

A FIELD STUDY OF OCELOTS (*FELIS PARDALIS*) IN PERU

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Three-quarters of the world's cat species are small (< 20 kg), and for most of these, little or nothing is known of their behavior in the wild (Guggisberg, 1975). The only effective way to follow and study small wild cats is radio-tracking. Many radio-telemetry studies of bobcats (*Lynx rufus*) have made this the best known of small wild species (e.g. Bailey, 1974 ; papers in *Bobcat Research Conference*, 1979 ; Knowles, 1985), yet even for these, there are large gaps in our knowledge, such as foraging dynamics and the nature of the mating system. Simultaneous studies of ocelots (*Felis pardalis*) have been carried out in habitats that span the species' entire range : Texas scrub (Navarro, 1985 ; M. Tewes, *pers. comm.*), Brazilian Pantanal (Schaller, 1984), Venezuelan llanos (Sunquist and Ludlow, 1985), and Amazonian rainforest (this study). These are the first detailed studies of populations of small tropical felids.

The present work on ocelots was part of a larger study which had the goal of evaluating the roles of all major felid predators (ocelot, puma, and jaguar) in the ecology of an undisturbed rainforest community (Emmons, 1987). The methodology chosen, of continuous following of radio-tagged animals on foot, yielded information on individual and social behaviors that are not usually recorded by the more usual method of daily or hourly locations taken from afar. Because these observations are unique, they are given here in detail so that they will be available both for future comparison and for other interpretations of their meaning.

STUDY AREA AND METHODS

Ocelots were studied at *Estación Biologica de Cocha Cashu, Parque Nacional Manu*, Madre de Dios, Peru, between August 1982 and February 1985. The study area is on the alluvial floodplain of the Rio Manu. Most of it is covered by mature evergreen rainforest ; natural sucesional vegetation occupies the river margins behind seasonally exposed beaches, and there are several swamps in poorly-drained low spots. The year is divided into marked dry (June to October-November) and rainy (October-November to May) seasons. In the rainy season about 20-30 % of the study area is covered by shallow standing

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water. Several times a year the river floods its banks, briefly (2-3 days) inundating larger areas. One catastrophic flood has been recorded since 1973 : heavy rains of the « El Niño » of 1982 caused the river to flood about 90 % of the study area for 5 days. Terbogh (1983) includes more detailed descriptions of the climate and vegetation.

Cocha Cashu is isolated from human settlements and protected from hunting by humans. All land travel in the study area is by foot on a network of about 46 km of trails distributed on 7.5 km². Because of the difficulty of monitoring larger areas on foot, the aim of the study was to describe predator-prey relations on a well-defined, small area. It was not possible to follow the movements of animals outside it.

Trapping

Ocelots were trapped in either home-made box-traps (1982 only) or wire-mesh bobcat traps (National Live Traps) baited with live chickens. The traps were disguised with vegetation and the chickens were fed daily through the back of the trap to avoid leaving human odor at the entrance. Traps were placed on trails frequently used by ocelots. In 1983 cable leg-snares manufactured by Michael Lembeck were also used. These succeeded in capturing individuals that would not enter traps. Ocelots did not damage their legs when snared : although the foot was sometimes swollen below the snare, the skin was never broken by the cable. After an initial struggle that flattened the surrounding vegetation, snared cats lay down and remained quiet. Captured ocelots were injected with ketamine hydrochloride and chlorpromazine by means of a Telinject blowgun, and while anesthetized were weighed, measured, examined, photographed, tattooed on the ear, and fitted with a radio collar. They were held in a darkened, covered trap for about 4-6 h and released after recovery from anesthesia. At the end of the study animals were placed in dense vegetation near the capture site and allowed to recover and depart undisturbed. Nine individuals (Table I) were captured a total of 18 times (8 trapped, 10 snared), with no known lasting injuries from capture procedures.

Ocelots were tracked on foot with a hand-held, Yagi antenna and earphone. Signal range was usually 200-500 m, but varied from about 50 m to 2 km, depending on intervening vegetation density. Bearings were taken from mapped trail markers. When an animal was stationary, its location was triangulated from three points and verified every 15 min. When it was moving, bearings were taken almost continuously (every 1-4 min). A focal ocelot was tracked for sample periods ranging from 1-5 days (usually 3-5 days), during which time it was followed continuously from mid-afternoon to about an hour after dawn. Its location was checked once around mid-day, and continuous tracking was attempted before the Ocelot began its nightly activity. However, because of their highly irregular behavior, ocelots were sometimes already moving when a tracking period was begun. Sample periods were of uneven length because it was often difficult to locate a cat that had moved. In a few samples, ocelots were followed for 24 hours per day. The tracker walked on trails and kept well behind and out of sight and earshot of the animal followed. The cat's activities could not be seen. Every 30 min frequencies of other collared cats were checked and bearings of all cats in range were taken at every location interval. Several times a week the study area was searched for day-resting sites of collared animals, but all were not always found. Ocelots were followed for 1,310 h, including 69

TABLE I
Ocelots captured during study.

Hours followed included only periods when the ocelot was the focal cat followed (spot locations and records when another cat was focal not included).

Ocelot	Date first capt.	Last recorded	No. capt.	Mass at capture, kg	Hours followed	Home range, Km ²	Age
F1	22/X/82	8/II/85	3	8.8;8.3;10.6	532.7	2.48	middle-aged, prime adult
F2	4/XI/82	26/V/84	5	8.5;8.3;7.8;7.5	136.7	1.15 (1)	very old broken canine
F4	26/VIII/83	4/IX/84	1	7.0	199.2	1.64 (2)	subadult at capture
M3	16/VIII/83	26/I/84	1	9.0	55.5	1.22 (3)	subadult/young adult
M5	13/IX/83	2/VII/84	1	9.0	105.4	{ 1.33 (3) 3.0 (1,2)	subadult at capture
M6	17/IX/83	12/XII/83	2	12.0;11.0	115.9	5.86 (1)	very old, worn broken & decayed teeth
M9	20/II/84	10/I/85	3	11.5;10.8;11.4	164.9	8.1 (1)	late middle age, broken canine
M8	21/XII/83		1	11.5	transient		young adult
F13	1/X/84	30/XII/84	1	9.1	transient		young adult

(1) Northern boundary of home range based on few locations, area may be underestimated.

(2) Home range after apparent establishment of a territory.

(3) Home range while still subadult on presumed parental territory.

entire nights and 21 partial days or nights, excluding spot checks of day-locations.

Ocelot activity on the study area was also monitored from tracks as described in detail in Emmons *et al.* (in press). Diet was studied by analysis of feces (Emmons, 1987).

Home ranges were defined as the minimum polygon connecting all outer radio-locations.

RESULTS

ACTIVITY PATTERNS

Circadian Activity

The nine ocelots captured (Table I) included adults and subadults of both sexes. Seven were residents of the study area and two, M8 and F13, were evidently transients. All analyses of activity are based on residents. Activity is here strictly defined as horizontal movement as shown by several sequential radio-locations. « Resting » is defined as lack of displacement for more than 20 min. Single spot checks of daytime locations did not contain activity information. Immobile or « resting » ocelots might be engaged in significant activities such as feeding, but these were not determinable.

The daily activity of individuals was highly variable and unpredictable, ranging from no displacement at all to more than 12 h of continuous movement, encompassing any hours of day and/or night. However, most activity was nocturnal and followed a typical pattern (Fig. 1). An ocelot usually rested in a den site from shortly after dawn until afternoon. It began to move between 1600 h and 1830 h, and remained active most of the night, with a midnight rest period, until it returned to a den after dawn. Males and females showed similar patterns (Fig. 1), but activity peaks during the last half of the night were about two hours displaced for the different sexes (note that if activities of the two sexes were averaged, the clear bimodal pattern would be obscured).

