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MOVEMENT PATTERNS AND FOOD HABITS OF FOUR SYMPATRIC CARNIVORE SPECIES IN BELIZE, CENTRAL AMERICA

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ABSTRACT. Four species of sympatric carnivores (3 felids: 1 mustelid) were studied using radio telemetry for 21 months in Belize, Central America. Body weights ranged from 4 to 12.5 kg. Two species (jaguarundi, *Herpailurus yagouaroundi*; tayra, *Eira barbara* were diurnal; two species (ocelot, *Leopardus pardalis*; margay, *Leopardus wiedii*) were nocturnal. All four species traveled about 6.5 km in a 24-hr period, but there were large differences in home range sizes (10 to 99 km^2). Home range area was not correlated with body weight. No significant habitat associations were found for any species. Vertebrate prey, especially mammals, provided 95-98% of the ingested energy for the three felids. Tayra diets included a high frequency of fruit, but the caloric contribution of fruit could not be assessed. No significant similarities were found in the diets of the four species. Collected data were used to speculate about interspecific interactions and the large home ranges exhibited by jaguarundi.

RESUMEN. Cuatro especies de carnívoros simpátricos (3 félidos: 1 mustélido) fueron estudiados utilizando radio telemetría por 21 meses in Belize, America Central. El peso del cuerpo varió de 4 a 12,5 kg. Dos especies (jaguarundi, tayra) fueron diurnas; dos especies (ocelote, margay o tigrillo) fueron nocturnas. Las cuatro especies se movieron alrededor de 6,5 km en un periódo de 24 horas, pero hubieron grandes diferencias en los tamaños de ámbitos de hogar (10 a 99 km^2). El ámbito de hogar no estuvo correlacionado con el tamaño del cuerpo. No se observaron asociaciones significativas con habitats determinados por parte de ninguna de las especies. Los vertebrados, especialmente mamíferos, proveyeron entre un 95-98% de la energiá ingerida por los tres félidos. La dieta de tayra incluyó un alto porcentaje de frutas, pero la constribución calórica de esta no pudo ser estimada. No se encontraron diferencias significativas en las dietas de las cuatro especies. La información obtenida fue utilizada para especular acerca de las interacciones interspecificas y el ámplio ambito de hogar exhibido por jaguarundi.

INTRODUCTION

Descriptions of resource partitioning (i.e. time, space, food) among sympatric species can be used to determine the factors governing species co-existence and whether, or at what level, competition exists. Some authors disagree whether species co-existence is random or non-random (Connor and Simberloff, 1984; Gilpen and Diamond, 1984).

There is also debate about competition and its effects on co-existence patterns (Dickman, 1984; Thomson, 1980).

Co-existence patterns among sympatric species with close taxonomic affinities (i.e. guilds) have been examined by Dickman (1984), Emmons (1980) and Feinsinger (1976) among others. Among similar sympatric carnivores, positive correlations exist between body size and prey size and between co-existence and body size difference (Rosenzweig, 1966). That is, in stable carnivore communities larger carnivores take larger prey, and size differences exist between members that serve to reduce possible competition. Four sympatric, synchronously active Namib desert carnivores co-existed by the extreme diet specialization of two species and broad differential resource use by the other two (Bothma et al., 1984). Studies of pairs of felid species have each suggested that differential habitat use may be important in reducing competition, especially if the species are synchronously active or utilize the same prey (Norton and Lawson, 1984; Schaller and Crawshaw, 1980; Seidensticker, 1976).

At the outset, the present study's objectives were to examine movement patterns, diet, and habitat use of two previously unstudied small felids: jaguarundi (*Herpailurus yagouaroundi*) and margay (*Leopardus wiedii*). The study was expanded to include two other sympatric species, the closely related ocelot (*Leopardus pardalis*) and the morphologically similar tayra (*Eira barbara*). The study was conducted in the Cockscomb Basin, Belize simultaneously with a study of jaguar (*Panthera onca*) ecology (Rabinowitz and Nottingham, 1986).

The Cockscomb Basin is one of the few locations where all five known felid species in Belize are sympatric (*P. onca*, *Puma concolor*, *L. pardalis*, *L. wiedii*, *H. yagouaroundi*). Cooperatively. we hoped to gather data about puma ecology, thereby making it possible, for the first time, to characterize an entire felid community in sympatry. However, we were unsuccessful in attempts to capture puma.

When combined with other studies, the data gathered in this study provide insight into individual species' ecological needs, the effects of sympatry, and the adaptability of species across their range.

MATERIALS AND METHODS

Most of the data were collected by the author in the Cockscomb Basin Forest Reserve in south-central Belize in 1985-1986. Additional information was provided by other investigators and local residents. The Cockscomb Basin encompasses about 250 square kilometers and is contiguous with the Chiquebul Forest Reserve (166 km^2) to the West. The elevation of the eastern portion of the Basin ranges from near sea level to 600 m, while a series of ridges to the.west culminate in Victoria Peak, the highest point in the country. The central, and largest, portion of the Basin is relatively flat with low rolling hills. Three large rivers exit the Basin and provide drainage for the numerous creeks and streams in the area. The vegetation is subclimax moist, tropical forest, maintained by irregular hurricanes. Selective timbering throughout much of this century has created large patches of second growth vegetation at different successional stages.

Historically, Maya Indians have intermittently occupied the Cockscomb Basin, including the construction of a minor ceremonial site. Employing slash and burn agriculture, the Indians further disrupted the area. They shot cats opportunistically as potential pests, and hunted other animals sporadically for food. The Maya's last occupancy ended in January

1985 when the Basin was given governmental protection from milpa agriculture and hunting.

The climate may be divided into two seasons: dry and wet. The dry season (February to May) is typified by hot, cloudless days and temperate nights. Rainfall is sparse and sporadic. The wet season (July to December) is characterized by the rapid build-up and release of heavy downpours during the day and night. As much as 20 mm may fall in a single shower. In July 1984, 60 cm of rain fell in 54 hours. Walker (1973) stated that the average annual rainfall is 250 cm. Average daily high temperatures vary from 22° to 32° C, and low temperatures (December) may fall as low as 8° C. January and June are transitional months. Throughout the year day length varies from 10.5 to 12.5 hours.

