of the Association of American Geographers* 82(3): 369–385.
- Descola, P. (1994). *In the Society of Nature: A Native Ecology in Amazonia*. Translated from the French by Nora Scott. (Originally published in 1986), Cambridge University Press, New York.
- Dirzo, R., and Miranda, A. (1991). Altered patterns of herbivory and diversity in the forest understory: A case study of the possible consequences of contemporary defaunation. In Fernandes, G. W., Price, P. W., Lewinson, T. M., and Benson, W. W. (eds.), *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*, Wiley, New York, pp. 273–287.
- Dunning, J. B. (ed.) (1993). *CRC Handbook of Avian Body Masses*, CRC Press, Boca Raton, Florida.
- Eduards, C. R. (1986). The human impact on the forest in Quintana Roo, Mexico. *Journal of Forest History* 30(3): 120–127.
- Eisenberg, J. F. (1981). *The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior*, University of Chicago Press, Chicago, Illinois.
- Eisenberg, J. F. (1983). *Ateles geoffroyi*. In Janzen, D. H. (ed.), *Costa Rican Natural History*, University of Chicago Press, Chicago, Illinois, pp. 451–453.
- Eisenberg, J. F. (1989). *Mammals of the Neotropics: The Northern Neotropics. Volume 1, Panama, Colombia, Venezuela, Guayana, Suriname, French Guiana*, University of Chicago Press, Chicago, Illinois.
- Eisenberg, J. F., and Thorington, R. W., Jr. (1973). A preliminary analysis of neotropical mammal fauna. *Biotropica* 5(3): 150–161.
- Emmons, L. H. (1984). Geographic variation in densities and diversities of non-flying mammals in Amazonia. *Biotropica* 16(3): 210–222.
- Emmons, L. H. (1990). *Neotropical Rainforest Mammals: A Field Guide*, University of Chicago Press, Chicago, Illinois.
- Foerster, C. R., and Vaughan, C. (2002). Home range, habitat use, and activity of Baird's Tapir in Costa Rica. *Biotropica* 34(3): 423–437.
- Freese, C. H. (1983). *Cebus capucinus*. In Janzen, D. H. (ed.), *Costa Rican Natural History*, University of Chicago Press, Chicago, Illinois, pp. 458–460.
- Glander, K. E. (1983). *Alouatta palliata*. In Janzen, D. H. (ed.), *Costa Rican Natural History*, University of Chicago Press, Chicago, Illinois, pp. 448–449.
- Glanz, W. E. (1982). The terrestrial mammal fauna of Barro Colorado Island: Censuses and long-term changes. In Leigh, E. G., Jr., Stanley Rand, A., and Windsor, D. M. (eds.), *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*, Smithsonian Institution Press, Washington, DC, pp. 455–468.
- Glanz, W. E., Thorington, R. W., Jr., Giacalone-Madden, J., and Heany, L. R. (1982). Seasonal food use and demographic trends in *Sciurus granatensis*. In Leigh, E. G., Jr., Stanley

- Rand, A., and Windsor, D. M. (eds.), *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*, Smithsonian Institution Press, Washington, DC, pp. 239–252.
- Godoy, R., Brokaw, N., and Wilkie, D. (1995). The effect of income on the extraction of non-timber tropical forest products: Model, hypotheses, and preliminary findings from the Sumu Indians of Nicaragua. *Human Ecology* 23(1): 29–52.
- Gómez-Pompa, A., Flores, J. S., and Sosa, V. (1987). The “Pet-kot”: A man-made tropical forest of the Maya. *Interiencia* 12(1): 10–15.
- Good, K. (1995). Yanomami of Venezuela: Foragers or farmers—which came first? In Sponsel, L. E. (ed.), *Indigenous Peoples and the Future of Amazonia: An Ecological Anthropology of an Endangered World*, Arizona Studies in Human Ecology, University of Arizona Press, Tuscon, Arizona, pp. 113–120.
- Gordon, B. L. (1982). *A Panama Forest and Shore: Natural History and Amerindian Culture in Bocas del Toro*, The Boxwood Press, Pacific Grove, California.
- Greenberg, L. S. Z. (1992). Garden hunting among the Yucatec Maya: A coevolutionary history of wildlife and culture. *Etnoecológica* 1(1): 23–33.