Although the activity diagrams (Fig. 1) show two periods of decreased nocturnal activity, the modal number of times that individuals rested after they began to walk at night was one, for both sexes. Males (N = 20 nights) had a mean of 1.1 ± 1.0 rests per night, with a surprising 30 % of nights that they did not rest at all from the time they left their den for the night's activity, to when they stopped at dawn. Females, in contrast (N = 34 nights), rested a mean of 1.8 ± 1.1 times per night, and walked without rest on only 6 % of nights.

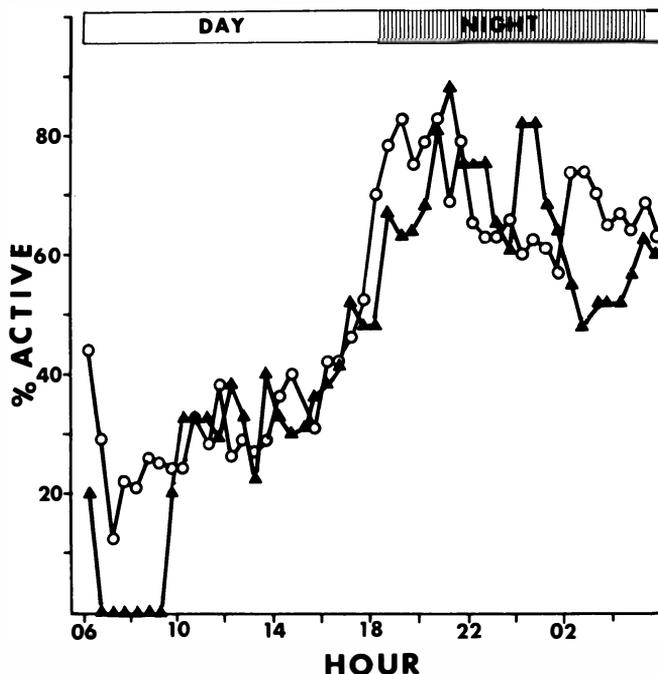


Figure 1. — Circadian activity of male (solid triangles) and female (open circles) ocelots. Data from continuously followed residents only. Summed over 30 min periods : 1 record/cat/period followed ; cat considered active or inactive according to how it spent the largest part of a period. Based on 2,467 records, male + female N/period = 20 - 80. 0700-1200 h had smallest samples.

Amount of Activity

Ocelots spent large amounts of time walking (Table II). Despite irregular day-to-day activity patterns, the average nightly movements of individuals were highly uniform. Most samples did not include all daylight hours when ocelots could be active. The minimum amount of daylight activity missed in sampling can be estimated from the (straight line) distance that ocelots moved between last morning, and first afternoon radiolocations, when cats were tracked on sequential nights. For females, on 11 of 25 days they were in the same place in the morning and afternoon, and I assume that they were inactive. On 14 days, they moved a mean of 514 ± 296 m between locations, or about 1.7 h of activity at the standard movement rate (Table II). Males did not move before afternoon sampling began on 10 of 19 days. On the other 9 they moved a mean of 526 ± 446 m, or for about 1.4 h of activity. Thus, for about half of the days sampled, 100 % of the activity was followed, and for the rest, about 90 %.

The resident adults, F1, M6, and M9, and the non-territorial subadult, M3, were active for equivalent average periods per night (Table II). Two subadults that were apparently setting up territories, F4 and M5, had longer average activities. A very old female that was losing her territory (F2) had shorter activity, but several nights of her sample she was engaged in unusual social interactions (see below) and her movements may have been atypical.

TABLE II
Activity of ocelots (means and SD).

Includes only samples of entire nights (N). Data for F1 excludes period when she was lactating.

Ocelot	N	Mean h followed/day	Mean h active (range)	Mean km moved/day	Mean rate travel km/h
F1	18	14.22 ± 2.5	9.38 ± 1.8 (7.4 -11.58)	3.7 ± 1.3	0.37 ± 0.1
F2	5	13.38 ± 0.9	6.67 ± 3.1 (3.2 -10.39)	1.8 ± 0.7	0.27 ± 0.4
F4	9	16.07 ± 2.6	11.29 ± 3.9 (6.33-17.27)	3.48 ± 0.8	0.30 ± 0.1
M3	4	13.88 ± 1.0	9.92 ± 3.8 (4.6 -13.25)	3.5 ± 0.7	0.36 ± 0.1
M5	7	14.92 ± 2.4	10.67 ± 1.9 (7.85-13.28)	3.5 ± 1.1	0.32 ± 0.1
M6	5	13.98 ± 1.5	9.3 ± 4.0 (3.59-12.98)	4.05 ± 2.4	0.46 ± 0.1
M9	3	20.42 ± 3.6	9.88 ± 3.3 (6.17-12.47)	3.6 ± 1.3	0.36 ± 0.1

Rate of Travel

Ocelots traveled at two typical rates. Most of their activity appeared to be spent in hunting, which consisted of slow and steady movement, with an occasional pause, at a rate close to 0.3 km/h. All age classes and both sexes seemed to hunt in precisely the same way, at the same rate of travel, as far as could be determined by their movements. When an ocelot appeared to be

heading for a destination, without hunting (e.g. when traveling to a known chicken kill), it traveled at 0.8 to 1.4 km/h, probably a fast walk. Territorial animals, males more often than females, sometimes traveled their boundaries walking without pause at this faster rate.

Resting Sites

During the day, ocelots rested in sheltered spots. Most were in tangled treefalls, several in buttress cavities between the roots of large trees. Each ocelot used many rest sites ; some sites only once, some many times. It was rare for an ocelot to return to the same spot on sequential days, with the exception of females with kittens. Generally ocelots seemed to rest at a site near where the night's activities had brought them, but sometimes at dawn they walked deliberately for a long distance in a direct line to a favored site. Rest-sites were scattered throughout the home range, but some general areas were used much more often than others. Individuals whose home ranges overlapped used some of the same sites.

FOOD HABITS AND HUNTING BEHAVIOR

Diet

The diet of ocelots at Cocha Cashu is described in Emmons (1987). Briefly summarized in terms of numbers of prey identified from feces (N = 177), the diet included 32 % spiny rats (*Proechimys*, three species, Echimyidae), 28 % other small rodents (mostly *Oryzomys* spp.), and 6 % marsupials, for a total of 66 % small mammals ; 5 % large rodents (> 1kg) ; 5 % bats and arboreal mammals other than opossums ; 11 % birds ; 12 % reptiles ; and 2 % fish. This diet suggests opportunistic hunting behavior : any kind of mammal, bird or reptile of appropriate size was evidently taken. Small terrestrial mammals, the bulk of the diet, were taken in approximately the same proportions that they occurred on the study area (as estimated by trapping efforts), with no evidence of specialization on certain prey species. The large rodents, *Myoprocta*, *Dasyprocta*, and *Agouti*, the latter two probably at the upper limit of ocelot prey-size, were taken mostly as juveniles and in inverse proportion to their size, not in proportion to occurrence (Emmons, 1987).

Wet and dry-season diets had similar proportions of major prey (Table III). Lizards seem more important in the dry season, when leaves are dry and their movements are easily heard. Insects, of almost no importance in terms of biomass eaten, were also found mainly in dry-season feces.

The circadian activity of the ocelots at Cocha Cashu was clearly reflected in their prey (Emmons, 1987) : of all mammalian prey individuals found in feces, 91 % were of nocturnal species, and 9 % of diurnal ones. The nocturnal concentration of activity by ocelots is probably a direct result of a diet principally of small mammals, which are almost all nocturnal in rainforest.

I estimated that the average adult ocelot eats 558-837 g of meat per day, and that the mean total prey biomass represented in each ocelot fecal sample found on the study area was 748 g, or about the expected daily consumption (Emmons, 1987). The mean number of prey per fecal sample was 3.0 ± 1.4 .

TABLE III
Seasonality of ocelot diets.

Percentage of total number of individuals of prey items identified in feces.
 Wet season (Dec.-May) N = 32 prey ; dry season (Jun.-Nov.) N = 134 prey.