No systematic survey has been done on the flora or fauna of the Cockscomb Basin. The combined efforts of several researchers have identified approximately 300 species of birds and 20 species of reptiles. Appendix 1 contains a list of mammal species seen, caught, or found in fecal remains in the Cockscomb Basin.

To capture study animals, fourteen bobcat-sized live traps (Tomahawk, Inc.) were baited with live chickens. Chickens were restricted to the back of the trap by chicken wire. Traps were distributed along roads and trails and near streams in the eastern portion of the Basin. Captured animals were immobilized with ketamine hydrochloride (20 mg/kg BW). Dosage responsiveness varied among the species captured. Individuals exhibiting premature activity were maintained in a relaxed state with injectible valium (5 mg). All immobilized animals were sexed, weighed, measured, and examined for relative physical condition. Most were fitted with radio transmitter collars manufactured by Telonics Inc. (Mesa, Az.). Some collars also contained mercury tip-switch activity monitors.

Collared animals were monitored on a scheduled 6-, 12-, or 24-hr basis. However, animal movements sometimes reduced or eliminated the ability to maintain monitoring schedules. Four 5-element yagi antennas were attached to 10 m bamboo poles. With one central antenna, the other three were arranged at 120 degrees from each other relative to the central antenna. During monitoring periods compass headings from the central antenna were paired with the peripheral antenna that produced the maximum angle. Peripheral antennas were erected 269 m, 398 m and 439 m from the central antenna.

Some animals ranged so widely that they could only be located by aerial telemetry. A 2-element yagi antenna was attached to each wing strut of the aircraft and signals were carried through coaxial cables to a switch box connected to a receiver. Both antennas were monitored until a signal was received. Using the antenna receiving the strongest signal, the animal was located by flying a reduced square. The location was determined from map landmarks and compass headings taken from known map reference points. Aerial surveys were conducted at average intervals of two weeks.

Activity and activity cycles were determined from visual observation, activity sensors in radio collars, and calculated relative travel rates from location data. During monitoring periods, radio locations were taken hourly, and the shortest distance between points was calculated. Because the actual path between points could not be determined, the results reflect the minimum estimate of hourly travel rates.

Food habit data were obtained almost exclusively from scat collections. Using size, shape, odor, and track evidence, it was possible to identify the species which had deposited each scat. Only scats which could be positively identified were collected. Analyses were performed using methods described in Johnson and Aldred (1982) and Johnson and Hansen (1978). Identification of fecal contents was as specific as possible. Mammalian identifications were made by hair medulla comparisons with reference collections or by other diagnostic characters. Fecal contents were expressed as a frequency of occurrence of all scats collected for that species.

The relative caloric contribution of ingested items could only be broadly estimated using from relative digestibilities calculated for domestic cats (Greaves and Scott, 1960) and the per gram dry weight caloric content of closely related taxa (Cummins, 1967). Comparison of diets between species were made by using proportional similarity indices (Greig-Smith, 1964) and correlation coefficients.

To estimate the relative abundance of potential prey, line transects were sampled in four different successional areas. Thirty-six Sherman traps were baited daily with oatmeal and peanut butter and checked twice daily for one week in each habitat. Captured animals were identified and released, and the data for each monitoring period were lumped. Areas selected were: abandoned cornfields (old field), dry second growth forest, moist second growth forest, and mature subclimax forest. Capture rates and species captured are listed in Appendix 2.

Radio location data were transformed to rectangular coordinates using the AIDA program written for Apple II micro-computers. Home range areas and shapes were calculated using the MCPAAL program written for IBM micro-computers. Home range area was calculated by minimum convex polygon and harmonic mean methods. Tests conducted by Stuwe (pers. comm.) revealed minimum convex polygon estimates to be more accurate, and these values were accepted.

RESULTS

Jaguarundi

Four jaguarundi (two adult males: two adult females) were captured, but only three could be fitted with radio collars. These animals were monitored for periods ranging from 10 to 14 months. See Table 1 for body parameters. An examination of nipples indicated that each female had had at least one litter, though neither was lactating at the time of capture (February 1985, June 1985).

Of the two color phases known to occur among jaguarundis, each was represented by a male and female, suggesting no association between coat color and age or sex. Although one black individual was seen, the dark color phase animals were grayish in appearance. Light phase animals were deep reddish brown. In contrast to Weigel (1961), no facial markings were found on any animal. Jaguarundi tracks are easily distinguished from other small cats because the toe pads are much more elongated and oval than those of other species.

Jaguarundi were essentially diurnal, but some movement was recorded for all hours (Fig. 1). All but one of the sightings (n = 11) of jaguarundi were made during the day. No differences were found in relative travel rates between seasons or individuals, so the data were pooled (n = 194). From the few data available, jaguarundi were slightly more active on moonlit rather than dark nights. Daily activity increased markedly about 0400 hr and peaked about 1100 hr, and then decreased steadily until 1300 hr. After 1800 hr (approximate mean sunset) activity levels dropped below 100 m/hr, indicating only residual activity. On only a few occasions during the night was an animal inactive for more than two consecutive hours.

Daily movements were similar between sexes. Jaguarundi exhibited a pattern of long, unidirectional movements. In general, daily travel paths crossed themselves infrequently and often ended well away from the starting location. Hourly movements (n = 215) ranged from 1 to 2253 m with a mean hourly movement of 253 m (± 342 m) for consecutive daily locations. Mean nocturnal movements (1800 to 0600 hr) were 90 m/hr while diurnal movements were significantly different (277 m/hr) (Chi-square; $p < 0.05$). The total distance traveled during a 24-hr period averaged 6.60 km ($n = 5$).

While both sexes exhibited long, unidirectional movements, there were intersexual differences in land tenure. Female (J2) moved 4 km to the West and was recaptured four days after initial capture. Over the next two weeks she moved 12 km further West. At that time, long range movements ceased, and for the next 12 months she occupied a range of 12.94 km^2. Using all the locations. the total area used during the study was 20.11 km^2 (Table 2; Fig. 2). This type of movement could be associated with subadult disperal, but physical examination had revealed her to be sexually mature. The toothwear and discoloration was that of an adult cat.

