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Comparative feeding ecology of felids in a neotropical rainforest

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Summary. Diet and habitat use of jaguar, puma, and ocelot, and populations of their mammalian prey, were studied in an undisturbed rainforest in southeastern Peru. Analysis of scats (feces) showed terrestrial mammals to be the chief prey of all three felids, but reptiles and birds were also numerically important in the diets of ocelot and jaguar. Prey diversity is high and the cats evidently take any readily captured vertebrate. For major terrestrial mammal prey of felids, density, biomass, prey/predator ratios, and annual offtake from the study area are estimated. All three cat species seem to hunt by opportunistic encounter of prey. Most mammalian prey species were taken in about the ratios of occurrence, but peccaries were taken by jaguar more often than expected. Most prey of jaguar have a body weight of >1 kg, those of ocelot, ≤ 1 kg. Jaguar often used waterside habitats, where they captured caiman and river turtles. Puma did not use these habitats or resources, although the puma prey sample was too small for much inference. The possible effects of felids on study area prey populations are discussed. Large and small cats partition prey at the body weight region where prey switches from low to high reproductive rates.

Introduction

The diets of many species of mammalian carnivores are well documented (see Gittleman 1983 and Bekoff et al. 1984, for extensive bibliography) and new prey-species lists from new localites bring few surprises. Studies of predator-prey relations for mammalian carnivores are scarcer, and for the most part limited to temperate zone, single-species examples, such as wolf-moose (Mech 1970), puma-cervid (Hornocker 1970), and lynx-hare (Parker et al. 1983); or to tropical savannas, including the best-studied of all predator-prey communities: the Serengeti (Schaller 1972; Sinclair and Morton-Griffiths 1979; Waser 1980).

Felids are the only large mammalian predators found in all three tropical rainforest regions of Africa, Asia, and the Neotropics. As for most mammalian taxa except primates, less is known about the ecology of rainforest populations than about those in other habitats. The only tropical rainforest carnivore that has been well-studied is the tiger (Schaller 1967; Seidensticker 1976; Sunquist 1981), and this, moreover, in partially open habitats with grassland. Leopards have been the object of some studies in dry habitats (Schaller 1972; Muckenhirn and Eisenberg 1973; Seidensticker 1976), and there is a list of prey for the leopard in Ivory Coast rainforest (Hoppe-Dominik 1984), but published information on the diets of other entirely rainforest populations of large Carnivora is chiefly anecdotal. The largest neotropical felids, jaguar and puma, have been studied in grassland/forest mosaic in Brazil (Schaller and Vasconcelos 1978; Schaller and Crawshaw 1980), and Mondolfi and Hoogesteijn (1987) have compiled an extensive review of the diet and natural history of jaguar in Venezuela. Diets of puma have been recorded for temperate South America (Wilson 1984; Yáñez et al. 1986).

The aim of this study was to describe the diets, habitat use, and prey population base of a community of three felid predators; ocelot, puma and jaguar; on a plot of undisturbed lowland tropical rainforest in southeastern Peru, and to analyse the relationships of the felids to each other and to the array of prey.

Study area and methods

This study was done at Estación Biologica de Cocha Cashu, Parque Nacional Manu, Dpto. Madre de Dios, Peru (ca. 11°22′S, 71°22′W), from August 1982 to February 1985. The study area is undisturbed, lowland evergreen tropical rainforest in the floodplain of the Rio Manu. Its climate and vegetation are described in Terborgh (1983). The area around Cocha Cashu is uninhabited and has not been hunted by humans since establishment of the Park in 1968. Prior to 1968 it was hunted sporadically by itinerant skin- and subsistence hunters.

The only access to Cocha Cashu is by boat and once there, the only land transport is by foot. Because of the difficulty of monitoring large areas on foot, the object of this study was to examine the predator-prey interactions that look place in a limited zone of about 7.5 km^2. Three species of felids were common on the study area: jaguar (*Panthera onca*), puma (*Felis concolor*), and ocelot (*Felis pardalis*). The three other cat species that do or could occur in the region were not encountered during this study.

Analysis of diet

Felid diets were studied by analysis of scats (feces). These were collected whenever found during five months in 1982, 11.5 months in 1983–84, and sporadically for 10 months subsequently. The scats were stored in plastic bags in 10% formalin or 70% ethanol. For analysis, they were broken up and washed with water over a fine-mesh screen, dried, and examined under a microscope. Hair was compared with reference slides of hair from mammals trapped at Cocha Cashu or from specimens in the United States National Museum. Plastic impressions were made of some hair samples and surface scale patterns examined under Nomarsky optics. Hard parts (bones, teeth, nails, scutes) were compared directly with museum specimens of mammals and reptiles. The minimum number of prey in a scat was counted from hard parts; hair only was counted as one prey of that species.

Scats were identified by their association with tracks, with a trapped individual, with a radio-monitored individual, or by size and presence of hair ingested while grooming. The maximum width of each piece of a dropping was measured and a scale established from scats of known origin. Scats of puma and jaguar could not be distinguished with certainty by size, but ocelot and "big cat" scats differ significantly. Because no other small cat species was identified on the area during the study, all small cat scats are assumed to be those of ocelot.

Prey identified from separate scats is assumed to represent independent captures. This assumption seems justified because in general only big cats feed on prey that is consumed in several meals. So few big cat scats were found, and these spread widely in time, that there are only two cases where the same prey individual could be represented in two scats. For ocelot, there were also only two cases where scats including the same large prey item were found on the same or sequential days. In all these cases, I have counted the two incidences as a single prey. In the environment on the study area, fresh scats in the forest are usually destroyed within hours by dung beetles and trigonid bees. Only those consisting of mats of coarse hair, or those placed in dry sunny areas (beaches) survive a few days.

