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Ecology and behaviour of the Jaguar (*Panthera onca*) in Belize, Central America

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(With 3 figures in the text)

Five adult male Jaguars and a translocated subadult female Jaguar were captured and followed by radio-telemetry in Cockscomb Basin, Belize. One adult male Jaguar, two resident female Jaguars, and a Puma were followed only by their tracks. Radio-collared males maintained overlapping ranges of 28–40 km², while resident females moved in minimum areas of 10 km² within the ranges of individual males. Despite range overlap, evidence of aggression or sign of more than one large cat in the same area simultaneously was uncommon. Such avoidance behaviour suggested some means of communication. Visual marking in the form of faeces and scrapes were found uncovered along roads and trails in areas of overlap between the cats; such marking could have helped in boundary delineation as well as spatial and temporal positioning. Males often remained in small areas of 2·5 km² for up to two weeks, a behaviour made possible by abundant prey. This behaviour may have facilitated avoidance with other Jaguars. Faecal analysis indicated opportunistic feeding on 17 prey species. Armadillo, Paca and brocket deer accounted for 94% of the available terrestrial prey and comprised 70% of the identified prey in the faeces. All Jaguars were primarily nocturnal, though activity varied between animals. The translocated female showed changes in activity patterns when feeding upon cattle. At least one Puma travelled within the ranges of several male Jaguars and appeared to be feeding on smaller prey items. The behavioural and ecological plasticity exhibited by the Jaguars in this study is beneficial for an animal whose habitat is rapidly diminishing.

Contents

Introduction

The Jaguar (*Panthera onca*) is the largest land predator throughout Central and South America, yet remains one of the least studied large cats in the world. Except for recent research in

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the Pantanal region of Mato Grosso, Brazil (Quigley & Crawshaw, unpubl. data; Schaller & Vasconcelos, 1978; Schaller & Crawshaw, 1980), knowledge of Jaguar behaviour was primarily anecdotal (see Guggisberg, 1975). This study, conducted between March 1983 and December 1984 in Belize, presents the first detailed ecological data on Jaguars in Central America.

Study area and methods

The study was conducted in the Cockscomb Basin of southern Belize. This area of 425 km^2 consists of subtropical wet forest, 0–600 m in elevation, with an average rainfall of 250 cm/yr (Walker, 1973). Numerous streams traverse the basin, merging into 3 major waterways. The climate is characterized by a distinct dry season (March through May) and wet season (June through February). Over the last 50 years, selective timbering and hurricanes have created dense secondary forest in many parts of the basin, with an upper canopy of 14–30 m.

Outside the study area, land use includes cattle and swine ranching, citrus crops and Mayan Indian settlements practicing slash and burn agriculture. The field station, Guam Bank, was located 10 km into the basin at an abandoned logging camp and Mayan settlement. Thirty-four km of logging roads and trails in the basin were utilized for trapping and monitoring Jaguars.

Jaguars were captured using dogs to tree the cats or with traps baited with live pigs. Captured animals were immobilized with Ketamine hydrochloride (Parke, Davis & Co., Detroit, MI) administered at 22 mg/kg body weight and fitted with radio-collars containing activity monitors (Telonics, Mesa, AZ). Attempts were made at least 3 times weekly to locate collared Jaguars using directional antennas on the ground, from tall trees, or from aircraft. Locations were used to ascertain home ranges using a modified minimum area method (Mohr, 1947). Home range boundaries were drawn around open fields and pastures when the Jaguar was known to avoid such areas.

Activity data were divided into categories based upon pulse rate and changes in signal strength over 2-min periods. Categories included: active pulse rate with frequent changes in signal strength (travelling), active pulse rate with no changes in signal strength (locally active), and inactive pulse rate (resting). When possible, activity was monitored at 15-min intervals for 24 h. Differences in overall activities between cats were examined by pooling locally active and travelling categories. Nocturnal activity was defined as sunset to sunrise (18.30–06.30 h).

Portions of the road system were travelled daily. Tracks observed on roads and trails were used to document movements of uncollared Jaguars and a Puma (*Felis concolor*). Though differences between the tracks of adult male Jaguars were not always apparent, track measurements combined with known locations of collared males helped identify uncollared adult male Jaguars. Male and female Jaguars or Jaguars and Pumas could be differentiated by size and shape of the track (Schaller & Crawshaw, 1980).