Males traveled over much larger areas than females. After release, males (Jl and J3) remained in the area of capture for 8 and 10 days respectively. Male Jl began to move intermittently but steadily away from his capture point. After three months he was 22 km to the West of his point of capture. Monitored from the air, Jl moved 12 km in a two-week period in November-December 1984. For the next three months he remained in an area of 30 km^2. In a nine-day period in March 1985, Jl moved 17 km back to the vicinity of initial capture. He was located from camp for nine days before he began to move again. He returned in the same general direction as before, but slightly to the North. In August 1985, he had begun a second return to camp when his transmitter failed. He was subsequently sighted to the East of camp. His home range area was 99.98 km^2.

Male J3 displayed similar movement patterns, moderate daily movements which progressed steadily into long range movements. On 28 June 1985, all three collared animals were located within 2.5 km of each other, and Jl and J2 were only 400 m apart. During August and September 1985, J3 emigrated from the Basin to the south. This movement required climbing a 400 m high ridge. After five months outside the basin, he began to move back in again. The home range area calculated from all locations was 88.32 km^2.

All jaguarundi were captured in second growth habitats, but afterward moved steadily toward more mature forest. All were captured near streams, and location data suggest a preference for riparian habitats. One den site was located in the bank of a small stream and appeared to be an abandoned paca (*Agouti paca*) den. Of the locations plotted in areas of second growth, jaguarundi were found more frequently in old field habitats than any other type (Chi-square, $p < 0.05$).

The association of jaguarundi with old field habitats is supported by the food habit data. Small mammals were found in over 90% of the scats collected ($n = 46$). The species found most frequently was *Sigmodon hispidus* (47.7%) (Table 3), and this species was trapped more frequently in old fields than other habitats (Chi-square; $p < 0.02$). *Didelphis marsupialis* (13%) also occurred commonly in the scats. Arthropods (71.4%) were found more frequently than any other diet item,and small birds (21.4%) were second only to *S. hispidus*. However, vertebrate prey contributed 95.1% of ingested energy: mammals contributed 87.6% of the total energy. Although seeds were found in 11.3% of the scats, it was not possible to accurately estimate the amount of fruit eaten or the energy contained in each fruit species. No reptile, amphibian or fish remains were found in any of the scats sampled, but there is no evidence to suggest they are excluded from the diet.

Margay

Only two margays (2 males) were trapped during the study, and it was possible to collar only one for a period of six months. After six months, the male slipped his collar. That individual was a young adult male, containing complete adult dentition, but showing little toothwear or discoloration. Furthermore, the testicles were not fully descended or enlarged. Both margays were more dosage sensitive to ketamine hydrochloride than other felids, and each had prolonged recovery periods and slightly greater ataxia once ambulatory. Both were captured in an area of late second growth forest with some relatively large trees still standing.

Margays were seen only three times and only at night. Travel data taken from sequential locations (n = 110) revealed strongly nocturnal activity (Fig. 1). The highest rates of travel occurred from 0100 to 0300 hr and decreased to a low rate at 1200 hr. Again from 2100 to 2400 hr travel rates varied from 300 to more than 500 m/hr. During the hours 0700 to 1100 and 1300 to 2000 hr the activity was reduced from the highest rates and varied from 100 m/hr to 280 m/hr. The data did not reveal any differences in movement rates with ambient moonlight.

During daylight hours the margay was located by homing in on his radio signal. Without exception, resting areas were in trees from 7 to 10 m above the ground. Rest areas were usually a tangle of lianas and vines or the bole of a cohune palm (*Orbignya cohune*). No single resting spot was used repeatedly, but some were revisited. In the area where the margay was found few trees with large cavities could be found. During the day, the male moved after 2 to 3 hours of inactivity, possibly to another resting spot. All traveling was done on the ground, although in other parts of Belize, margay were reported moving through the top of closed canopy forests.

The margay traveled in one direction from the daily starting point and returned along essentially the same path with little variation. Hourly movements varied from 0 to 1189 m and an hourly average of 273 m/hr for all hours. During the day, movements were 197 m/hr and during the night 305 m/hr. Total daily distance traveled was 6.65 km for four diel monitoring periods. The calculated home range area was 10.95 km^2 (Table 2; Fig. 3). This area included the narrow defile of the entrance road and the disturbed areas around the research camp. The margay used all habitat patches at some time, but spent significantly (Chi-square, $p < 0.01$) more time in late second growth forest. Movements consisted of 2- to 3-day forays into areas of early second growth followed by a return to older forest for 5 to 6 days. Over time, the male spent more time in the western portion of his range.

Scats (n = 27) were found infrequently. Areas around known roost trees were searched, but no middens were found. Typically, scats were covered with dirt or leaves, and rarely deposited in conspicuous locations. The number of different taxa (n = 7) included in the diet was fewer than any of the other species studied (Table 3). Vertebrate prey accounted for 96.2% of all calories ingested although arthropods (33.3%) and fruit (14.4%) were found frequently. Small birds were found in 29.2% of the scats. Arboreal rodents, *Sciurus deppei* (22.2%) and *Ototylomys phyllotis* (48.1%) were the most frequently consumed mammals. *Reithrodontomys gracilis* (18.5%) and *Marmosa* spp. (18.5%) were found equally.

One margay was seen at night in the lower branches of a tree. It had recently killed an unidentified rodent and was eating it crouched on a small branch 5 m above the ground. Once seen, it demonstrated its arboreal adaptations by descending the tree trunk to 3 m in a head down manner, carrying the prey in its mouth. Running quickly out onto a small branch, it leaped nearly two meters onto the small branch of another tree. Then it quickly climbed that tree and disappeared.

Ocelots

Three ocelots (1 male: 2 females) were trapped, and a male and a female were radio-collared and monitored for periods of 12-16 months. The male was a subadult/adult, and the female was an adult (Table 1). The third (uncollared) ocelot was an older adult female in an advanced state of physical deterioration. Her coat appeared mangy and lacked luster, and she was infested with numerous ticks and bot fly larvae (*Haematobium*).

The collared adult female had been captured and collared initially by another investigator in April 1984; shortly afterward the collar failed. She was captured again in November 1984 about 750 m from the original capture location. She was recaptured again in December 1984 and March 1985. In April 1984 she was lactating, but she was not lactating or palpably pregnant at any subsequent capture.

A subadult male was captured in March 1985 about 400 m from the point where the female had been first captured. Based on size, testicular development, toothwear, and capture location, the male was at the approximate age to be the offspring of the collared female. No other females were seen or captured in the same area.