Prey taxon	Wet season	Dry season
<i>Proechimys</i>	28	33
Cricetine rodents	26	27
Marsupials	9	5
Large mammals (> 1 kg)	6	7
Arboreal mammals & bats	9	5
Birds	13	10
Snakes	6	4
Lizards	0	6
Crocodylians	0	1.5
Fish	0	3
No. samples containing :		
Insects	0	13
Grass	0	8

This number should thus approximate the number of prey killed each day per ocelot. The mean distance traveled/ocelot/active period followed was 3.2 ± 1.5 km (N = 57, excluding data on F1 with kittens). Ocelot hunting success can therefore be roughly estimated at 0.9 prey captured per km walked. Ocelots traveled at a mean rate of 0.36 ± 0.11 km/h (N = 57, one night's activity = one sample), so the frequency of prey capture was roughly one per 3.1 h of walking. Because ocelots certainly were not hunting all the time that they were walking, the capture rate while actually searching for prey should be somewhat higher.

Hunting Behavior

Ocelots were rarely sighted : I saw them only 21 times during 16 months in the field, and 14 other sightings were reported by assistants on the project and others at the field station. Because direct data on hunting behavior is so difficult to obtain, the most indicative observations are given in detail below.

Ocelots were seen attacking prey four times : one unsuccessfully rushed a flock of trumpeters (*Psophia leucoptera*) ; one rushed a tinamou and caught it ; and one crouched on a log, then pounced at, and missed, a rat below.

In June 1986, 18 months after the end of the study, C. Mitchell (*pers. comm.*) was following a group of squirrel monkeys that had been foraging for two hours on and near the ground, when a radio-collared ocelot attacked and killed one. Following the attack, the monkeys all moved up to 15 m.

While radio-tracking, I heard three attacks on unidentified prey : in all three, the cat was moving slowly and steadily prior to the attack. In one case there was a sudden crash and indeterminate squawk, but the cat moved on, evidently unsuccessful. In another, there was a thrashing and gurgling from the location of a cat hunting on the waterside : this was followed by 40 min of immobility, presumably to feed on a captured prey. In the third, a cat changed direction and passed by me, stopping to watch me briefly from a trail, then continued moving slowly. When he was about 50 m from me in a dense treefall area, there was a loud, prolonged, monkey-like screaming and chocking followed by silence. The ocelot remained in this area for 67 min, presumably feeding.

When F1 was hunting one afternoon, she turned and headed straight for a group of squirrel monkeys (*Saimiri sciureus*) 250 m away, just as I first heard them moving up the lake-shore. When she arrived near the monkeys, they suddenly reversed direction and quickly moved back down the lake, perhaps, alarmed by her. She did not follow. Monkeys were four times heard alarming loudly over followed ocelots (brown capuchin, *Cebus apella*; spider, *Ateles paniscus*; and howler, *Alouatta seniculus*, monkeys), and a group of guans (*Penelope jacquacu*) also mobbed an ocelot. While we followed collared ocelots, three agoutis (*Dasyprocta variegata*), a rabbit (*Sylvilagus brazi-liensis*), and a flock of wood quail (*Odontophorus* sp.), ran alarmed from near the cats.

At a study site in Ecuador, I was sitting by a trail at night when a rabbit hopped by. Within a few minutes, a ocelot followed it up the trail, nose to the ground, sniffing intently. I also saw ocelot F1 sniffing deliberately down a trail.

After the first heavy rain of each wet season, fish (*Leporinus friderici*, Anostomidae) spawn in hundreds for one day in a tiny, shallow stream that feeds the lake (Cocha Cashu). On 16 November 1982 and 1 January 1984 ocelots fed on these fish : tracks with fish remains were found on the banks ; and a male ocelot was seen by the stream each year, one (M9) resting with his belly so distended that he was reluctant to move.

These observations, and the pattern of movements shown during radio-tracking, suggest that ocelots hunt chiefly by slow walking until prey is opportunistically encountered. Olfaction has been considered of little importance for prey location by felids (Leyhausen, 1979), but the above observations suggest that ocelots can follow prey odor trails. Ocelots hunted entirely terrestrially. They caught birds on the ground and were never seen traveling arboreally, although they sometimes rested on elevated fallen trunks.

USE OF SPACE

Home Range Distribution

Ocelots occupied the entire study area. Only one marked individual (F1) stayed on the area throughout the study. Adult females had non-overlapping home-ranges that appeared precisely contiguous and completely filled the study area (Fig. 2a). An exception is described under « Interactions » below. We did not capture female « Fx » on the west side of the lake, but female ocelot tracks were always present on this area. Assuming that she occupied all of the space between F1 and F4, the home range of Fx was 1.98 km², or about the same size as other female ranges. Males likewise occupied apparently exclusive areas, which overlapped three or more adult resident females (Fig. 2). Large male subadults occupied areas within, but smaller than, the ranges of their presumed mothers (Fig. 2a, b). I consider that the resident adults were territorial.

Pattern of Home Range Use

The nightly path of adult ocelots seemed deliberately chosen. They walked in smooth lines or long loops, almost never doubling back, and almost always covering a major part of a territorial boundary each night. The pathways chosen on sequential nights were usually different, with the result that the entire home-range boundaries were visited every 2-4 days. Individuals had favorite routes that they used repeatedly, many of which coincided with our trails, so that the trail system itself probably influenced home range use. Resident adults used their territorial boundaries more often than the interior of their territories, giving rise to « donut »-shaped use patterns (Fig. 3a). In contrast, a subadult male on the same home range did not show preferential use of boundary areas, suggesting that the movement patterns of adults were not responses to a

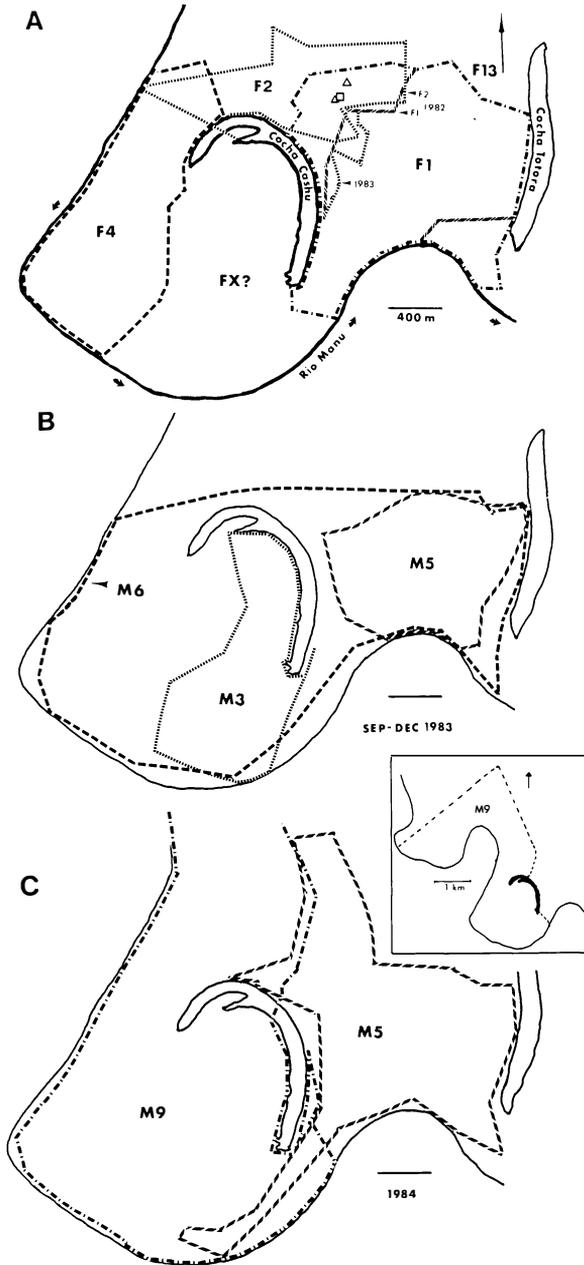


Figure 2. — A. Territories of female ocelots. F1, 1982-1985 ; F2, 1982 and August-September 1983 ; F4 after establishment of territory, March-July 1984 (F2 was no longer present) ; F13, October-December 1984 ; Fx, presumed territory (more than one female may have sequentially used this area. Triangles = dens where F2 had kittens in 1982 ; square = den where F1 had kittens in 1984. B. Home ranges of adult male M6 and subadults M3 and M5, September-December 1983. Note position of subadult ranges in relation to female ranges (A). C. Male territories 1984. Inset shows M9's entire known range.