Felid use of the study area

Felid presence on the study area was recorded by: (1) quantitative monitoring of tracks on prepared tracking areas during the dry seasons of two years (Emmons et al. 1987); (2) recording the presence of tracks at other times and locations, and other sign such as scrapes, scats, the roaring of jaguar, and direct sightings; and (3) radiolocation of radiotagged individuals (9 ocelot, two jaguar, one puma). The study area is enclosed on three sides by a loop of the Rio Manu and an oxbow lake, so that it was clear whether a cat was in or out of it.

Estimation of prey density and size

Densities of larger mammals on the study area were estimated by day and night transect census (Emmons 1982, 1984), or in the case of capybara, from known groups. Small mammals were estimated by monthly capture-mark-release trapping on a 4 ha grid during 12 months of 1983–84 and 5 months in 1979 (methods in Emmons 1982, 1984).

Biomass of small mammals was estimated from the actual mean body weights of all members of the population trapped, including juveniles. For larger mammals, a mean weight was estimated at about 3/4 of adult weight of animals captured on the study area, field-collected museum specimens, or the literature (field weights only).

Results

Use of the study area by felids

Temporal use. Ocelots were permanent residents of the study area: three adult females and their young had most of their home ranges within the area, while a dominant male had part of his range on it, for an estimated population of about 0.8 ocelot/km^2. Breeding females had non-overlapping territories, young occupied the mother's territory, and dominant males overlapped more than one female range (details to be described elsewhere). Ocelots hunted solitarily and terrestrially.

Big cats (jaguar and puma) were recorded on the study area on 178 of 530 days, or on 33.5% of all possible days. Of these, jaguar were recorded on 20% of days, and puma on 14%. These figures represent only a minimum prescence, as big cats certainly sometimes escaped detection, especially during the rainy season, when tracks are washed away and many trails flooded. In any month, big cats were recorded in the area on 12% to 60% of all days. Two puma and three to five jaguar shared the area.

With the following few exceptions, both puma and jaguar were solitary. In 1982, a female jaguar traveled with a cub. A pair of jaguar of unknown sex, with small female-sized feet, traveled together, entering the region several times from May to July 1984. This may have been a pair of siblings recently become independent. During three and a half weeks, from 11 Aug to 6 Sep 1983, the male puma that used the study area appeared to be consorting with the female, as they were three times on the area simultaneously, although not recorded on the same part of it. At no other time during the study were they noted in the area on the same day. Only one other lengthy interaction was observed: on five of the six days 8–13 Sep 1983, jaguar roared from in and around the study area in six episodes of up to two hours each. At least two jaguar were involved, one of which was a male.

There is evidence that the big cats avoided each other temporally both intra- and interspecifically: of 199 big-cat/days (an individual big cat known to be on the area during a 24 h period, excluding the jaguar kitten), recorded on the study area, two big cats were simultaneously present on only 20 days, and on one day, three. Most of these instances were the few interactions described above, but even with these, when two cats were present, they were usually on opposite sides of the study area. Only twice were tracks of two individuals found on the same day crossing the same spot or trail section. One of these was the above-mentioned pair of jaguar that traveled together, the other a jaguar and puma traveling in opposite directions.

Ocelots and big cats did not appear to avoid each other: tracks of both were found on the same trail 14 times, often superimposed, either large or small cat following the other down a trail.

All three species have behaviors which could facilitate temporal avoidence. Puma mark their path with frequent scrapes (this study; Seidensticker et al. 1973); but jaguar of both sexes go through episodes of intense scraping (every few hundred m, always urinating and occasionally defecating on the scrapes) only at long and irregular intervals, suggesting more restricted social context than scraping by puma. All three species often claw horizontal logs that lie across trails, and both male and female ocelot spray trailside vegetation with pungent urine. Only jaguar were heard to give long-distance vocal signals. Roaring, by both males and females, was rare, and may have been stimulated by detection of another jaguar nearby, as the most intensive bouts involved counter-calling between two individuals.

For both puma and jaguar, radio-tracking and footprints showed similar patterns of behavior: an individual typically entered the study area, circulated widely within it for 3–10 days, left the area, and then returned several weeks later. Each cat usually visited about once a month, or less.

Habitat use. Within the small confines of the study area, there was one clear-cut difference in habitat use between puma and jaguar. Tracks of jaguar and puma were recorded in the forest on the study area on equivalent numbers of days (35 and 32, respectively); whereas jaguar tracks were recorded on river or lake margins on 39 d, but puma tracks on only five d (one record/day/habitat type/individual; dry season only, when beaches and lake margins were exposed). All of the latter five puma records were tracks of the male, who habitually left the study area by swimming the river from a particular spot. He was once seen sunning on a log there, the only sighting during the study of a puma out in the open. In contrast, jaguar were often seen resting, sunning or walking on beaches or lake edges, and their tracks could be followed for thousands of meters along exposed beaches and mudbanks in the dry season.

Ocelot intensively used all areas: forest, river, and lake edges, but unlike jaguar, which used them day or night, ocelot only frequented exposed areas at night (Emmons et al. 1987).

Hunting behavior. The primary hunting method of all three felid species, reconstructed from tracks and from movements during continuous radio-tracking, appeared to be extensive walking until prey was encountered. A jaguar was seen walking along the lake edge and charging at a limpkin, which it missed. Three track sequences on the beach showed a jaguar walking steadily along the river edge and charging a basking caiman or turtle from distances of 7 m to 30 m (all three chases were unsuccessful). A reliable local hunter described to me being attacked by a jaguar that jumped down at him from a high horizontal log above a trail. Ocelots were seen attacking prey three times: twice by rushing at large birds, once by crouching in wait on a log, then pouncing at a rat below.