Travel rates for ocelots are similar to those of margay (Fig. 1). Ocelots were most active in the early morning and late evening hours. Activity decreased steadily to a low point at 1300 hr and began to increase rapidly afterward. From 1600 to 2000 hr, activity increased slowly, but then rose sharply again from 2100 to 2400 hr. Activity during daylight hours was sporadic but not uncommon. Diurnal activity occurred more frequently on overcast or rainy days, perhaps a consequence of darker skies or a need to find more secure shelter. Commonly, one or two inactive hours were followed by a single movement and more inactivity. Frequently at night, two hours of activity were followed by one hour of inactivity.

Location data indicate that ocelots intensively used their ranges. Frequently, their movements backtracked or crossed themselves. Hourly movements varied from 0 to 2809 m with an average hourly distance moved of 329 m. Average total travel distance for 24 hr was 6.35 km (n = 8). Home range areas for the adult female and subadult male were 14.68 km^2 and 31.21 km^2 respectively (Table 2; Fig. 3).

Their ranges were entirely within areas of second growth vegetation and included only small areas of late second growth forest. The female used all of her range equally and demonstrated no habitat preferences (Chi-square, $p > 0.25$). The male remained in old fields and early successional forest for two months after capture. During the final two months of monitoring, the male moved to the eastern portion of his range into areas of late successional forest. During that time, forays into old field areas became much less frequent.

Food habits of ocelots were obtained from scats (n = 49) collected from all parts of the Cockscomb Basin. Mammals constituted the most frequent prey items, and vertebrate remains were found in 48 of 49 scats and constituted 98% of ingested energy (Table 3). *D. marsupialis* and *Philander opossum* occurred most frequently. Brocket deer (*Mazama americana*) (n = 3) and tamandua (*Tamandua mexicana*) (n = 1) each were found rarely, but indicate that ocelot may take larger prey than the other small felids. Armadillo (*Dasypus novemcinctus*) were found in ten (20.4%) of the scats. Birds, fruit, and arthropods were found less frequently than for any of the other species studied.

Tayra

Three tayra (2 males: 1 female) were trapped and monitored for periods ranging from 3 to 13 months. All three individuals were adults (Table 1). Tayra, unlike margay, metabolized ketamine more rapidly than expected. To maintain an acceptable level of immobilization, dosages administered were more than twice those given to felids. All three animals were captured during rainy season months (October, December, January), and all were trapped near streams. Tayra always penetrated the wire and consumed the bait, while the felids rarely did. In addition, tayra frequently damaged the trap itself, bending the heavy gauge wire of the trap. On one occasion, based on tracks and hair, a trapped tayra ate the chicken and bent the wire sufficiently to tunnel out of the trap. Tayra were rather docile when approached in a trap, although they produced constant panting-growling vocalizations.

Data on travel rates (n = 236) suggest that tayra were strongly diurnal (Fig. 1). No movements were recorded between 0100 and 0500 hr. After 0600 hr. travel increased dramatically and remained at fairly high levels until 1600 hr. Peak activity occurred between 0700 and 0900 hr. The low level of travel rates from 2100 to 2400 hr probably represent only residual activity. These data were partially confirmed by data collected from one male fitted with an activity monitor. Calculated as a percentage of total readings, the activity curve for a single male tayra closely approximated the shape of the travel rate data.

Daily movement paths were predominantly unidirectional with little or no crossing or backtracking. Hourly rates of travel varied from 0 to 2704 m and 353 m/hr for all movements. Evening movements averaged 55 m/hr while daytime movements averaged 398 m/hr. Total daily movements averaged 6.89 km (n = 7).

Range utilization patterns demonstrate that tayra did not range far on an annual basis (Table 2; Fig. 4). Male T3 had a calculated home range of 2.11 km^2 which probably reflects the short monitoring period (3 mos.). Male T2 and female T1 had home range sizes of 24.44 km^2 and 16.03 km^2, respectively. Individuals remained in an area from one to three days before moving to another. The home ranges of male T2 and female T1 included a major river, South Stann Creek. Both crossed the river frequently at high and low water levels. Habitat associations varied between individuals and while the female was located more frequently in old fields, the males were found in early second growth (Chi-square; $p < 0.01$). No specific den sites were located.

No tayra middens were located during the study, and food habit data were gathered from collected scats (n = 31). Fruit (67.7%) and arthropods (58%) were found more frequently than other categories. Tayra were seen often in or near mamey trees (*Calocarpum mammosum*). Maya Indians reported observing tayra eating mamey fruit. Among vertebrates, *S. hispidus* and *Rattus rattus* occurred most frequently. Fecal data suggest tayra eat fruit, insects, and small vertebrates. Another researcher reported seeing a tayra pursue a brocket deer (*M. americana*) across an open field.

Tayra were seen on 15 occasions for periods varying from 1 to 15 minutes. On four of these occasions, 2 adult-sized individuals were seen traveling together. Frequently, animals were seen trotting, turning their heads from side to side. Animals stopped frequently, repeated the head turning behavior, and appeared to be sniffing the air. Observations from local Indians suggest that tayra use their olfactory ability to select the ripest fruits in fruiting trees. Tayra are strong and agile climbers and display good balance on branches of all sizes. A collared male was seen climbing a small tree (15 cm diameter) and then leaped about 2 m to the fronds of a large cohune palm. Tayra were curious while in the trees but maintained continual panting-growling vocalizations.

Interapecific Interactions

Besides the four species studied, several other carnivores also inhabited the area (Appendix 1). Gray fox (*Urocyon cinereoargentatus*) were captured three times. Opossums and raptors were also attracted by bait chickens and trapped: *D. marsupialis* (n = 75), *P. opossum* (n = 46), collared forest falcon (*Micastur semitorquatus*) (n = 5), roadside hawk (*Buteo magnirostris*) (n = 3), and white hawk (*Leucopternis albicollis*) (n = 3). It was beyond the scope of this study to assess the ecological impact of these potential competing species on the four focal species.

Home ranges of the four species overlapped considerably. There are no data to suqgest any interspecific spatial avoidance by olfactory, visual, or vocal means. Track evidence suggests that conspecifics could be found well inside established ranges. Jaguarundi demonstrated significant patch preferences for old fields whereas margay preferred late second growth forest. The most common vertebrate item in jaguarundi scats, *S. hispidus*, was found in siqnificantly greater numbers (Pearson correlation; $p < 0.001$) in old field habitats than any other (Appendix 2). Both ocelot and tayra had no strong habitat preferences and could be found in all patch types.