- Grenand, P. (1992). The use and cultural significance of the secondary forest among the Wayapi Indians. In Plotkin, M., and Famolare, L. (eds.), *Sustainable Harvest and Marketing of Rain Forest Products*, Island Press, Washington, DC, pp. 27–40.
- Gross, D. R. (1975). Protein capture and cultural development in the Amazon Basin. *American Anthropologist* 77(3): 526–549.
- Hames, R. B. (1979). A comparison of the efficiencies of the shotgun and the bow in neotropical forest hunting. *Human Ecology* 7(3): 219–252.
- Hames, R. B. (1980). Game depletion and hunting zone rotation among the Ye'kwana and Yanomamö of Amazonas, Venezuela. In Hames, R. B. (ed.), *Studies in Hunting and Fishing in the Neotropics. Working Papers on South American Indians*, Bennington College, Bennington, Vermont, pp. 31–66.
- Heany, L. R. (1983). *Sciurus granatensis*. In Janzen, D. H. (ed.), *Costa Rican Natural History*, University of Chicago Press, Chicago, Illinois, pp. 489–490.
- Herlihy, P. H. (1986). A cultural geography of the Emberá and Wounan (Chocó) Indians of Darién, Panama, with emphasis on recent village formation and economic diversification. Unpublished Ph.D. Dissertation, Louisiana State University.
- Herlihy, P. H. (1997). Central American Indian peoples and lands today. In Coates, A. G. (ed.), *Central America: A Natural and Cultural History*, Yale University Press, New Haven, pp. 215–240.
- Hernández-Camacho, J., and Cooper, R. W. (1976). The nonhuman primates of Colombia. In Thorington, R. W., Jr., and Heltne, P. G. (eds.), *Neotropical Primates: Field Studies and Conservation. Proceedings of a Symposium on the Distribution and Abundance of Neotropical Primates*, National Academy of Sciences, Washington, DC, pp. 35–69.
- Herrera, F. A., and González, R. (1964). Informe sobre una Investigación Etnográfica entre los Bokotá de Bocas del Toro. *Hombre y Cultura* Tomo I(3): 56–81.
- Hill, K., Padwe, J., Bejyvgi, C., Bepurangi, A., Jakugi, F., Tykuarangi, R., and Tykuarangi, T. (1997). Impact of hunting on large vertebrates in the Mbaracayu Reserve, Paraguay. *Conservation Biology* 11(6): 1339–1353.
- IUCN (2003). *2003 IUCN Red List of Threatened Species*. Obtained from website, <http://www.redlist.org>, July 26, 2004.
- Johnson, A. (1989). How the Machiguenga manage resources: Conservation or exploitation of nature? In Posey, D. A., and Balée, W. (eds.), *Resource Management in Amazonia: Indigenous and Folk Strategies*, New York Botanical Garden, New York, pp. 213–222.
- Jorgenson, J. P. (1993). Gardens, wildlife densities, and subsistence hunting by Maya Indians in Quintana Roo, Mexico. Unpublished Ph.D. Dissertation, University of Florida, Gainesville.
- Kalmbach, E. R. (1943). *The Armadillo: Its Relation to Agriculture and Game*, Game, Fish and Oyster Commission and United States Fish and Wildlife Service, Austin, Texas.

- Kaufmann, J. H. (1983). *Nasua narica*. In Janzen, D. H. (ed.), *Costa Rican Natural History*, University of Chicago Press, Chicago, Illinois, pp. 478–480.
- Leeuwenberg, F. J., and Robinson, J. G. (2000). Traditional management of hunting by a Xavante Community in Central Brazil: The search for sustainability. In Robinson, J. G., and Bennett, E. L. (eds.), *Hunting for Sustainability in Tropical Forests*. Biology and Resource Management Series, Columbia University Press, New York, pp. 375–394.
- Leigh, E. G., Jr., Rand, A. S., and Windsor, D. M. (1982). *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*, Smithsonian Institution Press, Washington, DC.
- Leopold, A. S. (1959). *Wildlife of Mexico: The Game Birds and Mammals*, University of California Press, Berkeley.
- Linares, O. (1976). "Garden Hunting" in the American Tropics. *Human Ecology* 4(4): 331–349.
- Loiselle, B. A., and Blake, J. B. (1992). Population variation in a tropical bird community: Implications for conservation. *BioScience* 42(11): 838–845.