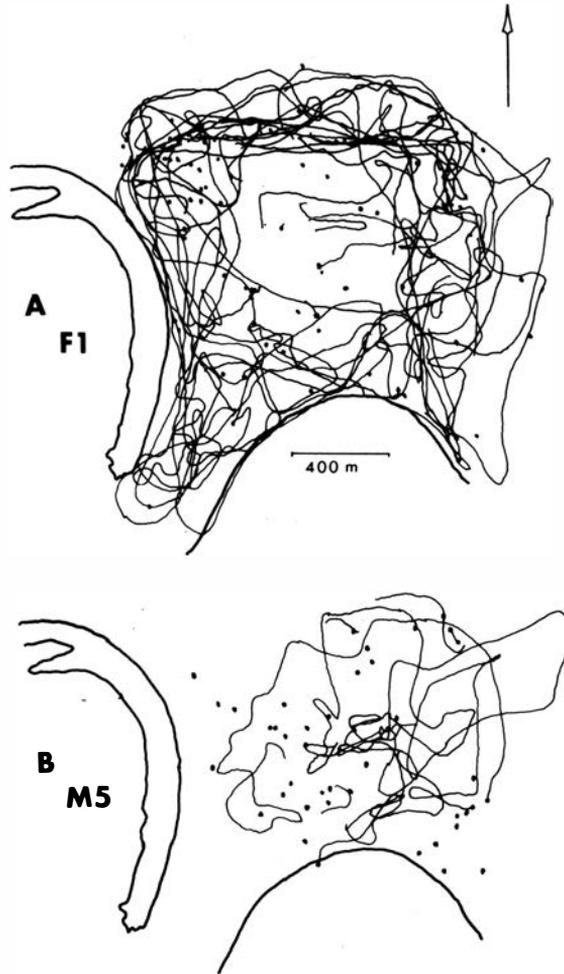


Figure 3. — Patterns of home range use. A. All itineraries and points recorded for F1 from 19 September 1983-24 June 1984. Note intensive use of border areas. B. All itineraries and points recorded for subadult M5, September-November 1983, on the same ground. Note lack of use of borders.

particular distribution of prey (Fig. 3b). There was no difference in the pattern of home range use between wet and dry seasons.

Marking Behavior

Ocelots had several types of marking behavior that could be involved in spacing through advertisement of presence. Both males and females sprayed trailside vegetation, leaving a strong odor similar to spray of male house cats. No visual marks were usually present where ocelots had sprayed. This was generally on leafy trailside vegetation, or sometimes on a rotten log or stump.

Scraping the ground with the hindfeet, a behavior common to many felids (Bailey, 1976 ; Sunquist, 1981 ; Rabinowitz and Nottingham, 1986), was rare in ocelots on the study area ; only five instances were recorded, one of these a group of four scrapes within a few meters of each other. Five scrapes each measured 10×15 cm and one, 10×28 cm. Most bore the imprint of one or both hindfeet. In one case, a male had both urinated and defecated on his scrape, and seemed to have dragged his anal region on the ground after defecation. Leafy vegetation had been sprayed at two scrapes probably made by a female (see below).

Both males and females left their feces prominently on trails. A map of where we found them (Fig. 4) shows a highly non-random distribution. Of 50 locations, 40 were on the edge of the river, lake, or a stream, and also on a territorial boundary. Sand substrates were preferred (31 sites) over other types of ground (19 sites). In two dry seasons we prepared « slicks » for recording tracks, by transporting fine beach sand to points on the trail system (Emmons *et al.*, in press). Ocelots left feces on six of these small sand patches (Fig. 4). Enders (1935) and Sunquist and Ludlow (*pers. comm.*) report ocelot « latrines », of dozens of feces in one place. No large accumulation was found at Cocha Cashu, but there was a tendency for repeated use of certain places : feces were deposited (by males when tracks could be identified) seven times on one of our sand slicks at a border trail-crossing (Fig. 4). An accumulation of about five was found under a house in a deserted guard station near the study area, and a cluster of three was found on a small beach. A 600 m strip of sandy riverside path (of 46 km of trails) yielded 10 of the 50 deposits. Because riverside and lakeside territorial boundaries that did not abut directly with neighbours had 17 of the fecal deposits on F1's territory, but her most heavily used north boundary (Fig. 3a), which did abut neighbours, contained only three (two of these on streambanks), it seems likely that waterside and sand substrate had more influence on fecal deposition than boundary position alone. Of 38 deposits on F1's territory, only six were not on a boundary, four of these six not on sand.

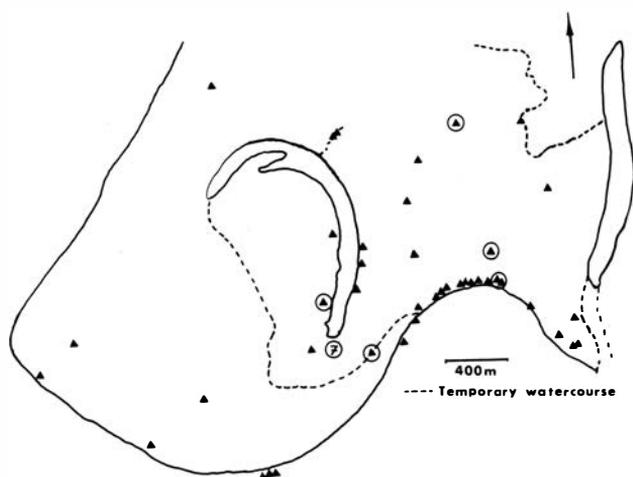


Figure 4. — Sites where Ocelot feces were found on the study area (triangles). Circles = « slicks » of beach sand, one used seven times (see text).

Ocelots left abundant evidence of tree-scratching. The fine scratches made by ocelots are easily distinguished from the deep, wide claw-marks of jaguar and puma. All ocelot scratch-marks I found were on horizontal logs near the ground, most were on logs fallen across, or beside, trails. Some logs were used repeatedly throughout the study. All three felid species scratched logs of a particular consistency : the wood or bark was just soft enough for them to be able to dig in the claws and pull them backwards through the wood with some resistance. Hard, fresh wood, or soft, rotten wood was not used.

SOCIAL INTERACTIONS

Two ocelots were seen together only once in 37 sightings, the others were alone. In contrast, continuous following of collared individuals showed that they often met each other (Table IV). Interaction levels of individual cats can not be compared because a key animal, Fx, was not collared, so that M3, M6, M9, F2, and F4, who spent time on her presumed territory, probably had unrecorded interactions while they were followed. The encounters (Table IV, plus two other encounters recorded during spot checks), can be summarized thus : adult females and their presumed young, 10 ; adult male (M6) and his presumed sons, 7 ; adult female with adult female, 9 ; adult female with adult male, 7 ; two subadults, 2 ; adult female and « unrelated » subadult, 2 ; and adult male with adult-male, 0. Although the data consist only of the relative positions of radio signals, much can be inferred from the observed interactions in light of the histories of the individuals.

TABLE IV
Social interactions between collared ocelots.
Encounters recorded during radio-tracking.

Ocelot	Encounters while followed (1)	Encounter rate, h (2)	Distribution of encounters						Grand total
			F2	F4	M3	M5	M6	M9	
F1	9	32	8	1	0	6	2	1	18
F2	5	21.9		4	1	1	1	0	15
F4	8	24.9			2	0	0	1	8
M3	1	55.5				0	4	0	7
M5	5	21.1					3	0	10
M6	7	16.6						0	10
M9	0	—							2
Total	35								70

(1) Number of encounters recorded while Ocelot was focal cat being followed.

(2) Mean number of hours focal cat was followed per recorded encounter (August 1983-July 1984 only).