Prey distribution by size and taxon

The 104 scats analysed for this study included 62 from ocelots, comprising 177 prey (excluding arthropods); 25 from jaguar, with 40 prey; 7 from puma, with 12 prey, and 10 from unidentified "big cats" with 22 prey, for a total minimum of 251 prey. The taxonomic distribution of prey taken is remarkably wide (Table 1). Ocelot and jaguar, for which there are the best samples, evidently take all vertebrate taxa which they can handle. Terrestrial mammals are the primary prey of all three species, but reptiles are also a major component of the diets of ocelot and jaguar at Cocha Cashu. Approximately equal percentages of arboreal mammals, bats, birds, and fish are taken by jaguar and ocelot alike (Table 2). These prey, likely to be taken by rare encounter of a vulnerable individual, are relatively unimportant components of all diets reported here.

Table 1. List of prey taxa identified from felid scats, and number of each prey found in total sample for a given species. Small rodents are identified to genus only. There are three species of *Proechimys* and about six species of *Oryzomys, sensu latu,* at Cocha Cashu [all specific characters of *Proechimys* are lost in digestion, and most dental characters of Oryzomyines eroded beyond certain recognition, although a few species (not listed) were identified]. Total no of scats analysed = 104: ocelot = 62; jaguar = 25; puma = 7; unidentified big cat = 10

Taxon	Adult mass	Ocelot	Jaguar	Puma	Big cat	Total
Small mammals (≤1 kg)						
Marsupials						
Didelphis marsupialis	1.0	2	1			3
Metachirus nudicaudatus	0.42	2	1			3
Marmosa cinerea	0.15	3				3
Marmosa noctivaga	0.08	2				2
Marmosa spp.		1				1
Total		10	2			12
Bats						
Artibeus fuliginosus		1				1
Micronycteris sp.		1				1
Unidentified		1		1		2
Total		3		1		4
Small rodents and rabbits						
Oryzomys spp. large	0.07	38			3	41
Unident. mice, small		8				8
Mesomys hispidus	0.2	1				1
Proechimys spp.	0.28	56		2	1	59
Sciurus spadiceus	0.6	1	1			2
Sylvilagus brasiliensis	1.0	2				2
Total		106	1	2	4	113
Larger mammals (>1 kg)						
Large rodents						
Agouti paca	8.0	1	2	3	1	7
Dasyprocta variegata	4.0	3	3	4	1	11
Hydrochaeris hydrochaeris	45		1			1
Myoprocta pratti	1.5	5				5
Total		9	6	7	2	24
Other large terrestrial						
Mazama americana	30		2		1	3
Nasua nasua	4.5				1	1
Tamandua tetradactyla	5.0		1			1
Tayassu tajacu	25		6		4	10
Total			9		6	15
Arboreal mammals						
Saguinus fuscicollis	0.4	1				1
Saimiri sciureus	1.0	1			1	2
Ateles paniscus	9.0		1		1	2
Unidentified primate		1				1
Bassaricyon alleni	1.0	1	1			2
Coendou prehensilis	4.5	1				1
Total		5	2		2	9
Total mammals						177

Table 1 (continued)

Taxon	Adult mass	Ocelot	Jaguar	Puma	Big cat	Total
Birds		19	4			23
Snakes		9		2	3	14
Lizards		8	1		1	10
Snake/lizard		2				2
Snake egg					1	1
Geochelone denticulata	~7		6			6
Podocnemis unifilis	~6		2			2
Platymys platycephala			1			1
Caiman unidentified		2	3			5
Fish		4	2			6
Snails			1			1
Total						71
Other (no. scats with)						
Insects		14				
Grass		7	12			
Unidentified scaly lumps		2	1			
Total number of prey		177	40	12		

Table 2. Distribution of felid prey by size and taxonomic group, from all scats collected in Rio Manu region and identified to species of origin. Percent of minimum total number of prey individuals in scats (Table 1)

Prey type	Total prey (%)		
	Ocelot (n=177)	Jaguar (n=40)	Puma (n=12)
Small rodents, opossums	66	8	17
Large rodents (≥1 kg)	5	15	58
Other large mammals	0	23	0
Arboreal mammals, bats	5	5	8
Birds	11	10	0
Reptiles	12	33	17
Fish	2	5	0

The three cats concentrate on different taxa (Table 1). Of reptiles, ocelots primarily ate snakes and lizards (9% of items in the diet) while jaguar fed on turtles, tortoises and caiman (30%). The small sample for puma included only snakes. Among mammal prey, small rodents made up 59% of the diet of ocelots at Cocha Cashu, with spiny rats (*Proechimys* spp.) the single most numerous item (32% of prey). The staples of jaguar were ungulates and large rodents (>2 kg), with collared peccary (*Tayassu tajacu* 15%) and agouti (*Dasyprocta variegata,* 10%) the most important. Puma fed chiefly on two large rodents, agouti (33%) and paca (*Agouti paca,* 27%); but the sample is too small for confident inference.

There is relatively little overlap in prey weight between ocelot and jaguar. Most mammal prey of ocelot (92%) weigh less than one kg, most mammal prey of jaguar (85%), more than one kg. The small sample of puma prey falls in the weight region where jaguar and ocelot diets overlap (1–10 kg).

Between them, ocelot and jaguar take prey across the entire weight range of mammal species at Cocha Cashu. The sole exception is that tapir, which are common in the area, were not found in scats of this sample.

Selectiveness of predation

Prey taken vs prey density. These felids will evidently eat almost any type of prey; but is hunting directed, or random? Comparison of prey frequency in scats with independent estimates of population density is possible only for terrestrial mammals. Ocelots took small mammals (<1 kg) in ratios close to those shown by trapping (Table 3a). The slightly fewer *Oryzomys* and opossums caught by ocelots is likely to be because the latter are somwhat scansorial, but *Proechimys* are entirely terrestrial. There is thus no evidence for selection between small mammal prey by ocelots. In contrast, the distribution of large prey eaten by ocelots is not in proportion to their occurrence, but in inverse order of size (Table 3b). Adult paca (8 kg) are surely too large a prey for ocelot, which probably only take the occasional juvenile. Moreover, at least two of the three agouti (4 kg adult) eaten by ocelots were subadult or juvenile.