Faeces collected along roads and trails were used to determine food habits using a reference collection of hair and bone from known prey species. Faecal content was analysed in terms of percent occurrence (the number of times a particular species was found as a percentage of all species identified). Random transects were cut in the forest to assess prey availability. The dense understorey did not allow for a visual census so an index of relative abundance was developed by recording any sign of prey species within a metre of either side of the transects. Species were primarily identified by tracks. Armadillos (*Dasypus novemcinctus*) could also be identified by diggings and dens, while Agoutis (*Dasyprocta punctata*) and Pacas (*Agouti paca*) could be identified by chew marks on nuts from Cohune palms (*Orbignya cohune*). Numbers of individuals of a species were based upon measurements, freshness of sign, direction of travel, and proximity of sign to each other.

Measurements of skulls and hides from Jaguars throughout Belize were used to assess physical parameters. Age categories were determined from tooth eruption, coloration, attrition (Almeida, 1976) and, when possible, from cranial suture closure, assuming the same general anatomical progression for Jaguars

as for the African lion (*Panthera leo*) (Smuts, Anderson & Austin, 1978). Jaguars were classified as subadults (2–3 years), mature adults (4–10 years), or old adults (>11 years).

Results

Physical parameters

Six mature adult male Jaguars averaged 57·2 kg in weight (S.D. = 6·3 kg), 190·5 cm (S.D. = 14·0 cm) in total body length and 55·7 cm (S.D. = 4·8 cm) in tail length. Using hide measurements, no significant differences (Mann–Whitney *U* Tests) in total body ($P = 0{\cdot}14$) or tail lengths ($P = 0{\cdot}06$) were found between males ($n = 7$) and females ($n = 5$). Male Jaguars had significantly larger skulls than females (*M–W* Tests) with respect to zygomatic breadths ($P = 0{\cdot}02$) and mandibular lengths ($P = 0{\cdot}02$) but showed no significant differences in greatest lengths ($P = 0{\cdot}20$) and basal lengths ($P = 0{\cdot}06$) (Table I). Compared to nine adult Jaguars in the Pantanal of Brazil (Schaller, unpubl. data; Schaller & Vasconcelos, 1978), Belizean Jaguars were significantly smaller (*M–W* Tests) in total body length ($P = 0{\cdot}01$), weight ($P = 0{\cdot}0008$) and skull measurement with respect to basal length and zygomatic breadth ($P = 0{\cdot}0001$).

TABLE I

Skull measurements (mm) from Jaguars of known sex in Belize, Central America

Sex	Greatest length	Basal length	Zygomatic breadth	Mandible length
Males				
Mean	232	198	163	156
S.D.	26	12	8	9
n	16	14	16	10
Females				
Mean	216	182	150	143
S.D.	13	17	11	9
n	3	5	5	5

Home range and movements

Four mature adult male Jaguars, radio-tracked continuously for 3–14 months ($n = 236$ locations), averaged home ranges of 33·4 km² (28–40 km², S.D. = 5·5 km²). Two uncollared females moved within minimum areas of 10 km² and 11 km². A cattle-killing subadult female, collared and transplanted into Cockscomb, left the basin and settled near a cattle pasture. She travelled within a 10 km² area ($n = 26$ locations) until killed (Rabinowitz, 1986).

Consecutive daily locations of collared males indicated they often remained within small areas ($\bar{x} = 2{\cdot}5$ km², S.D. = 0·6 km², $n = 16$) for an average of seven days (range 4–14 days) before shifting, in a single night, to other parts of their range. On two occasions, two different male Jaguars were located hourly between 20.00 and 05.00 h. They travelled within areas of 3 km² and 2·5 km², averaging linear movements of 0·7 km/h and 0·8 km/h, respectively.

Land tenure

During the first year of the study, the monitored roads were used by at least five mature adult male Jaguars, two females, and a Puma (Fig. 1). Home ranges of the female Jaguars did not overlap and their movements were restricted within the ranges of individual adult males. Home ranges of males overlapped with adjacent adult males. The most extensive overlap observed was with Jaguar #525, who travelled at least 50% of the monitored roads. His range was overlapped 80% by at least four male Jaguars, a female Jaguar, and a Puma. The extent of range overlap among the other collared Jaguars could not be accurately determined due to lack of data of Jaguars in the surrounding areas.