Parent-Young Interactions

A. Father-Young

Encounters of adults with subadults comprised almost half of all interactions. The old male on the study area in September 1983, M6, with worn

and yellowed teeth, a broken canine, a decayed premolar, and patches of mange, was the likely father of the subadults on his territory. This assumption seems supported by his tolerance for the two, 80 % grown males (M3, M5) in his range.

M6 usually denned on the W side of the lake, in the territory of Fx, on which M3 was also living (Fig. 2). His interactions with M3 were often lengthy : on 10 October the two were together in the same place from 22 01-01 03 h, when they moved, and M3 followed M6 for 500 m until they stopped and remained close to each other until 05 00 h. On 12 October M6 was at a den when M3 arrived, stayed with him for 30 min, then left. On 13 October both were together in a den for more than 30 min, when M6 left, leaving M3 stationary. In contrast, the 3 meetings between M6 and M5 were brief : they simply encountered each other while traveling, and each continued on his way.

It was clear that the subadult males did not try to avoid the adult male, that they quite often met him, and in the case of M3, sought him out. It may be of note that M6 was not observed interacting at all with his presumed daughter, F4.

B. Female-Young

The 6 encounters of F1 with M5 were usually brief meetings while both were traveling. In one case they moved together for 15 min, in another, M5 walked a long way to a den where F1 was at dawn. He remained there all day, but she had left by mid-day.

The interactions between F2 and F4 were difficult to interpret because it is not certain whether they were mother and daughter, and because F2 was losing her territory while F4 did not yet have one. I was lucky to be following F4 when F2 chased her from her territory : F4 had walked from a part of F1's territory across part of F2's and straight to a favored den of F2, where she rested for 45 min in the middle of the night. When F2 arrived there at 00 43 h the two females spent 31 minutes together, and moved 100 m. F4 then walked away with F2 following closely. After 300 m F2 stopped following, and I passed her so as not to lose track of F4, who moved rapidly for about 400 m then slowed. F2 slowly began to follow F4 again, about 1/2 to 1 hour behind (she must have been following an odor trail). This continued until they reached the river edge at dawn, where both stopped. F2 stayed near, but not with, F4, until 13 30 h, when she retraced her path of the night before. F4 continued on, and was never again recorded in the area where she had met F2. F2 followed F4 for a total of 1 400 m. At a later date in another location, F4 moved quickly away when F2 approached, then moved back again when F2 walked on.

Although often on F1's territory from September to December 1983, F4 was not recorded meeting F1 then. During the day she used areas on the south end of F1's territory, where F1 rarely went by day. In contrast to the subadult males, F4's few encounters with adults from September to December 1983 appeared antagonistic.

Interactions Between Adults

A. Female-Female Interactions

The relationship between adult females F1 and F2 was complex. F2 was old, with faded pelage, a broken canine, and a missing incisor when first captured in 1982, but well-fleshed despite lactation. When caught a year later she weighed 250 g less and had three healed, and one open, sores. F1 was middle-aged and robust, with no deterioration of her fine condition between years. In 1982, when both presumably had young kittens, the borders of the two abutted sharply, with virtually no overlap (Fig. 2a). In September 1983 F1 had

encroached on a corner of what had been F2's range the year before (including the dens where F2 had kept her litter), but F2 also still used this area.

During a sample when F2 was followed in September 1983, she spent 3.75 entire days with F1 in about 16 ha of the « disputed » area. For two whole nights the females stayed within 50-300 m of each other, each moving around from time to time, but never meeting. The next two nights, F2 was stationary during the day and night, but F1 left, then returned at 03 00-04 30 h, and stayed near F2 until daylight. On the fifth night, F2 hunted, but once again returned to the same general area. At 03 23 h she met F1 on a different part of her territory about 400 m away, that F1 also took over.

F2 at this time showed a predilection for bait chickens in traps, and she was caught in, or robbed, several on both her own and F1's territories. She moved around the entire lake, sometimes in her old territory, sometimes on that of F1 or Fx. On 22 December she was captured on Fx's area, shortly after a damaging encounter with another animal, probably a paca or capybara. She had 17 deep slit puncture wounds on her underparts and legs : one nipple was bitten off, and a foreleg was hot and swollen from toe to shoulder. She had lost 0.5 kg. Amazingly, she survived, and had healed wounds when caught again February 2, but had lost another 250 g. During recovery, she took to raiding chickens in the camp clearing, even in broad daylight, with people watching. By March her activity had become restricted to a little-used riverside border of F1's territory, and in April she crossed the river out of the study area and lived for several months more on a cliff opposite. The displacement of F2 from the study area therefore took 6-7 months.

B. Male-Male Interactions

No encounters between territorial adult males were recorded during radio-tracking, but the movements of marked animals describe the replacement of one male by another. The old male, M6, was last located on 12 December 1983. Had he died on the study area, we would have found his stationary radio, so presumably he departed. The date M9 arrived on the study area is unknown ; but on 1 January 1984 he was seen at close range on M6's former territory, (the spot pattern on his throat was sketched), and he was first captured on 20 February 1984. From then until the end of the study a year later M9 occupied the western half of M6's former territory (Fig. 2c).

C. Male-Female Interactions

Three of the six recorded encounters between adult males and adult females were brief meetings, after which the cats went separate ways. On 14 March 1984, M9 was with F4 (now a territorial adult) at a rest site spot-checked during the day (data not in Table V). On 27 March M9 met F4 briefly, but after she walked on, he followed her at a distance of more than 150 m for over 3 h, covering about 900 m before splitting off without meeting her again. In contrast, on 18 October 1983, F2 followed M6 after a brief meeting, walking more than 150 m behind and to the side for 1.2 h, from Fx's territory into that of F1 (800 m).

REPRODUCTION

Temporal Pattern

Information on reproduction is largely circumstantial. Three or four litters were apparently born on the study area from March-August 1982 to July 1984 (Table V). As shown by F2, who was lactating when first captured, nursing females used the same den day after day, a behavior never otherwise seen. F1 was in the same den May 1, 7, 14, and 17 1982, after which she was monitored daily. She used only that den until 6 June, when she resumed a behavior of changing dens every day. She presumably gave birth about the first week in May, and lost her kittens a month later. When she was recaptured on 18 August, she was 2 kg heavier than normal and perhaps pregnant again. The interval between successive litters of F1 was two years, and Fx evidenced the same pattern (but Fx could have been more than one individual).

TABLE V

Reproductive history of female ocelots on the study area.

Presence of « Fx » inferred from tracks and home range space : more than one female could have used this home range sequentially. HR = home range, AD = adult, SA = subadult.

Ocelot	August-December 1982	August 1983-March 1984	April-July 1984
F1	Has weaned SA on HR (tracks)	Large SA M5 on HR becomes AD	Has kittens May, lost June, pregnant August ?
F2	Lactating 4 September	Probable SA daughter F4 leaves HR	Leaves study area
Fx	Has kitten on HR (tracks)	Large SA M3 on HR	Kitten tracks on HR
F4	Is young kitten	Wanders	Becomes territorial

We searched for dens with kittens when F1 and F2 were absent. F2 moved to another fixed area 350 m away after three searches, perhaps disturbed by our odors. When I searched this three weeks later, she moved again, but her new site was not located. Despite 10 searches, the dens with kittens were never found. All three den areas were treefall zones of many fallen trunks and vines, with vegetation so dense one had to crawl on hands and knees to explore parts of it. The second den of F2 and sole den of F1 were in the same area : a swamp with low, thick vegetation and fallen trees that was also a favored day-rest area of both females when they did not have kittens (this site was on the part of F2's 1982 territory that was taken over by F1 in 1983).

Behavior of A Lactating Female

F1's activity increased dramatically during lactation (Table VI). The time she spent moving when she was supporting a litter of about a month old reached a maximum of 93 % of a 24 h period, or over double her usual activity of about 40 % of the day. After she presumably lost her litter, her activity decreased to 52 % of 24 h.