Jaguar took agouti, paca, deer, and capybara in similar ratios to those estimated for the study

Table 3. Relative densities of major, terrestrial mammalian prey estimated on the study area compared to relative numbers of those species in felid diets determined from scats. **a** Mean monthly small mammal densities estimated by trap-mark-release on a grid. **b** Large mammal densities estimated by transect census, calculated by King method (Emmons 1982)

a Small mammals	Density on study area		Rel. no. in scats
	No./km^2	Rel. no.	Ocelot
Proechimys spp.	230	100	100
Oryzomys spp.	180	78	65
Opossums	50	22	16

b Large mammals	Density on study area		Rel. no. in scats		
	No./km^2	Rel. no.	Ocelot	Jaguar	Puma
Tayassu	5.6	108		200	
Myoprocta	5.3	102	166		
Dasyprocta	5.2	100	100	100	100
Agouti	3.5	67	33	67	75
Mazama	2.6	50		67	
Hydrochaeris	1.6	31		33	

area (Table 3b). Peccary, in contrast, were taken more often, suggesting that either success rate per encounter is higher, or that they are sought out. Peccary usually travel in groups and generally walk in single file, leaving a strong odor and visible trail, and they are often noisy. Jaguar should be able to detect them from a distance, and their herding behavior may make it hard for them to excape pursuit by hiding.

Puma also took agouti and paca in close to the proportions of occurrence (Table 3b). Although the sample size of 12 prey is far too small to be conclusive, the dominance of large rodents suggests that puma did not preferentially seek peccary as do jaguar.

Circadian activity of prey

The mammalian prey of ocelots and big cats differs in representation of diurnal versus nocturnal activity (Fig. 1). Numerically, most prey species of ocelot at Cocha Cashu are nocturnal, while most prey of jaguar and puma are diurnal, or diurnal/nocturnal, although nocturnal prey are also well represented. These results are a natural consequence of the relationship between body-size and activity cycle in rainforest mammals: most small mammals are nocturnal; intermediate-sized mammals are nocturnal or diurnal; and the largest mammals are diurnal/nocturnal (Emmons et al. 1983).

The activities of the felid predators in turn reflect those of their prey. Ocelots are chiefly active at night, with much less activity by day (Emmons et al. 1987), whereas jaguar are almost equally active day and night (Schaller and Crawshaw 1980). Body size of mammalian prey thus constrains prey and predator circadian activity alike.

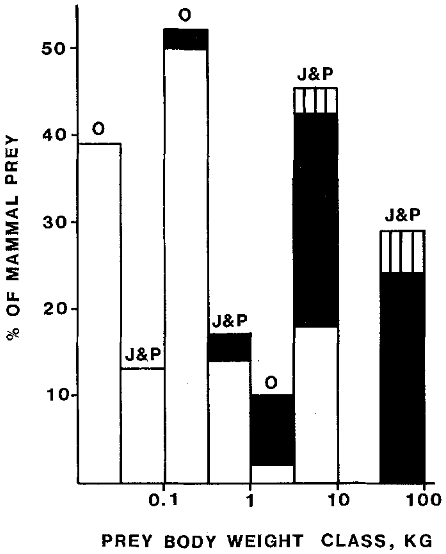

Fig. 1. Circadian activity of mammalian prey of ocelot (*O columns*) and jaguar and puma (*J&P columns*) as a function of prey body weight class. *Open bars* nocturnal prey; *black bars* diurnal prey; *striped bars* nocturnal/diurnal prey

Table 4. Estimated food consumption by felids

Species	kg meat/ day	g/day/ kg cat	Reference
Puma (captive)	1.2	34	Altman and Dittmer 1973
Puma (wild)	1.9–2.7	32–45[a]	Hornocker 1970
Jaguar (captive)	1.4	34	Altman and Dittmer 1973
Lion (wild)	6.8	43[a]	Schaller 1972:457
Tigress (wild)	5–6	34–41[a]	Sunquist 1981
Jagouaroundi (captive)	0.6	60–90	Altman and Dittmer 1973
Lynx (captive)	0.6	60–90	Altman and Dittmer 1973
Lynx (wild)	~1.0	~110[b]	Parker et al. 1983

[a] My calculations based on weights reported in the same articles: puma, 59 kg; lion, 160 kg; tigress, 145 kg

[b] Crude, based on Parker et al.'s estimate of about one hare/day

Estimated food consumption

Mass of prey in scats. I could not measure prey consumption by any of the cats studied, but estimates can be derived from the literature (Table 4). The agreement between the estimates from different sources is close, with big cats consuming 34–43 g/d/kg and ocelot-sized cats 60–90 g/d/kg. The puma and jaguar at Cocha Cashu are generally small. The captured female puma weighed 29 kg, the female jaguar weighed 31 kg, and the male, 37 kg. All were adults in good condition. From the track sizes of the captured big cats and the others known on the study area, the average puma and jaguar would each weigh about 34 kg, and would eat 1.2 to 1.4 kg/d. The average adult ocelot weighed 9.3 kg and should eat 558 g to 837 g/d. Female ocelots on our study area killed three tethered chickens; each time they ate about half of the chicken during the night, and returned the next night for the other half. The chickens weighed about 1.5 kg, so the ocelots ate about 0.75 kg per meal, or about 88 g/d/kg ocelot.

The mean biomass of mammalian prey represented in each ocelot scat is 688 g. If bird, reptile, and fish prey items are estimated to average 100 g each, then the total animal mass represented per scat would be 748 g. This is about the amount expected to be eaten in a day by an ocelot-sized cat (Table 4).