The four species were divided temporally with jaguarundi and tayra active diurnally and ocelot and margay active nocturnally. The activity curves of the studied species intersected between 0600 and 0700 hr and 1500 and 1600 hr. All four species shared arthropods and small birds in their diet. *D. marsupialis*, *R. rattus*, leaves, and fruit were shared by three species (Table 3). On the whole, diets among the four species were different. Pairwise Pearson correlation coefficients calculated from all possible combinations revealed insignificant negative correlations between: jaguarundi-ocelot, ocelot-margay, and ocelot-tayra. Interestingly, the coefficient of correlation of jaguarundi and tayra diets was $R = 0.694$ (df = 16; $p = .001$), but a proportional similarity index (Greig-Smith, 1964) revealed that although many identical items were eaten, the level of consumption similarity was only 40.3%. Similarity indices done on all other pair combinations revealed none greater than 56.0% (tayra-margay). Correlation coefficients weight presence or absence of an item more than its frequency of occurrence. Similarity indices weight items eaten by only one species as well as items eaten by both.

DISCUSSION

Ocelot

Recently, four studies have intensively examined ocelot ecology in Texas (Tewes, pers. comm.), Peru (Emmons and Terborgh, in litt.), and Venezuela (Ludlow, 1986: Sunquist et al., this volume), and other general information is available from a variety of sources (Guggisberg, 1975; Mondolfi, in litt.; Rengger. 1830). Ocelots range in weight from 7 to 13 kg, are generally nocturnal but can be active at any time, and eat predominantly small to medium mammals. This conforms well with the data gathered in Belize. However, there are differences in specific aspects of their ecology.

Sunquist et al. (1986) found that ocelots exhibited a punctuated movement pattern with stops less than 60 mins. and traveled an average of 2.0 km (females) and 3.8 km (males) during 6-hour sampling periods. This agrees with my data except that when expanded to 24 hours total movements may be nearly twice as long. Interestingly, ocelots moved further each day in Venezuela than Belize, but maintained smaller home ranges. Ludlow (1986) and Sinquist et al. (this volume) calculated mean home ranges of 2 to 3 km^2 (females) and 9 to 10 km^2 (males) while in Belize the female's home range was 14.28 km^2 and the male's home range 31.21 km^2. The differences batween males could be accounted for because my male was a subadult and likely to move more widely in search of suitable and available range. But a nearly five-fold difference among adult females suggests a real contrast between sites, possibly in densities of equivalent prey species.

Habitat associations vary, but whenever forest areas are present, ocelot seem to prefer them. In the habitat mosaic study area of Venezuela, ocelots preferred gallery forests and only occasionally wandered into the sandhills (Sunquist et al., this volume). Working in more mesic and xeric habitats, Tewes (pers. comm.) studied ocelots in the thorn scrub and marshland of coastal southeastern Texas.

Among all studies, there is agreement that ocelots prey primarily on small to medium mammals. In Belize, opossums and armadillos occurred most frequently in the scats. The presence of a tamandua in a scat is surprising because of their formidable claws as defensive weapons. Rengger (1830) indicated that small deer and peccaries were also prey items. Sunquist et al. (this volume) found that after mammals, reptiles accounted for 18% of the diet and birds only 4%, while Emmons and Terborgh (in litt.) reported almost equal occurrences of birds and reptiles.

In Belize, birds occurred in 18.3% of the scats and no reptile remains were found. This could be due to the small sample size (n = 49) or possibly reduced reptile populations in study area, which overlapped greatly with recent human habitation. Working in the primary forest of southeastern Peru, Emmons and Terborgh (in litt.) suggest that in spite of high mammalian proportions in the diet and foraging bouts of 7 to 11 hours, female ocelots may be unable to find sufficient food for their litters resulting in greater kitten mortality due to starvation.

Habitat associations, dietary preferences, and home range size result from prey density and the density of conspecifics and competitors. Home range exclusivity may be maintained by fecal scrapes, scratching posts, and urine spray marking. These were not observed in Belize. Rengger (1830) reported that ocelots lived as couples, hunting independently, but cooperatively defending the home range. This was not observed in the present study. Furthermore, there was no evidence for use of toilets as reported by Guggisberg (1975).

The large home range of the subadult male and few captures suggest a low population density or a low replacement rate. In March 1986 a large unidentified individual (presumably male) was seen walking slowly on a dirt road near camp at 1930 hr. Possibly his presence caused the change in range observed for the subadult male. A few months before the project began, a prime male was killed by hunters in the middle of the female's home range. The reports of animals shot prior to this study, plus the lack of sign and captures during the study, suggest a reduced population. I believe the low replacement rate may be due more to continued human hunting pressure than ecological factors.

Tayra

This study provided some of the first ecological data about this relatively unstudied species. There is wide agreement that they are diurnal. Kavanau (1971) reported that tayra were active about 89% of the daylight hours, but only 2.1% of the evening hours. They became active after dawn and inactive before dusk. Although they infrequently moved for more than 10 sec continuously, they are active about 48 min of each hour. This agrees with data collected in Belize and is consistent with activity levels of omnivorous mammals (Kavanau, 1971). Tayras were active throughout the day, moving a total of about 6.5 km, but showed no activity from 2400 hr to 0500 hr. Sunquist et al. (this volume) found that a female exhibited a bimodal pattern of activity with peaks in morning and afternoon and traveled 2.0 km in a 6-hr period.

The Venezuelan tayra had a home range of 2.25 km^2 during lactation, and 9.0 km^2 at other times. In Belize, the female had a home range nearly twice as large. The large difference in male home ranges is likely due to the short monitoring period for the second male. The amount of overlap displayed by tayras in Belize contradicts the home range patterns of elongate mustelids (Powell, 1979). Powell did admit that tayras may not fit his criteria because they exhibit less sexual dimorphism and less carnivory than other elongate species. In this study, tayras showed no habitat preferences while at other sites they avoided open areas and showed a tendency toward arboreality (Kaufmann and Kaufmann, 1965). Although rapid and agile climbers, tayras were most frequently found on the ground, but went into the trees if disturbed.