In the period surrounding parturition F1 showed unusual behaviors. A group of four scrapes was found near her northern border on 10 April, and

TABLE VI
Activity of F1 before, during, and after lactation.

Periods when F1 was followed continuously only (1).
F1 presumably gave birth about 1 May and lost her litter about 6-9 June 1984.

Date	No. h followed	No. h active	Km traveled
16-17 April	25.8	9.47	1.8
18-19 May	21.9	18.64	6.7
19-20 May	24.0	13.16	5.9
2-3 June	23.55	21.86	7.2
23-24 June	23.42	12.25	6.7

(1) Data for the entire samples : on the five nights 16-20 April, she was active for a mean of 9.83 h/night and moved an average of 3.28 km/night ; on 17-20 May, she was active a mean of 17.3 h/day and moved an average of 7.2 km ; and of a sample of 34.27 h on 2-3 June, two days and the included night, she moved for 30.85 h, for a distance of 8.8 km.

while she was followed on 15 April she left a fresh scrape in the middle of a trail at the base of a large tree. Another scrape was found on her eastern boundary 12 May. These were the only ocelot scrapes found on her territory during the study. Those of 10 April and 12 May were associated with a strong odor of cat spray. Although only one of these scrapes was known to have been made by F1, it seems likely that she also made the others, given the rarity of this behavior and its location and temporal clustering on her home range.

On the first day F1 was followed after she had given birth (17 May), she walked for 11.48 h and covered 9.1 km between 18 00 h and 05 49 h, the greatest distance traveled in a night by any ocelot followed during this study. She walked in a great circle around almost her entire home range boundary, and stopped only once when she returned for 32 min to her den. On 19 May, and when she was next followed on 2 June, she again visited almost all of her home range boundary during a single night. In no other sample period did she cover most of her boundary in one night : typically she would do so during the course of two or three sequential nights.

Fates of Young on the Study Area

Captive ocelots acquire permanent canines at 8 months (Cisin, 1967). Two captive males reached 70 % of adult weight at 12-13 months, 80-87 % of adult weight at 18 months, and adult weight at 24-30 months (Cisin, 1967). It is likely that females reach adult weight earlier than males, as in margays (Petersen and Petersen, 1978). Ocelots M3, M5, and F4, captured from mid-August to mid-September 1983, had their permanent canines and were all 77-80 % of the mean weight of adults captured during the study (females = 8.8 kg, N = 3 ; males = 11.7 kg, N = 3). They were thus probably 14-18 months old at capture, and born from April-August 1982.

M5 was almost certainly the son of F1. The tracks of a youngster restricted to F1's home range in August-December 1982 were probably his. From September to December 1983 he had a smaller home range within hers and had frequent interactions with her, and some with the dominant male at that time,

M6. M5 remained entirely within F1's territory until 23 December 1983, when he was first located 500 m to the northwest. By March 1984 he had expanded his home range to include not only that of F1, but also a large area to the north, presumably that of another female. In a sample in March, he behaved like a territorial male, in two days patrolling 11.3 km of largely border areas. M5's radio signal was last located on 14 April, but it seems likely that the transmitter failed and he remained on the same territory, at least through August 1984, when he was seen on his former area (in F1's range) and his transmitter verified to be dead.

The expansion of M5's territory occurred when M6 was replaced by M9. M9, therefore, did not take over the whole area formerly used by M6, but only half of it, the rest was retained by M5, now probably two years old (Fig. 2c). M9 remained in the same area until at least January 1985, without expanding into M5's territory.

M3 was older than M5 at first capture and appeared adult but not full grown. I believe he was the son of Fx, for he occupied a smaller home range within her presumed area (Fig. 2b) from August to December 1983. He had frequent interactions with the adult male, M6, yet remained within the latter's territory. He abruptly left the study area in January 1984, just after the disappearance of his presumed father, M6, and arrival of M9. It seems likely that M9 evicted him. In October 1984 his skeleton was found about 5 km outside of the study area. He had died long before, seemingly of severe head injuries received several weeks before death : a zygomatic arch was broken and partly rehealed, and there was a partly rehealed gouge in the cranium above one eye ; but the most serious injury was a stab-wound that had penetrated the eye-socket, probably destroying the eye. The scar in the orbit from this latter wound is exactly fitted by the canine tips of specimens of adult male ocelots (US National Museum), and the gouge in the cranium is consistent with the same weapon. As Jaguar and Puma have much wider canines, and would probably have killed outright an ocelot held by the head, it seems likely that M3 died as a result of a fight with another ocelot.

F4 seemed strongly tied to the study area, and was restricted to it although she was already wandering widely throughout it when first captured in August 1983. I believe that she was born on it, most likely the daughter of F2, nursed in September 1982, but there is no direct evidence for this. She had four encounters with F2 when she was followed during her wandering phase, and none with F1.

In September-October 1983, F4 was usually on the south end of F1's territory during the day, although in a sample in October she traveled widely at night across the areas of F1, F2 (where she was chased), and Fx. On 10 October she left the study area and crossed the river, but returned by 20 October. In November she was on F1's territory on 5 days, and Fx's on 3 days. In December-January 1984 she started to be found on her future territory, but in February still occasionally appeared on Fx and F1's ranges. From 4 March to July she occupied a well-defined zone on the riverside between Fx and the former territory of F2 (Fig. 2a). Her movement patterns during 5 nights in March were typical of an adult, territorial, female. No data were collected in August, but on 1 September F4 was found crossing F1's territory, with F1 apparently following several h behind. On 2 September F1 met F4 for a few min, followed her for 200 m, met her again and traveled with her for another 200 m, spent an hour stationary with her then followed her again and rested

near, but not with her for 5 h. The next morning F4 left the study area, with F1 following far behind her to the edge of her territory. A month later, F4 was located once about 5 km downstream from the study area. In the 5-6 months that F4 maintained a territory, at an estimated age of two years, she did not appear to give birth to kittens. Her only two recorded encounters with an adult male (M9) were while she held a territory.

Mating System

It is likely that a territorial adult male is dominant on his territory and has most access to females with territories within his, but neighbouring males might also enter an estrus female's range. Because F1's presumed son M5 became the territorial adult male on her territory, the question arises whether M5 fathered her litter born in May. The gestation period of ocelots is 69-85 days (Hemmer, 1976 ; Fagen and Wiley, 1978). A litter born on 1 May would therefore have been conceived from 5-21 February (but she could have given birth up to two weeks later). Although it was not part of his usual area, M9 was recorded entering F1's territory, along the lake edge border only, on 26 February, 2 March (when he rested near her during the day), and again on 6 June 1984 (just after she lost her litter). He thus was near her at close to the time she would have bred.

Transients

A large young-adult male, M8, was caught on the riverside in July 1983. His radio signal was never heard after his release, and we assumed that he left the area. However, his freshly dead body, with radio non-functional, was found on the study area 13 months later (August 1984). The cause of death was not apparent. Because it is not certain if or how long the radio functioned, nothing can be said about his movements. The largest female captured during the study, F13, was caught in Fx's range on 1 October 1984. The next day she was on F1's territory and F1 spent 4 h in her vicinity. A week later she was on the west border of F1's range, where she may have acquired an adjacent territory (outside the study area, Fig. 2a), because she was several times located there until late December. From 17 September 1983 to July 1984 (when most ocelots had collars), there were three clear sightings of uncollared ocelots on the study area, involving at least two cats. Because suitable habitat may all be occupied by territorial residents that remain until old age, as in the case of M6 and F2, most young and very old ocelots are likely to become transients.

DISCUSSION

Activity

Navarro (1985) and Schaller (1984) plot circadian activity of ocelots in Texas and the Pantanal of Brazil. The activity pattern in Texas (summer) is quite similar to that found in this study, except that the whole pattern is shifted about six hours to the right, with the least active period in the afternoon rather than morning ; probably a result of high afternoon temperatures. Pantanal ocelots show a completely different pattern of fairly constant moderate activity

levels throughout the 24 h. This may result from measuring activity by spot checks of transmitter activity-sensors, rather than horizontal movement ; but Navarro also used the latter method. Sunquist and Ludlow (1985) report ocelots in Venezuelan Llanos to rest during the day and become active at sunset. Because ocelots, like many other felids (Guggisberg, 1975), appear well adapted for hunting both day and night, their circadian movements are probably locally fitted to probabilities of prey encounter. As in the present study (Emmons, 1987), both Enders (1935, for Panama) and Sunquist and Ludlow (1985) found small nocturnal rodents to dominate ocelot diets.