For big cats, the mean total mammalian biomass represented per scat is 9.2 kg. The approximate weight of meat on tortoises can be estimated from the weight of live animals minus the weight of empty carapaces. For *Geochelone denticulata* in Brazil, this is 4.4 kg per animal (D. Moskovits pers. comm.). *Podocnemis unifilis* I weighed were in the same range as *Geochelone,* and are assigned similar weights. The mass of turtle/tortoise meat represented in big cat scats is thus about 43 kg. If an estimated weight is added for other reptiles, birds and fish, the total mean biomass represented per scat is 12.3 kg for jaguar, or about 8 d food; and 4.4 kg for puma, or 3 d food. For the larger sample of all big cat scats, the mean total biomass per scat is 10.6 kg.

Several factors can influence the degree to which scats represent the amount of prey killed or eaten. It is unlikely that a scat represents a single day's food: parts of a meal with different digestibilities have different retention times in the gut and may be excreted for several days. The largest prey species (deer and capybara, relatively small by nonrainforest standards), would probably be about 75% consumed (all but the skull, larger bones and digestive tract: the feet are found in scats). For smaller prey such as pacas, all but the digestive tract is eaten. Finally, jaguar may abandon major parts of their large prey uneaten (Schaller and Vasconcelos 1978).

The prey numbers reflected in jaguar scats thus should represent the amount of biomass killed, but probably not the amount of mass eaten, whereas ocelots eat the whole of their small prey (except intestines) and the biomass calculated from numbers of prey in a scat is a good approximation of biomass eaten. For puma, the use of prey in rainforest is unknown, but in Idaho large prey are closely guarded and completely eaten (Hornocker 1970). The small prey in puma scats at Cocha Cashu could be easily eaten in one meal (cf. Hornocker 1970), thus these scats probably reflect the biomass both killed and eaten. This seems supported by the relatively smaller biomass represented per puma scat.

Ocelots probably produce scats at a regular rate, as they hunt small prey almost every day. For big cats the rate is probably irregular, and depends on irregular capture of large prey. The numbers of scats found at Cocha Cashu have the same crude relationship as the known temporal use of the area by different species (ocelots 100%, jaguar, 20%, Puma, 14%); for identified scats the proportions are: ocelot:jaguar:puma, 100:37:11; but total big cat scats (including unidentified) are 58% of the number of ocelot scats found. The recorded big cat use of the area (34% of the time) must be an underestimate, but nonetheless jaguar scats are overrepresented, perhaps they kill relatively greater amounts of prey than do puma or ocelot.

Impact of felid predators on mammalian prey

The following analyses are based on three assumptions: (1) that the scats are a random sample of all scats produced; (2) that if big cats produced scats on the study area derived from meals eaten outside it, those scats sample prey populations of similar structure to that on the study area; and (3) that the probability of finding a scat of any cat species is the same; thus, that the relative numbers of prey in the scats represent an equivalent sample of what the predators have taken from their environment over an equivalent time. This last seems reasonable because the cats have similar behavior in that they all intensively use the same trails, where their scats are found. The puma and jaguar data are in some cases combined, because they are predators of the same prey range. We can thereby include "big cat" scats that were not identified to species. Omitted from this sample are scats collected sporadically after I left Cocha Cashu, although these are included in other analyses and Table 1.

Relative numbers of prey taken. If the total numbers of terrestrial mammalian prey represented in the sample of scats are plotted by body weight class (Fig. 2A), small mammals predominate, as might be expected from the larger contri-

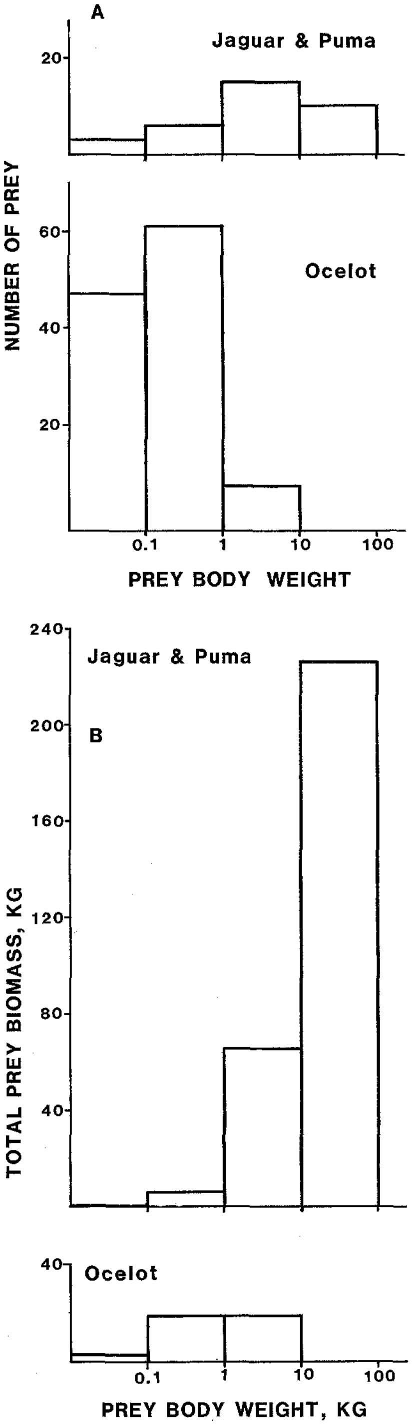

Fig. 2. Crude numbers (**A**) and biomass (**B**) of terrestrial mammalian prey represented in scats, as a function of prey body weight class

bution by ocelot prey, from both larger number of scats (60) and larger mean number of prey/scat (x = 3.0 ± 1.4), when compared to the big cats (N = 36; x = 1.7 ± 0.7 prey per scat). When the same prey numbers are converted to biomass (Fig. 2B), there is a dramatic reversal in importance, only part of which is due to classical Eltonian pyramid relations. The standing crop numbers and biomass of selected, terrestrial prey species on the study area can be compared with the representation of those species in the sample of scats (Fig. 3). It is apparent that in either numbers or biomass, large species are preyed upon to a relatively greater extent than small ones. If this converted into terms of the area occupied by the standing crop of prey represented by all individuals of a species in the scat sample (Table 5), we see that: (1) the terrestrial prey is divided by weight into two classes of under or over 1 kg. Within each size class, felid predators are taking roughly equivalent proportions of each prey species; and (2) as expected, arboreal and scansorial species are taken relatively rarely. This phenomenon is not related to predator species: acouchys (*Myoprocta*) were taken only by ocelots in this sample, but were taken in the same relative numbers as big cats took larger prey. Agoutis (*Dasyprocta*), which are prey of all three cats, had the highest predation level.