Two mature adult males, #780 and #525, died during the first year. Within a month of both deaths, an adjacent male, #333, started shifting into the former range of #780, while #545 moved west into the former range of #525. Both Jaguars maintained portions of their former range (Fig. 2). The vacancy resulting from the shift of #545 was filled within six weeks by a mature adult male Jaguar moving in from outside the basin. This Jaguar, #380, was captured, collared, and followed for five months until killed by a hunter.

Despite home range overlap, it appeared unlikely that male Jaguars often had aggressive encounters. Of five male Jaguars captured 10 times over 20 months, only #525 showed a scar in the facial region that might have been caused by physical aggression.

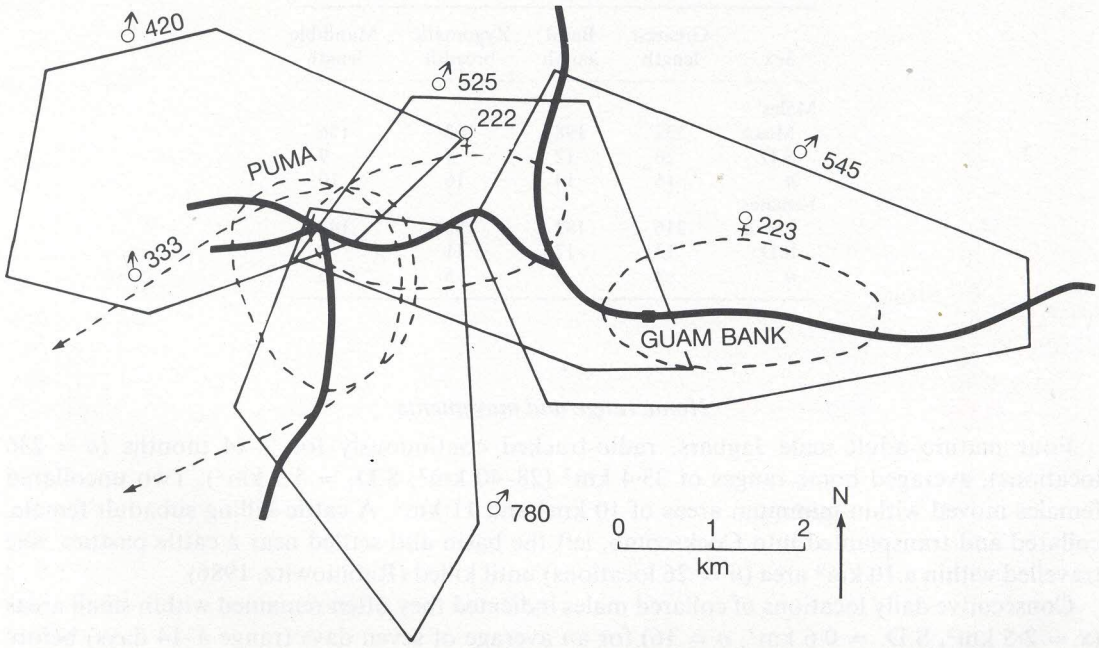

FIG. 1. Home range overlap among five adult male Jaguars, two female Jaguars, and a Puma in the Cockscomb Basin, Belize, March 1983–December 1983. —— Ranges determined by radio-telemetry; - - - ranges determined by tracking and sighting; ▬▬ timber roads.