Home Range Size

Navarro (1985) reported a female ocelot home-range in Texas of 2.07 km², and an adult male range of 3.5 km² ; while Schaller (1984) found two females to range 0.8 and 0.9 km². Ocelot home-range sizes in Texas subtropical scrub, Brazilian Pantanal and Peruvian evergreen rain forest, are thus surprisingly similar. This can be contrasted with the more than 10-fold variation in home-range size of female Puma, which in Texas are reported to range an average of 1,032 km² (McBride, 1976, cited in Anderson, 1983, N = 4), but in the Brazilian Pantanal, only 82 km² (Schaller, 1985, N = 1).

All ocelot home ranges thus far described are the size of the smallest known for bobcats, which have similar body weight (e.g. Lembeck and Gould, 1979). This is two orders of magnitude smaller than the largest bobcat ranges of about 100 km² (Zezulak and Schwab, 1979). Reported ranges vary throughout this scale, and it is clear that bobcats are extremely flexible in adjusting home range size to available resources. The small amount of data thus far available for ocelots does not suggest a similar flexibility.

A reason that bobcats might have more variable home range size than ocelots is that they occupy a much wider range of habitats, from Sonoran desert to Boreal coniferous forest. Ocelots, although geographically widespread, appear restricted to densely vegetated or forested portions of open biomes (Navarro, 1985 ; Sunquist and Ludlow, 1985). The range of microhabitats occupied by ocelots is therefore smaller than suggested by the general geographic pattern.

Home range size of females is probably a product of the interaction between prey abundance and how it is related to foraging time. There is a basic difference between the prey of ocelots at Cocha Cashu, and that of bobcats. About 60 % of the diet of ocelots consists of rodents so small that three or more are needed per day (Emmons, 1987). The modal prey of bobcats is rabbits, and these and larger mammals such as Mountain Beaver, deer fawns, porcupines and marmots, make up 70-80 % of the diet (Kitchings and Storey, 1979 ; Berg, 1979 ; Brittel *et al.*, 1979). A single capture of one of these prey would feed a bobcat for a day or more.

Activity and Reproduction

Long circadian activity may be typical for solitary felids : Sunquist (1981) found tigers to be active about 15-16 hours/day and Rabinowitz and Nottingham (1986) reported jaguars active about 13.7 hours/day. Although these authors' methods were not strictly comparable to mine, high levels of

movement are evident. This contrasts sharply with the behavior of Serengeti lions, which on average spend only two hours a day walking (Schaller, 1972).

The energetic cost of reproduction has been measured in few wild species, but the data available for rodents and domestic mammals suggests that pregnancy usually increases caloric needs by about 25 %, while lactation requires an intake of 50 %-152 % above non-breeding maintenance levels (reviewed in Randolph *et al.*, 1977). For domestic cats, recommended food increase during pregnancy is 25 %, and during lactation, 150 % (Scott, 1976). F1's activity during lactation showed a maximum increase of 133 % over non-reproductive levels (Tables II, VI). This corresponds well with values for the cost of lactation and suggests that time spent active may be closely correlated with food requirements and hunting success. I believe that the pattern of increasing activity by F1 during lactation, to a maximum of 93 % of the day, suggests that she had great difficulty in catching enough prey to maintain her litter, and that she lost it when hunting demands reached unsustainable levels. The exclusive boundaries between F1 and F2 when they had kittens in 1982, the increased patrolling and marking behavior of F1 when she was pregnant and lactating in 1984, and the simultaneous disappearance of the formerly tolerated F2, all suggest that territorial behavior is intensified by females with young ; probably in an effort to sequester food resources.

Ocelots have a strong mode of one young per litter (mean 1.4, Cisin, 1967 ; Tewes and Schmidly, 1987. Gittleman, 1986 gives a mean litter size of 2.5, but his cited sources give no actual data). Ocelots also have one of the longest gestations and slowest growth rates in small felids (Fagen and Wiley, 1978). These parameters suggest adaptation to low expected rates of energy acquisition. Data collected during this study, including long circadian activity, in one case perhaps reaching unsustainable levels during lactation ; long support of male young on the parental home range ; and probable two-year interbirth interval ; are all consistent with this hypothesis. It takes much of each day for an ocelot to catch its food at Cocha Cashu, despite both high diversity and abundance of prey (Emmons, 1984 ; 1987). It can be predicted that ocelots might not be able to reproduce where prey density is much lower than that on the study area. This was supported by the total absence of ocelot sign in an area of low rodent density near Manaus where I worked for 5.5 months (Emmons, 1984).

Bobcats have different life-history parameters, despite similar body-size, sexual dimorphism and sometimes, land tenure system, to ocelots. They have 63 days gestation (Hemmer, 1976), mean litter of 2.6 (Britell *et al.*, 1979), and rapid postnatal development (Fagen and Wiley, 1978). All young emigrate from the natal territory just before 12 months of age, when the mother is about to give birth to her next (usually annual) litter (Kitchings and Storey, 1979 ; Lembeck and Gould, 1979 ; Zedulak and Schwab, 1979 ; Britell *et al.*, 1979). Litters are born in early spring (Berg, 1979 ; Britell *et al.*, 1979), when prey populations are low following winter mortality. Females are thus able to support 2-3 nursing young on low prey numbers.

I thus conjecture that ocelots are adapted to greater average difficulty catching prey than their temperate counterparts, the bobcats. Yet the density of ocelots at Cocha Cashu is high (est. 0.8/km² excluding transients), in the same range as the densest bobcat populations (Lembeck and Gould, 1979). If resources on an ocelot territory are borderline for lactation, why do ocelots not

expand their territory size, as bobcats apparently do when prey is scarce ? It may be that an increase in an ocelot's territory would not decrease its required foraging time, while it might increase the energetic costs of patrolling territorial boundaries. Data are needed on time spent foraging by bobcats in relation to reproduction and home range size.

Social Organization

The limited data presented here suggest that at Cocha Cashu breeding female ocelots have contiguous territories, and resident adult males have larger territories that overlap those of several females. The superficial distribution of ocelot home ranges during certain months of this project would not suggest territoriality, but the long-term pattern, with ages and probable relationships between individuals taken into account, is far more compelling. Territorial defense by solitary, nocturnal, forest mammals is almost never seen, but we were fortunate in recording four instances of what seemed to be direct territorial defense by females : 1) a 12 h pursuit of F4 by F2, after which F4 never was found on the area of encounter again ; 2) the final, 24 h pursuit of F4 by F1, after which F4 entirely left the study area ; 3) the interaction between F1 and the transient F13 as F13 crossed, and definitively left, F1's territory ; and 4) the several days of interactions between F1 and F2 on a piece of F2's territory taken over by F1. The fixed home-range boundaries and boundary-walking behavior of resident adults are also consistent with territoriality.

It was clear from the many encounters recorded during radio-tracking (Table IV) that while ocelots are solitary hunters, their patterns of movement bring them frequently, and to all appearances deliberately, into contact with other ocelots. Males and females meet outside of breeding periods, and independent male subadults often meet both parents. The unceasing patrol by adults of their territories should result in immediate detection of intruders, or conversely, show to a transient the presence of a territory holder.

F1 and F2 had no range overlap when both had young in 1982, but a year later F2 was « allowed » on the territories of female neighbours for about six months before she reduced her activity to an unused corner of F1's range, and then abruptly left the study area forever, when F1 became pregnant and showed intensified marking behavior (scrapes). A relaxation of intolerance between females that knew each other thus occurred when they were not breeding, but this ended when breeding resumed. F2's unique behavior of repeatedly killing chickens suggests impaired prey-catching abilities during the months before she left the area. F1 had already proven dominance by taking over part of F2's range and might have continued to tolerate F2 only because she posed no immediate threat and because they already had social ties.