Predator-prey ratios. If the big cat biomass at Cocha Cashu is taken at its minimum estimate (percent of cat/days, days with two cats present counted twice = 2 kg big cat/km^2), the ratio of big cat:prey species standing-crop biomass is about 136kg prey/kg big cat. This includes only major, large terrestrial mammalian prey of species found in scats (excludes tapir and white-lipped peccary) and is an underestimate of actual prey biomass, which includes other taxa as well.

The population density and biomass of ocelot is known more accurately (≈ 6 kg/km^2). For the major prey items of *Proechimys*, large mice (*Oryzomys*), acouchys, and agoutis, which comprise 89% of all mammalian biomass represented in ocelot scats, and for which I have standing crop estimates, the ratio is only 12 kg prey/kg ocelot. Even were this doubled, to include other prey, it would still show the striking effect of scaling on predator-prey ratios.

Absolute numbers of prey taken. From the amount of time spent on the study area, the standing crop of prey, and the calculated minimum food requirements, the approximate minimum offtake by felids of their prey on the study area can be estimated. If 20% of one jaguar-year is spent on the study area, the total offtake should equal about 110 kg of prey. From relative numbers in scats, 89 kg, or 12 kg/km^2 of this, is comprised of large rodents and Artiodactyla. For puma, with 14% presence

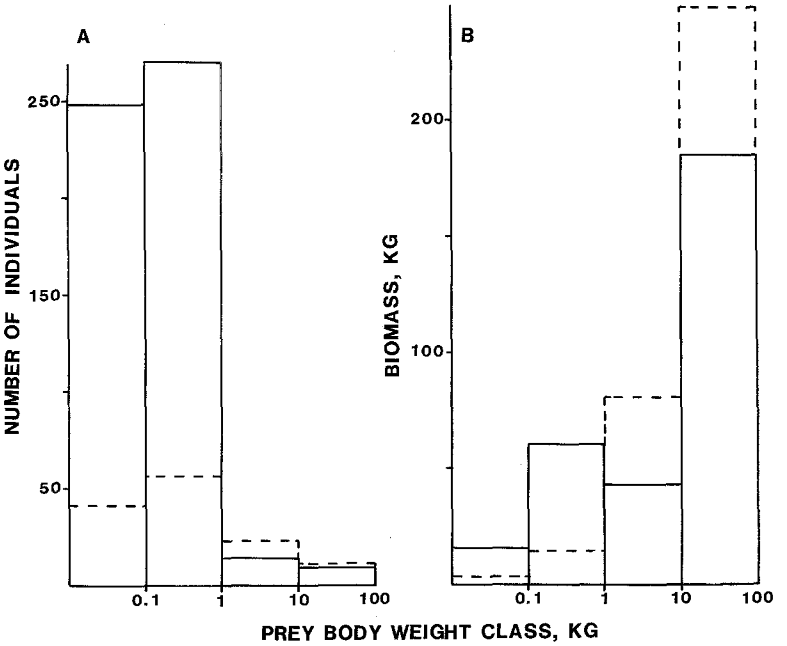

Fig. 3. Standing crop density/km^2 and biomass/km^2 on the study area of major, terrestrial, mammalian prey species (*solid lines*); compared with absolute numbers and biomass of the same species represented in the entire sample of cat scats (*dashed lines*), as a function of prey body weight class

Table 5. Area that would be occupied by a standing-crop of the total numbers of prey represented in felid scats. One scansorial species (*Sciurus spadiceus*) added for comparison with others, which are major, terrestrial prey. Species listed in increasing order of body size

Species	km^2
Oryzomys spp.	0.2
Proechimys spp.	0.3
Sciurus spadiceus	0.01
Myoprocta pratti	1.0
Dasyprocta variegata	2.3
Agouti paca	1.7
Tayassu tajacu	1.6
Mazama americana	1.2
Hydrochaeris hydrochaeris	0.6

on the study area, the same calculation gives an offtake of 10 kg/km^2. The standing crop biomass on the study area at Cocha Cashu, for these prey species only, is estimated at 271 kg/km^2. Together, the annual offtake by puma and jaguar would thus be about 8% of the standing-crop biomass. Note that this is a minimum estimate only, assuming minimum known occupancy of the study area by large felids, low mean felid body weights, and no gross wastage of prey (but balancing this is the likewise minimal estimate of prey density, based on direct census numbers, with no adjustments for animals missed).

The result of the same calculation for ocelots is a startling contrast: for an 8 kg cat that eats the lower value of 60 g/kg/d, for a total of 175 kg/year, or 135 kg/km^2/year average for the study area, the contribution of *Proechimys, Oryzomys,* and *Myoprocta* would be about 63 kg/km^2. However, the standing crop of these species is only 83 kg/km^2. For *Proechimys* alone the figure is 39 kg/km^2 eaten/year, of a standing crop biomass of 61 kg/km^2; or 64% of the total standing crop biomass.

Discussion

Predator-prey ratios

The mammalian prey/predator biomass ratios roughly estimated for Cocha Cashu, 135 kg prey/kg big cats, falls easily within the range of total mammalian large prey: large predator ratios of 94–301 kg prey/kg predator calculated by Schaller (1972:454) for five African savanna ecosystems. All of these are lower than Sunquist's (1981) estimate of 390–630 kg prey/kg tiger in Nepal, which to be comparable should also include leopard and dhole biomass. However, Sunquist (1981) estimates that tiger kill 8–10% of the standing crop of their prey per year; Schaller (1972:397) estimates that together, large Serengeti predators kill 9–10% of their standing crop of prey; while my estimate for big cats at Cocha Cashu is 8% of their large terrestrial mammalian prey. I believe that the similarity of these numbers is not coincidental, but reflects a limiting equilibrium state for large predators and large mammalian prey.