In Belize, fruit and insects were the most common elements of the diet followed by three species of rodents and then small birds. Reports were gathered in Belize and in Mexico concerning pursuit of deer by tayras (Leopold, 1959). No data exist to indicate that tayra prey on deer. In Panama, tayras showed a predilection for mamey fruit (*C. mammosum*) (Kaufmann and Kaufmann, 1965).

In Belize, tayras were seen several times in pairs, but an equal number of solitary individuals were seen as well. Reports and anecdotal information exist about tayras occurring in large groups. These are likely persistent family groups. Alston (1874-1882) did report seeing 15 to 20 individuals in the mountain pine ridge of Belize, but most authors agree that they are a solitary species (Cabrera and Yepes, 1940; Kaufmann and Kaufmann, 1965; Villa, 1948).

Margay

According to Grzimek (1975), "Almost nothing is known about the margay's life in the wild." This project was the first attempt to study margay ecology. Only two captures in twenty-one months suggest that the density in the selected study area was very low. This is supported by a lack of margay sign throughout the study. In areas of primary forest in Belize, margay are reported by local inhabitants more frequently, but the close resemblance to ocelot makes identifications of nocturnal cats equivocal. Throughout Mexico, Leopold (1959) found the margay to be rare.

Margays are nocturnal with the highest levels of activity between 0100 hr and 0500 hr. This was observed in captive animals as well (Peterson, 1974). The home range area (10.95 km^2) was larger than expected possibly because the male was a subadult, and the data may reflect dispersal movements. The length of daily movements corresponds well with other animals studied at the same site. Both margays were caught in forest areas, and the monitored male showed a preference for forests which is supported by other observations (Mondolfi, in litt.).

Adaptations of the hind limb, superlative balance, great leaping ability, and proportionately longer claws than other species make the margay well-suited for arboreality (Leyhausen, 1963). When leaping between branches, margay are completely outstretched, can catch themselves with a single paw, and have been known to leap 2.44 m vertically (Peterson, 1974: Leyhausen, 1963). Peterson reported that margay have the ability to "ricochet" off several objects such as branches without losing balance or speed.

Such agility allows margay to surprise and capture arboreal prey that constituted a majority of the diet in Venezuela (Mondolfi, in litt.). In Belize, *O. phyllotis* was the most common element of the diet found in scats. Several other arboreal species were also found. Margay took more birds and fewer terrestrial mammals than the other species studied. They also showed the second highest consumpton of fruit. Because no other males or any females were collared, it is impossible to comment on intraspecific interactions.

Jaguarundi

Previously unstudied, the jaguarundi has proved difficult to study despite of being widely distributed and the most commonly seen felid in Central and South America (Mondolfi, in litt.). Much of the prior information comes from Rengger's (1830) observations. Jaguarundis are strongly diurnal which is supported by several studies, however, Leopold (1959) reported anecdotal information indicating jaguarundis were nocturnal in parts of Mexico.

Total daily movements (6.5 km) were similar to other species studied in the Cockscomb Basin. However, home range areas were radically different. After an initial long move, the female, an adult at capture, has shown little movement for the next 12 months. Even so, her home range was not substantially different from ocelot, tayra, or margay home ranges. Home ranges for the males were over four times larger than the female's. Males showed little apparent cyclicity to movements within their ranges. These areas are several times larger than those reported for sympatric jaguars weighing nearly ten times more (Rabinowitz and Nottingham, 1986).

When near my camp, jaguarundis showed a preference for old field habitats, but much of their home ranges included older successional and primary forests. Guggisberg (1975) reported jaguarundi to be lowland marsh habitat species preferring the vicinity of streams. In Belize, jaguarundis were frequently found close to streams, although one male did wander up into the mountains, out of the basin, and away from the network of streams.

Their diet consisted of rodents, although insects were found most frequently in the scats, but represent few total calories. *S. hispidus* was the most common vertebrate species. Leopold (1959) believed jaguarundis specialized on gallinaceous birds; the diet in Venezuela was very similar to that found in Belize, although lizards were included in that diet (Mondolfi, in litt.).

The available data provide few explanations to the large home range sizes for male jaguarundis. Because similarly sized and even much larger species have much smaller home ranges in the same area, and the diet appears unspecialized, food can probably be eliminated. One explanation for the long distance movements may be related to males monitoring the reproductive state of females that also move widely. Even with such large home ranges, the two males' ranges overlapped for less than 25%. At one time both males were located in the area of overlap close to one another and very close to a resident female. When located next, both had moved well away from each other.

A second, less likely and equally unsupported explanation is that jaguarundis move widely to avoid competition from other carnivores. The carnivore community in the Cockscomb Basin is rich and varied (Appendix 1). Dietary data reveal that jaguars take smaller prey than predicted by their body size (Rabinowitz and Nottingham, 1986). This diet may increase the competitive pressure on smaller species (i.e. puma, ocelot, margay, tayra, jaguarundi, coati, cacomistle, and gray fox). As the smallest felid species, jaguarundi may have to move widely to catch sufficient prey because of the competitive pressures from three larger felids. However, diet similarity indices do not support this idea. Diet overlaps were not extensive, and the frequencies of occurrence in the scats of identical prey species were different for potential competitors. Home range and interactive data gathered elsewhere will help clarify this seemingly unusual situation. .

Prompted by McNab (1963), several authors have considered the determinants of home range size for a variety of animals (Gittleman and Harvey, 1982; Harestad and Bunnell, 1979: Mace and Harvey, 1983). Depending on the analysis, opinions appear to be divided as to whether body weight or metabolic rate is the most critical factor. Data collected in this study do not appear to align well with either point of view. Using either body weight or metabolic rate criteria, the home range size of male jaguarundis relative to similar-sized predators or even the much larger jaguar (Rabinowitz and Nottingham, 1986) is much too large. Even diet does not appear a likely candidate to explain such large home ranges.

The co-existence of taxonomically or ecologically closely-related species has also been the topic of much debate. Kiltie (1984), examining neotropical felids, found body size ratios separating sympatric species. He found that species with approximately equal body weights had approximately equal jaw gapes which correlates well with prey size. Size ratio differences possibly reduce competition for food. Rosenzweig (1966) found that among North American carnivores, co-existence is related to body size which is also related to prey size taken. Among raptors, closely related species differed greatly in size thereby avoiding competition (Schoener, 1984).