- McDade, L. A., Bawa, K. S., Hespdenheide, H. A., and Hartshorn, G. S. (1994). *La Selva: Ecology and Natural History of a Neotropical Rain Forest*, University of Chicago Press, Chicago, Illinois.
- McDonald, D. R. (1977). Food Taboos: A Primitive Environmental Protection Agency (South America). *Anthropos* 72(516): 734–748.
- Medellín-Morales, S. (1990). Manejo Agrosilvícola Tradicional en una Comunidad Totonaca de la Costa de Veracruz, México. In Posey, D. A. et al. (eds.), *Ethnobiology: Implications and Applications. Proceedings of the First International Congress of Ethnobiology*, Museu Praense Emílio Goeldi, Belém, Brazil, pp. 11–26.
- Mena, P., Stallings, J. R., Regalado, J. B., and Cueva, R. (2000). The Sustainability of Current Hunting Practices by the Huaorani. In Robinson, J. G., and Bennett, E. L. (eds.), *Hunting for Sustainability in Tropical Forests*, Biology and Resource Management Series, Columbia University Press, New York, pp. 57–78.
- Mittermeier, R. A. (1991). Hunting and its effect on wild primate populations in Suriname. In Robinson, J. G., and Redford, K. H. (eds.), *Neotropical Wildlife Use and Conservation*, University of Chicago Press, Chicago, Illinois, pp. 93–107.
- Nations, J. D., and Nigh, R. B. (1980). The evolutionary potential of Lacandon Maya sustained-yield tropical forest management. *Journal of Anthropological Research* 36(1): 1–30.
- Naughton-Treves, L. (2002). Wild animals in the garden: Conserving wildlife in Amazonian Agroecosystems. *Annals of the American Association of Geographers* 92(3): 488–506.
- Naughton-Treves, L., Mena, J. L., Treves, A., Alvarez, N., and Radeloff, V. C. (2003). Wildlife survival beyond park boundaries: The impact of slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. *Conservation Biology* 17(4): 1106–1117.
- Nietschmann, B. (1972). Hunting and fishing focus among the Miskito Indians, Eastern Nicaragua. *Human Ecology* 1(1): 41–67.
- Ojasti, J. (1991). Human exploitation of capybara. In Robinson, J. G., and Redford, K. H. (eds.), *Neotropical Wildlife Use and Conservation*, University of Chicago Press, Chicago, Illinois, pp. 236–252.
- Orejuela, J. E. (1992). Traditional productive systems of the Awa (Cuaiquer) Indians of Southwestern Colombia and neighboring Ecuador. In Redford, K. H., and Padoch, C. (eds.), *Conservation of Neotropical Forests: Working from Traditional Resource Use*, Columbia University Press, New York, pp. 58–82.
- Peres, C. A. (1994). Primate responses to phenological changes in an Amazonian Terra Firme Forest. *Biotropica* 26(1): 98–113.
- Peres, C. A. (2000a). Effects of subsistence hunting on vertebrate community structure in Amazonian Forests. *Conservation Biology* 14(1): 240–253.
- Peres, C. A. (2000b). Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. In Robinson, J. G., and Bennett, E. L. (eds.), *Hunting for*

- Sustainability in Tropical Forests*, Biology and Resource Management Series, Columbia University Press, New York, pp. 31–56.
- Peres, C. A., and Zimmerman, B. (2001). Perils in parks or parks in peril? Reconciling conservation in Amazonian Reserves with and without use. *Conservation Biology* 15(3): 793–797.
- Peterson, J. T. (1981). Game, farming, and interethnic relations in Northeastern Luzon, Philippines. *Human Ecology* 9(1): 1–22.
- Posey, D. A. (1984). A preliminary report on diversified management of tropical forest by the Kayapó Indians of the Brazilian Amazon. *Advances in Economic Botany* 1: 112–126.
- Posey, D. A. (1985). Indigenous management of tropical forest ecosystems: The case of the Kayapó Indians of the Brazilian Amazon. *Agroforestry Systems* 3: 139–158.
- Posey, D. A. (1998). Diachronic ecotones and anthropogenic landscapes in Amazonia: Contesting the consciousness of conservation. In Balée, W. (ed.), *Advances in Historical Ecology*, Historical Ecology Series, Columbia University Press, New York.
- Povillitis, T. (2002). What is a natural area? *Natural Areas Journal* 22(1): 70–74.