Sunquist and Ludlow (1985) reported that in Venezuela, home ranges of male ocelots had little overlap, but that females in some cases overlapped considerably. As seen above, this may or may not differ from ocelot social organisation at Cocha Cashu as interpreted herein. For bobcats, radiotracking studies show variable spatial organization, consisting of either overlapping (Zezulak and Schwab, 1979) or non-overlapping female territories, and larger male home ranges that overlap those of several females, with from extensive (Bailey, 1974 ; Berg, 1979 ; Lembeck and Gould, 1979) to no (Buie *et al.*, 1979) overlap with other males. The spatial organisation of cats may only make sense when the individual histories and relationships are known.

In bobcats (Bailey, 1974), a female territory is overlapped by the ranges of several males, which suggests a mating system based on a male dominance hierarchy, as in domestic cats. This seemed not to be the case in the small sample of ocelot ranges determined at Cocha Cashu, where each female was overlapped by only one territorial male. However, as M9 entered the edge of F1's range and met her, at close to the time of conception of her litter, males may have access to females around their borders, and females may have some choice of mates. Much more data are needed.

Adult males may have great influence over the social organisation around themselves. The arrival of M9 coincided with changes in the status of every collared ocelot on the study area, as follows : 1) disappearance of the old male, M6 ; 2) disappearance (and death ?) of young M3 ; 3) expansion of M5 into territoriality including half of old range of M6 ; 4) establishment of F4 in a territory on her presumed father's (M6's) old range ; 5) pregnancy of F1 ; and 6) consequent (?) final emmigration of F2 from the study area. Changes 3, 4, and 5 may have been unrelated to the change in adult males, but they closely coincided (December to March, 1984). Bertram (1978) reports a birth peak among lionesses, unrelated to the killing of cubs, several months after a new male has taken over a pride. It is worth exploring whether the same phenomenon exists in « solitary » felids.

The nature of ocelot social interactions was often enigmatic : what was happening when F1 and F2 spent many hours immobile but separate in « disputed » ground, or when F1 spent four hours with a transient before following her to her border ? Were the many hours M3 and M6 spent together part of a similar interaction, but one where the ageing M6 failed to attain dominance ? Or were the presumptive father and son simply friends that sought each other's company ? At least with females, territorial defense seemed to involve long interactions. It seems likely that challenges to territorial animals by transients may be frequent, and that tests of dominance may take hours or days.

The objectives of ocelots that followed each other were often equally unclear. In all cases, following succeeded a meeting, and the follower waited while the other cat walked a long way ahead, then fell in behind. The three cases where females followed other females to their territory borders can be interpreted as territorial defense ; but why did M9 follow F4, and F2 follow M6 ? My presence between the two cats may have disrupted some interactions, but this was not the case when F2 « chased » F4 out of her territory. The cats must have used olfaction to follow each other at night at > 100 m distances.

Dispersal of Young

F4 had apparently already begun dispersal by 80 % adult weight. Both young males, in contrast, used distinct small home ranges within female territories for another four months. F4 and M5 seemed to become territorial, and M3 emmigrated, at ages of 17-22 months, but these events coincided with the arrival of M9, and might have happened later had M6 remained in place. The young males were apparently allowed by both presumptive parents to remain on the parental territories for longer than was the young female, until they had reached a greater percentage of adult weight (but it is noteworthy that F4 was partially tolerated by two or three females, for she was not evicted from the study area as a subadult, although she apparently was, later, as an adult).

Ocelots probably have little chance of breeding unless they acquire territories. Because male territories are 3-4 times larger, there are fewer male, than female territories, and the variance in reproductive success is probably higher in males than in females. The outcome of competition between males may be decided by body weight and vigor : the death of M3 from a fight suggests physical combat does occur. Parent ocelots may invest more in sons than in daughters ; by allowing them to use the resources on their territories for longer ; so that sons can reach large size, and presumably, breeding-potential, before they embark on the risky life of transients. It would be interesting to know whether ocelot females that have raised daughters have a shorter interbirth interval than those that have raised sons (cf. Clutton-Brock *et al.*, 1982). A large subadult on the home range may reduce the likelihood that a female will find prey easily enough to support lactation.

CONCLUSION

I believe that these « solitary » felids have a network of social ties with other ocelots around themselves, and that their behavior towards other individuals reflects these ties and cannot be predicted or understood without knowledge of them. I have made many interpretations and inferences from a small sample of ocelots during a small part of their lives. Larger populations need to be studied for longer periods to test the generality of the behaviors I observed. The method of continuous following on foot of radiocollared ocelots yielded data on social interactions, itineraries, activity, and hunting behavior that would not have been collected by other means. The method is arduous and requires a good trail system and great care to avoid influencing the behavior of the animals followed (e.g. use of earphones), but with it, many remaining questions about the mating system, foraging energetics, reproductive behavior of females and long-term social organization of ocelots could be answered.

SUMMARY

A population of ocelots was followed by radio-tracking in a Peruvian rain forest. Two resident adult males, two adult females, and three subadults were radio-collared, as well as two transients. Ocelots were active at any time of day, but usually they rested in the morning, became active in mid — to late — afternoon, and continued activity until after dawn the following morning, with one rest period during the night. They spent an average of 9.6 hours walking per night.

Breeding females occupied mutually exclusive territories, but an old female was tolerated on their territories by her former neighbours when the latter had no dependent young. Apparent direct territorial defense by females was recorded four times. Adult males occupied large territories that overlapped three or more female ranges.

Circumstantial evidence indicated that females on the study area produced young about every other year. A lactating female increased her daily activity to a maximum of 133 % above normal, to 93 % of the time, before losing her lit-

ter. It is conjectured that she was unable to sustain the foraging demands of lactation.

An 80 % grown subadult female was already wandering, but two 80 % grown males occupied small ranges within their presumed mother's territories. The disappearance of an old adult male and establishment of another coincided with changes in the status of all collared residents. Although ocelots hunted, traveled, and usually denned alone, they often met : 37 encounters between collared cats were recorded during radio-tracking.

RÉSUMÉ

Une population d'ocelots a été suivie par radio-pistage dans la forêt hygrophile de Cocha Cashu, sud-est du Pérou. Des émetteurs-radio furent fixés au cou de deux mâles adultes résidents, de deux femelles adultes, de trois subadultes et de deux individus « nomades ». Les ocelots sont actifs à n'importe quelle heure du nyctémère ; ils se reposent généralement dans la matinée, s'activent au milieu ou en fin d'après-midi, et continuent à se déplacer jusqu'à l'aube du lendemain — avec une période de repos pendant la nuit. En moyenne, les ocelots se déplacent 9,6 heures par nuit.

Les femelles reproductrices occupent des territoires mutuellement exclusifs, mais une vieille femelle était cependant tolérée sur les territoires de ses anciennes voisines quand celles-ci n'avaient pas de jeunes dépendants avec elles. L'auteur a observé à quatre reprises des femelles défendant apparemment leur territoire. Les mâles adultes occupent de vastes territoires qui chevauchent ceux de trois femelles et plus.

Il semble bien que les femelles de la zone d'étude aient mis bas un jeune tous les deux ans. Une femelle allaitante a augmenté de 133 % au maximum son activité normale, ce qui représentait 92 % de son temps, avant de perdre sa portée. Il est probable que cet animal fut incapable de chasser assez pour faire face à ses dépenses d'allaitement.

Une femelle ayant atteint 80 % de sa taille adulte nomadisait déjà, alors que deux mâles de même taille occupaient encore de petites parties du territoire de leur mère présumée. La disparition d'un vieux mâle adulte, et l'arrivée d'un autre mâle, ont coïncidé avec un changement de statut de tous les ocelots résidents radio-marqués. Bien que les ocelots chassent, se déplacent, et gîtent isolément, ils se rencontrent souvent : 37 de ces rencontres furent observées.

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