In Belize, the margay, jaguarundi, and tayra all had about the same body weights, which means they should take similarly-sized prey. Fecal analyses revealed that there was diet overlap among the four species, but similarity indices revealed no significant correlations in consumption of prey species. Ocelots took larger species than the others, while tayras ate more fruit, margay diets included more arboreal species, and jaguarundi had a relatively broad diet. In a study of four sympatric African carnivores, Bothma (1984) found that 2 species were highly specialized while the others differed in the amounts of each prey species utilized.

Overlapping diets could possibly lead to some level of exploitative competition if all carnivores were hunting at the same time. Jaguarundis and tayras were diurnal and ocelots and margays nocturnal. All species were equally active shortly after dawn and before sunset. In a study of a hummingbird guild, Feinsinger (1976) found that similar species with similar foraging patterns move apart from areas of ecological overlap with time.

Three studies of dimorphic, sympatric felids found habitat partitioning occurred irrespective of activity periods or diet. In South Africa, the nocturnal leopard (*Panthera pardus*) and diurnal caracal (*Lynx caracal*) used habitat patches differently (Norton and Lawson, 1984), as did jaguar and puma in Brazil (Schaller and Crawshaw, 1980). Seidensticker (1976) found that synchronously active tigers and leopards used different patches of the same habitat. It is possible that the four species studied here differentially used the successional patches in a more fine- grained manner than could be discriminated in this project.

These data, when combined with those about jaguar ecology from the same location (Rabinowitz and Nottingham, 1986), provide insight into the community of medium- to large carnivores. Both studies failed to gather any data about pumas, so their place in the felid community remains a mystery.

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Table 1. Body parameters and capture data of four sympatric species in Belize.

Species Capture Date	Sex/Age*	Weight (kg)	Body Length (cm)	Tail Length (cm)	Ear Height (cm)	Pes Length (cm)
Jaguarundi						
Aug 84#	M-A	5.50	63	43.0	3.0	13.5
Feb 85#	F-A	3.75	53	40.0	3.0	12.5
Jun 85#	M-A	6.25	68	51.5	3.5	14.0
Jun 85	F-A	5.00	63	47.5	2.3	12.4
Margay						
Dec 84#	M-A	4.00	49	40.0	5.0	11.0
Jun 85	M-A	4.00	54	37.0	4.0	12.2
Ocelot						
Nov 84#	F-A	12.5	72	40.0	5.6	16.0
Mar 85#	M-SA	7.75	68	34.0	5.0	15.0
Jun 85	F-A	8.85	74	31.6	5.3	16.0
Tayra						
Oct 84#	F-A	4.90	61	41.0	1.4	10.0
Dec 84#	M-A	4.80	60	38.0	2.5	10.0
Jan 86#	M-A	5.50	56	40.0	2.4	12.0

*M = male; F = female; A = adult; SA = subadult
#Radio-collared

8.5-13.8.16

Table 2. Home range, monitoring period, and number of locations for nine radio-collared carnivores in the Cockscomb Basin, Belize (August 1984-March 1986).

Species	Individual Age/Sex*	Months Monitored	Number Locations	Home Range (km^2)
Jaguarundi	J1 A/M	14	106	99.89
	J2 A/F	13	62	20.11
	J3 A/M	10	84	88.32
Margay	M A/M	6	114	10.95
Ocelot	O1 A/F	16	285	14.68
	O2 SA/M	12	107	31.21
Tayra	T1 A/F	13	165	16.03
	T2 A/M	10	95	24.44
	T3 A/M	3	20	2.62

*A = adult; SA = subadult; M = male; F = female

Table 3. Frequency of occurrence of items in the scats of four sympatric carnivore species.

Dict Item	Jaguarundi (n=46)	Occlot (n=49)	Margay (n=27)	Tayra (n=31)
Arthropods	.717	.102	.333	.580
Small Birds	.217	.183	.292	.194
Marsupials				
Didelphis marsupialis	.130	.387	----	.096
Philander opossum	----	.306	----	----
Marmosa spp.	----	.122	.185	----
Edentates				
Tamandua mexicanus	----	.020	----	----
Dasypus novemcinctus	----	.204	----	----
Rodents				
Sciurus deppei	----	----	.222	----
Oryzomys palustris	.152	----	----	.225
Ototylomys phyllotis	.152	----	.481	----
Reithrodontomys gracilis	.086	----	.185	----
Sigmodon hispidus	.477	----	----	.323
Rattus rattus	.086	.102	----	.290
Agouti paca	----	.122	----	----
Artiodactyls				
Mazama americana	----	.061	----	----
Leaves	.065	.082	----	.065
Fruit	.108	----	.144	.677

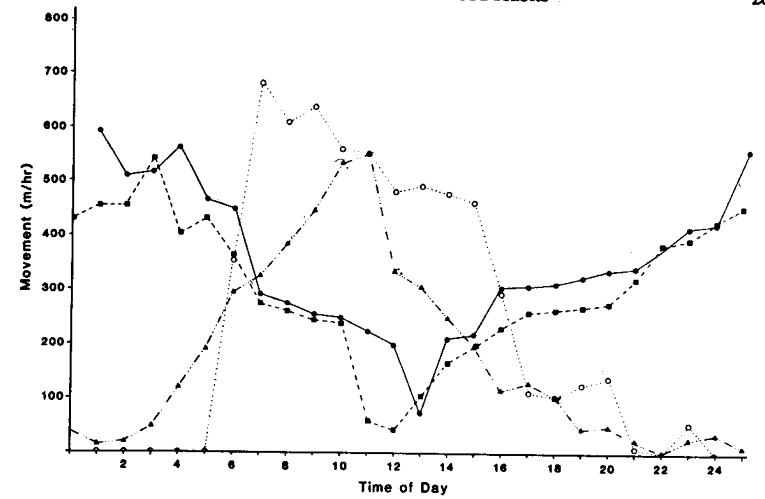

Figure 1. Activity Rates. Solid circle with solid line = Ocelot; solid square with dashed line = Margay; open circle with dotted line = Tayra; solid triangle with dotted line = Jaguarundi.