For ocelots, which eat small prey, the standing-crop ratio of 12 kg prey/kg ocelot, and annual offtake of 75% of standing-crop biomass of major terrestrial mammal prey, clearly reflects a different situation. For prey species with high reproductive rates, standing-crop biomass is obviously a poor estimate of the resource-base available to predators. When *Proechimys* consumption by ocelots is calculated as a function of potential productivity, 151 animals are estimated taken from a possible production of 2400 *Proechimys*/km^2, or 6% of the crop. This corrected offtake is now in the same range as that estimated for big cats and their prey. Even if we use higher estimates of mass eaten per day and biomass of ocelots, the consumption of *Proechimys* stays within an ecologically feasible range, with the predator-prey equilibrium close to that for large species.

The estimated high productivity of small rodents at Cocha Cashu is due almost exclusively to effects of short generation time: *Proechimys* breed year round, are pregnant again while lactating, and are reproductive at 3.5 months (Emmons 1982 and unpublished data). Although the litter size of *Proechimys* is small (mode = 2–3), a female can produce 18 descendants a year. In contrast, a capybara or peccary, with similar litter size, on average may produce only 2–3 young annually, with the first litter born at a maternal age of about two years. Large *Oryzomys* species likewise breed much of the year, but litter size and generation times are not known for Cocha Cashu.

Body size.

It is striking that two species alone, ocelot and jaguar, readily divide the entire size range of mammalian prey between them. This is possible because of the absence of truly large mammals in the Neotropics. The sizes of the cats divides them at a prey size of one kg, a point of scaling where prey species life history patterns switch from multiple to single litters per year and short to long generation times. For the known terrestrial mammal fauna of Cocha Cashu, 100% of species ≤ 1 kg adult weight should have multiple litters per year and early age of first reproduction. For terrestrial mammals > 1 kg, only one species, or 4%, should be in this category, and this species (*Didelphis marsupialis*), could equally be placed in the lower weight range (females breed at 700 g), which would split the species 100% into each category. Note that this division does not apply to arboreal mammals, of which many small species have low reproductive rates. The terrestrial species one kg and under are rodents, opossums, and a lagomorph, and I assume that species for which there are few data have life histories similar to those for which there is information.

Just above one kg in the body weight range of mammals in the community there is a marked decrease in species packing: there are 10 species > 0.4–$1.0 \leq$ kg; five species > 1–$4 <$ kg body mass, and 16 species ≥ 4–$8 \leq$ kg body mass. In a mammal community in African rainforest the primary consumers show a pronounced drop in species packing at the same point in the weight range (Emmons et al. 1983: Fig. 1).

The size-related life history difference of ocelot and jaguar prey has a number of consequences: high ocelot biomasses are supported by low standing biomass, but high productivity of prey; ocelots can defend small territories on areas of dense and predictable resources; most of their prey weighs less than 5% of their own body mass, and they spend many hours foraging to catch several prey each day (Emmons et al. 1987). Ocelot prey is mostly nocturnal, and ocelots are in competition for their prey with many snakes, raptors, and other small Carnivora of several families. Jaguar and puma, in contrast, have lower biomass in relation to their standing crop of prey, have consequently larger home ranges for their body mass, and appear not to defend territories although they avoid each other (Seidensticker et al. 1973; Schaller et al. 1984). They kill prey that generally weighs 10% to 80% of their own body mass, at intervals of several days (Seidensticker et al. 1973; Schaller and Crawshaw 1980). They have no other competitors but each other for large mammal prey, most of which is diurnal or diurnal/nocturnal.

The world's cats are sharply divided into large and small sizes: 0–10 kg, 21 species; 11–20 kg, 5 species; 21–35 kg, 0 species; 36–60 kg, 5 species; > 61 kg, 2 species (Guggisberg 1975; Gittleman 1983). I conjecture that this split corresponds generally to the prey life history pattern shift that occurs in terrestrial mammals at about on kg, with its concomitant shift of predator population, circadian activity, foraging strategy (many small prey), and social adaptation, as exemplified by ocelot and jaguar at Cocha Cashu.

In Asia, Africa and North America, healthy adults of the largest mammalian herbivores escape predation because of size alone (e.g. Schaller 1972; Sunquist 1981). It is likely that a predator energetically adapted to its median prey would be smaller than required to readily fell the prey at the largest end of the spectrum. Of the neotropical forest fauna, the tapir is four to six times heavier than the next largest species. Adult tapir would appear to be above the limit for easy prey of forest jaguar. Jaguar do attack tapir, but at least sometimes cannot bring them down (André 1904; Mondolfi and Hoogesteijn, in press; anecdotes reported to me by hunters).

In contrast, the species subject to heaviest predation are those whose size falls in the area of overlap between several predators. In the neotropical fauna agoutis are in this class (Table 1, Table 5), as are Thompson's gazelle in African savanna (Schaller 1972). For their size, such species might be expected to have particularly cryptic behavior or high reproductive rates to compensate for multiplied predation pressures. Species of body mass below one kg have many predators and high reproductive rates.

Prey diversity

Some studies show that the larger of a pair of similar, sympatric carnivores takes a larger range of prey than the smaller, because the larger takes large and small prey, and the smaller only small prey (Rosenzweig 1966; Gittleman 1983). For ocelot and jaguar, this is clearly not the case: in prey taxonomic richness or size, ocelot (24 mammal species eaten, small and medium sizes) are taking as wide a range as jaguar (16 mammal species eaten, medium and large sizes): in fact the prey range is almost exactly divided between them (34 non-flying mammal species ≤ 1 kg, 35 species > 1 kg at Cocha Cashu; list for small mammals probably incomplete).