- Redford, K. H. (1990). The ecologically noble savage. *Cultural Survival Quarterly* 15(1): 46–48.
- Redford, K. H. (1992). The empty forest. *BioScience* 42(6): 412–422.
- Redford, K. H., and Stearman, A. M. (1993). Forest-dwelling native Amazonians and the conservation of biodiversity: Interests in common or collision? *Conservation Biology* 7(2): 248–255.
- Reichel-Dolmatoff, G. (1996). *The Forest Within: The World-View of the Tukano Amazonian Indians*, Themis Books, Totnes, Devon.
- Reid, F. A. (1997). *A Field Guide to the Mammals of Central America and Southeast Mexico*, Oxford University Press, New York.
- Reitsma, R., Parrish, J. D., and McLarney, W. (2001). The role of Cacao plantations in maintaining forest avian diversity in Southeastern Costa Rica. *Agroforestry Systems* 53: 185–193.
- República de Panamá (2001). *Censos Nacionales de Población y Vivienda—Mayo 14 de 2000. Volumen 2, Cuadro 7: Población Indígena, Por Sexo, Según Grupo al que Pertenece y Edad: República de Panamá por Provincia. Censo 2000*. Obtained from website, <http://www.contraloria.gob.pa/censodepoblacion/>, October 31, 2003.
- Ridgely, R. S., and Gwynne, J. A., Jr. (1989). *A Guide to the Birds of Panama, with Costa Rica, Nicaragua, and Honduras*, Princeton University Press, Princeton, New Jersey.
- Robinson, J. G., and Redford, K. H. (1986). Body size, diet, and population density of neotropical forest mammals. *American Naturalist* 128(5): 665–680.
- Robinson, J. G., and Redford, K. H. (1991). Sustainable harvest of neotropical forest mammals. In Robinson, J. G., and Redford, K. H. (eds.), *Neotropical Wildlife Use and Conservation*, University of Chicago Press, Chicago, Illinois, pp. 415–429.
- Ross, E. (1978). Food taboos, diet, and hunting strategy: The adaptation to animals in Amazon cultural ecology. *Current Anthropology* 19(1): 1–36.
- Ruddle, K. (1974). *The Yukpa Cultivation System: A study of shifting cultivation in Colombia and Venezuela*. University of California Press, Ibero-Americana, Berkeley, Vol. 52.
- Russell, J. K. (1982). Timing of reproduction by Coatis (*Nasua narica*) in relation to fluctuations in food resources. In Leigh, E. G., Jr., Stanley Rand, A., and Windsor, D. M. (eds.), *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*, Smithsonian Institution Press, Washington, DC, pp. 413–431.
- Savage, J. M., and Villa, J. R. (1986). *Introduction to the Herpetofauna of Costa Rica*, Society for the Study of Amphibians and Reptiles, Contributions to Herpetology, San José, Costa Rica, Number 3.
- Seamon, J. O., and Adler, G. H. (1999). Short-term use of space by a neotropical forest rodent, *Proechimys semispinosus*. *Journal of Mammalogy* 80(3): 899–904.
- Silva, J. L., and Strahl, S. D. (1991). Human impact on populations of Chachalacas, Guans, and Curassows (Galliformes: Cracidae) in Venezuela. In Robinson, J. G., and Redford, K. H. (eds.), *Neotropical Wildlife Use and Conservation*, University of Chicago Press, Chicago, Illinois, pp. 36–52.

- Skutch, A. F. (1950). The nesting seasons of Central American birds in relation to climate and food supply. *Ibis* 92(2): 185–222.
- Smith, D. A. (2003a). Hunting, habitat, and indigenous settlement patterns: A geographic analysis of Buglé wildlife use in western Panama. Unpublished Ph.D. Dissertation, Department of Geography, University of Kansas, Lawrence, Kansas.
- Smith, D. A. (2003b). Participatory mapping of community lands and hunting yields among the Buglé of western Panama. *Human Organization* 62(4): 332–343.
- Smith, E. A., and Wishnie, M. (2000). Conservation and subsistence in small-scale societies. *Annual Review of Anthropology* 29: 493–524.
- Smole, W. J. (1989). Yanoama horticulture in the Parima Highlands of Venezuela and Brazil. *Advances in Economic Botany* 7: 115–128.