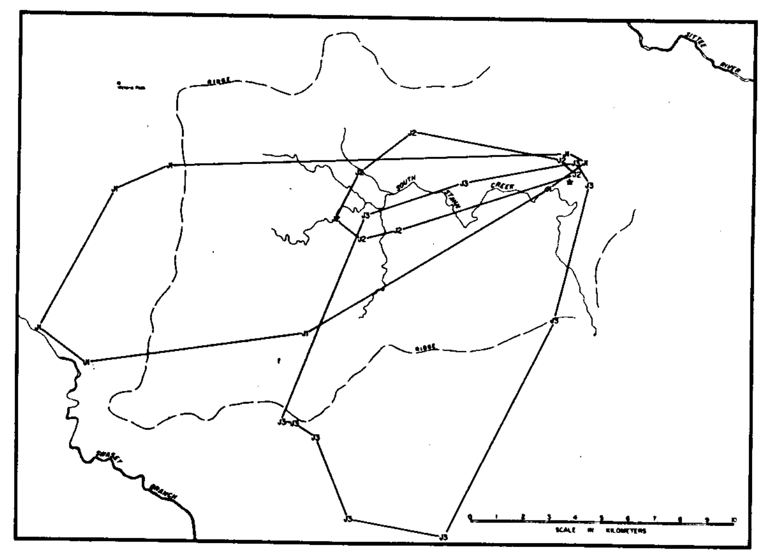

Figure 2. Home ranges of Jaguarundi.

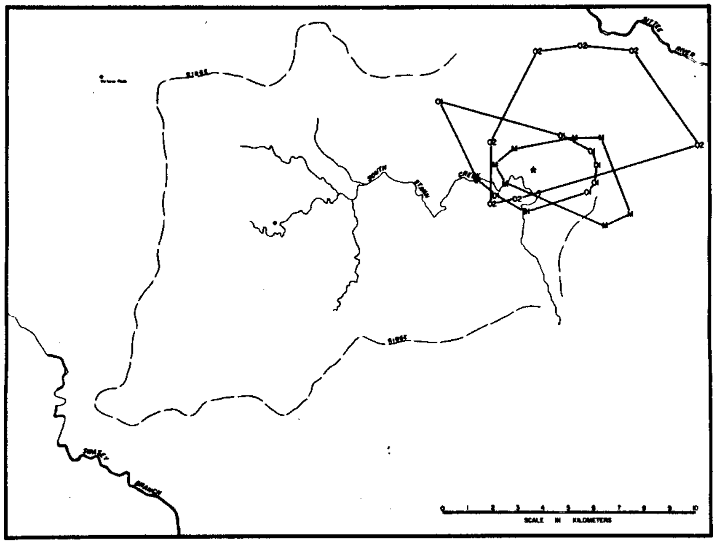
Figure 3. Home ranges of Ocelot and Margay.

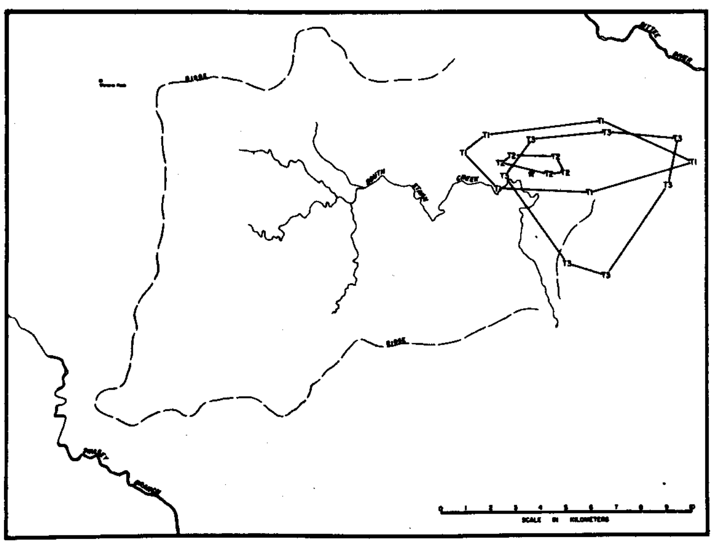
Figure 4. Home range of Tayra.

Appendix 1. Mammals (excluding Chiroptera) identified from Cockscomb Basin, Belize (June 1984-March 1986)

- Marsupialia
  - Didelphidae
    - *Chironectes minimus*
    - *Didelphis marsupialis*
    - *Philander opossum*
    - *Marmosa mexicana*
    - *Marmosa alstoni*
- Edentata
  - Myrmecophagidae
    - *Tamandua mexicana*
  - Dasypodidae
    - *Dasypus novemcinctus*
- Rodentia
  - Sciuridae
    - *Sciurus deppei*
  - Geomyidae
    - *Orthogeomys hispidus*
  - Cricetidae
    - *Oryzomys melanotis*
    - *Ototylomys phyllotis*
    - *Nyctomys sumichrasti*
    - *Peromyscus leucopus*
    - *Reithrodontomys gracilis*
    - *Sigmodon hispidus*
  - Muridae
    - *Rattus rattus*
  - Erethizontidae
    - *Coendou mexicanus*
  - Dasyproctidae
    - *Agouti paca*
    - *Dasyprocta punctata*
- Carnivora
  - Canidae
    - *Urocyon cinereoargentateus*
  - Procyonidae
    - *Nasua narica*
    - *Potos flavus*
    - *Bassariscus sumichrasti*
  - Mustelidae
    - *Mustela frenata*
    - *Eira barbara*
    - *Spilogale putorius*
    - *Conepatus semistriatus*
    - *Lutra longicaudis*
  - Felidae
    - *Panthera onca*
    - *Puma concolor*
    - *Leopardus pardalis*
    - *L. wiedii*
    - *Herpailurus yagouaroundi*
- Perissodactyla
  - Tapiridae
    - *Tapirus bairdii*
- Artiodactyla
  - Tayassuidae
    - *Tayassu tajacu*
    - *T. pecari*
  - Cervidae
    - *Mazama americana*

Appendix 2. Rodent trapping results in four habitat patches in the Cockscomb Basin, Belize, using a line transect (18 x 18 traps) summed for one week.

Species	Old Field	Dry, Open Woodland	Moist, closed Woodland	Subclimax Forest
Oryzomys palustris	24	1	---	---
Nyctomys sumichrasti	1	---	---	---
Reithrodontomys gracilis	14	---	---	---
Sigmodon hispidus	95	8	---	---
Peromyscus leucopus	47	20	6	5
Rattus rattus	---	4	13	---