Constraints of rainforest habitat

In contrast to the felid community in African savanna where as well as generalized hunters (leopard), specialized felids are adapted to cursorial pursuit of small game (cheetah, caracal), and communal pursuit of large game (lion) (Schaller 1972), rain forest appears to support only highly opportunistic solitary felid hunters (Schaller 1967; Seidensticker 1976; Sunquist 1981). The general hunting pattern seems to be that of extensive walking: doubtless because in dense forest prey is widely scattered throughout, cannot be seen for more than a few meters, and cannot be located at predictable sites such as waterholes. The high diversity of prey reported for rain forest leopard (Hoppe-Dominik 1984), jaguar in several habitats (Guggisberg 1975; Schaller and Vasconcelos 1978; Mondolfi and Hoogesteijn 1987), and jaguar and ocelot at Cocha Cashu, attests to the unpredictability of rain forest encounters. This lack of prey selection differs from the behavior of big cats in open habitats, where puma (Hornocker 1970), probably jaguar (Schaller and Vasconcelos 1978), tiger (Sunquist 1981), lion, and cheetah (Schaller 1972), focus on certain prey species.

Effects on prey populations

No doubt because of their opportunistic hunting, felids at Cocha Cashu took terrestrial mammalian prey species with remarkable evenness. Consequently, these predators should exert an equalizing influence on prey numbers, and they may be a cause of the surprizingly even densities of large terrestrial species on the study area. A possible bias in the results (Table 3b) is that the prey density estimates are derived in the same way that the cats presumably hunt: by my counting the number of animals met while I walked. Both census and cat encounters would thus have the same bias towards animals most easily detected. Nevertheless, that the relative numbers of major prey species taken by cats approximate my census ratios, reinforces the view of non-selective hunting behavior.

Comparable density estimates are available for only one other completely rain-forested habitat in the Neotropics, Barro Colorado Island, (BCI) Panama (Glanz 1982). BCI has a few ocelots, but puma and jaguar, formerly present, are now extinct. Large mammal populations, censused and calculated by the same means I used for Cocha Cashu, are: *Mazama americana,* 11/km^2; *Tayassu tajacu,* 9/km^2; *Agouti paca,* 20/km^2, and *Dasyprocta punctata,* 94/km^2 (Glanz 1982). There is a tenfold range of density difference on BCI between the same or equivalent species that at Cocha Cashu have almost equal densities. It is perhaps significant that agoutis (*Dasyprocta*), which I suggest should be adapted to the heaviest predation pressure because of their size, have achieved the highest populations in the absence of large predators.

That predators may limit numbers of prey does not imply that the prey are all, or always, limited by predation. Food is clearly limiting during some bad seasons or years (e.g. Foster 1982), but in other years, predation could limit prey population growth.

Mammal densities at Cocha Cashu.

A few comments on prey populations seem in order. Densities of large rodents and armadillos are low at Cocha Cashu. This is partly due to the floodplain habitat: up to 30% of the land surface is covered with shallow standing water for several months a year, with higher floods periodically. Armadillos disappeared after severe flooding in 1982. Numbers of agoutis, acouchys, and deer have varied from year to year since my first observations in 1979, but the most dramatic recent change in the fauna has been a drastic reduction of white-lipped peccary. Groups of scores were commonplace until 1979 (Kiltie and Terborgh 1983). Now, groups of less than 10 appear at rare intervals. The most likely cause of this extinction is epidemic disease, but whatever the cause, a major contributor to biomass and a prey species of jaguar was no longer of importance in the ecosystem during this study. It would clearly be imprudent to generalize mammal densities from Cocha Cashu either from year to year or to other localities.

Ecological differences between puma and jaguar

Puma overlap the entire geographic range of jaguar, so it can be assumed that they differ enough ecologically for stable coexistence. In the similar case of leopard and tiger, the smaller leopard takes smaller prey (Seidensticker 1976); but there is also evidence that in some regions leopards are restricted to habitats little used by tigers (Schaller 1967; Seidensticker 1976). Schaller and Crawshaw (1980) found puma and jaguar to be syntopic in the Pantanal, but there was a suggestion of spatial avoidance. I likewise have observed puma and jaguar to occur syntopically in terra firme rainforest in several regions of Amazonia, as they do at Cocha Cashu. In open habitats, jaguar appear to be much larger than puma (Schaller et al. 1984), but nonetheless the species overlap in size and take largely the same prey (Schaller and Crawshaw 1980).

The apparent temporal avoidance observed at Cocha Cashu between individual big cats of both species does not seem to involve interspecific, more than intraspecific, competition. It would clearly be counter-productive for a cat to use a trail just used by another that hunts the same prey.

From this limited study, only two interrelated differences were evident between the ecologies of puma and jaguar at Cocha Cashu. The intensive use of waterside habitats by jaguar, also noted by Schaller and Crawshaw (1980) and Guggisberg (1975), and avoidance of such areas by puma, is correlated with the quantitatively important presence in the jaguar diet of turtles, caiman, and fish. Turtles, caiman and tortoises have exceedingly hard integuments. Jaguar break the carapaces of chelonians to extract the meat. The massive head and stout canines of jaguar would seem better adapted to crushing resistant materials than are the relatively small head and thinner canines of puma, which have not been recorded killing large, armoured reptiles. Many of these reptiles are now scarce, but once they were common (Bates 1892), and jaguar predation on them was reported by early explorers (Humboldt 1853; André 1904). In the Pleistocence, five genera of large felids lived in North America (Anderson 1984). With the extinctions of large herbivores, all but two of these, puma and jaguar, subsequently disappeared. Its unique ability to use the once-abundant reptile resources of the Neotropics may be a key to the heavy build (Guggisberg 1975), predilection for wet habitats, and survival of the jaguar, which is now threatened not only by skin hunters and habitat destruction, but also by extinction of many of its prey, every species of which is intensively hunted by man.

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