- Smythe, N., Glanz, W. E., and Leigh, E. G., Jr. (1982). Population regulation in some terrestrial Frugivores. In Leigh, E. G., Jr., Stanley Rand, A., and Windsor, D. M. (eds.), *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*, Smithsonian Institution Press, Washington, DC, pp. 227–238.
- Sowls, L. K. (1983). *Tayassu tajacu*. In Janzen, D. H. (ed.), *Costa Rican Natural History*, University of Chicago Press, Chicago, Illinois, pp. 497–498.
- Stahl, P. W. (1996). Holocene biodiversity: An archaeological perspective from the Americas. *Annual Review of Anthropology* 25: 105–126.
- Stearman, A. M. (1995). Neotropical foraging adaptations and the effects of acculturation on sustainable resource use. In Sponsel, L. E. (ed.), *Indigenous Peoples and the Future of Amazonia: An Ecological Anthropology of an Endangered World*, Arizona Studies in Human Ecology, University of Arizona Press, Tuscon, Arizona, pp. 207–224.
- Steinberg, M. K. (1998). Mopan Maya forest resources in Southern Belize. *Geographical Review* 88(1): 131–137.
- Stiles, G. F., and Skutch, A. F. (1989). *A Guide to the Birds of Costa Rica*, Comstock Publishing Associates, Cornell University Press, Ithica, New York.
- Terborgh, J. (1975). Faunal equilibria and the design of wildlife preserves. In Golley, F. B., and Medina, E. (eds.), *Tropical Ecological Systems*, Springer-Verlag, New York and Berlin.
- Timm, R. M. (1994). The mammal fauna. In McDade, L. A., Bawa, K. S., Hespenheide, H. A., and Hartshorn, G. S. (eds.), *La Selva: Ecology and Natural History of a Neotropical Rain Forest*, University of Chicago Press, Chicago, Illinois, pp. 229–237.
- Timm, R. M., Wilson, D. E., Clauson, B. L., LaVal, R. K., and Vaughan, C. S. (1989). *Mammals of the La Selva-Braulio Carrillo Complex, Costa Rica*, Fish and Wildlife Service, United States Department of the Interior, North American Fauna, Washington, DC, 75.
- Townsend, W. R. (2000). Sustainability of subsistence hunting by the Sirionó Indians of Bolivia. In Robinson, J. G., and Bennett, E. L. (eds.), *Hunting for Sustainability in Tropical Forests*, Biology and Resource Management Series, Columbia University Press, New York, pp. 267–281.
- van Shaik, C. P., Terborgh, J. W., and Wright, S. J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24: 353–377.
- Ventocilla, J. (1992). *Cacería y Subsistencia en Cangandi, una Comunidad de los Indígenas Kunas (Comarca Kuna Yala)*. Quito, Ecuador: Ediciones Abya-Yala.
- Ventocilla, J., Herrera, H., and Núñez, V. (1995). *Plants and Animals in the Life of the Kuna*. Translated by Elisabeth King, University of Texas Press, Austin.
- Vickers, W. T. (1980). An analysis of Amazonian hunting yields as a function of settlement age. In Vickers, W. T., and Kensing, K. M. (eds.), *Working Papers on South American Indians*, Bennington College, Bennington, Vermont, pp. 7–29.
- Vickers, W. T. (1991). Hunting yields and game composition over ten years in an Amazon Indian Territory. In Robinson, J. G., and Redford, K. H. (eds.), *Neotropical Wildlife Use and Conservation*, University of Chicago Press, Chicago, Illinois, pp. 53–81.
- Wetzel, R. M. (1983). *Dasyopus novemcinctus*. In Janzen, D. H. (ed.), *Costa Rican Natural History*, University of Chicago Press, Chicago, Illinois, pp. 465–467.

- Wilkie, D. S., and Finn, J. T. (1990). Slash-burn cultivation and mammal abundance in the Ituri Forest, Zaire. *Biotropica* 22(1): 90–99.
- Yost, J. A., and Kelley, P. M. (1983). Shotguns, blowguns, and spears: The analysis of technological efficiency. In Hames, R. B., and Vickers, W. T. (eds.), *Adaptive Responses of Native Amazonians*, Academic Press, New York, pp. 189–224.
- Young, P. D. (1995). Bugle. In Dow, J. W., and Van Kemper, R. (eds.), *Encyclopedia of World Cultures. Volume VIII. Middle America and the Caribbean*, G. K. Hall & Co., Boston, Massachusetts, pp. 31–34.