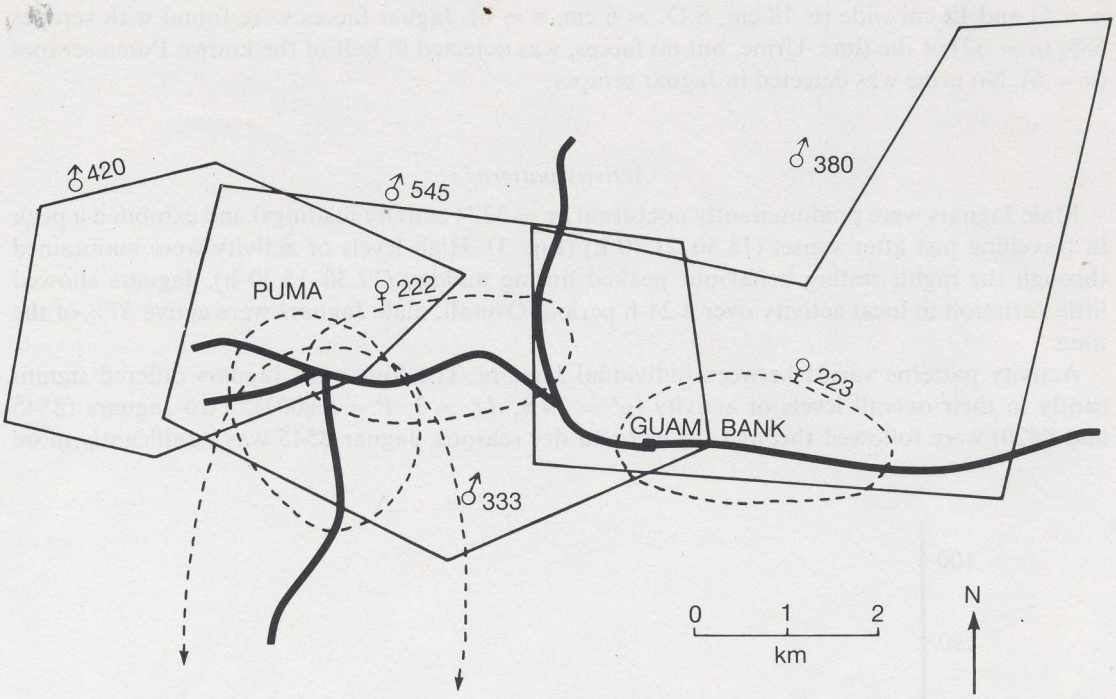

FIG. 2. Home range overlap among four adult male Jaguars, two female Jaguars, and a Puma in the Cockscomb Basin, Belize, January 1984–December 1984. Symbols as in Fig. 1.

Communication

Neighbouring radio-collared male Jaguars were rarely located near one another, and fresh sign from more than one large cat was rarely observed on the same portion of road at the same time. Faeces were deposited in open areas along roads and trails. Of 60 faeces recorded during 1983, 80% were found on 8 km of road in the area of overlap between Jaguars #525 and #545 and 20% on 5 km of road in the area of overlap between Jaguars #525, #780, #420, #333 and the Puma (Fig. 1). After the deaths and shifts in movements of several Jaguars, faecal deposition continued to occur most frequently in overlap areas. Of 149 faeces recorded along the road during 1984, 50% were between Jaguars #545 and #380, 46% between Jaguars #333, #545 and #420 and the Puma, and 6% in the range of female Jaguar #222 and male #545 (Fig. 2). Seventy-three per cent of all faeces were observed during the wet season.

Scrapes (n = 40) observed along roads were frequently recorded in areas of overlap, with 50% found between Jaguars #380 and #545 and 38% between Jaguars #420, #545, #333 and the Puma. Seventy per cent of the scrapes were documented on only seven days. During four of these days, fresh tracks and telemetry data indicated that two adult male Jaguars had travelled the same portion of road; on two other days, fresh tracks indicated a male Jaguar and a Puma had travelled the same segment of road. Fifty-five per cent of the scrapes were recorded during the wet season.

Jaguar scrapes averaged 37 cm long (18–58 cm, S.D. = 11 cm, n = 26) and 10 cm wide (7–19 cm, S.D. = 3 cm, n = 21), while Puma scrapes averaged 20 cm long (12–32 cm, S.D. = 7 cm,

$n = 6$) and 12 cm wide (6–18 cm, S.D. = 6 cm, $n = 6$). Jaguar faeces were found with scrapes 68% ($n = 37$) of the time. Urine, but no faeces, was detected in half of the known Puma scrapes ($n = 6$). No urine was detected in Jaguar scrapes.

Activity patterns

Male Jaguars were predominantly nocturnal ($n = 3274$ activity readings) and exhibited a peak in travelling just after sunset (18.30–21.30 h) (Fig. 3). High levels of activity were maintained through the night; resting behaviour peaked during midday (12.30–15.30 h). Jaguars showed little variation in local activity over a 24-h period. Overall, male Jaguars were active 57% of the time.

Activity patterns varied between individual Jaguars. The four male Jaguars differed significantly in their overall levels of activity ($\chi^2 = 34{\cdot}8$, $d.f. = 3$, $P = 0{\cdot}0001$). Two Jaguars (#545 and #420) were followed through the wet and dry seasons. Jaguar #545 was significantly more

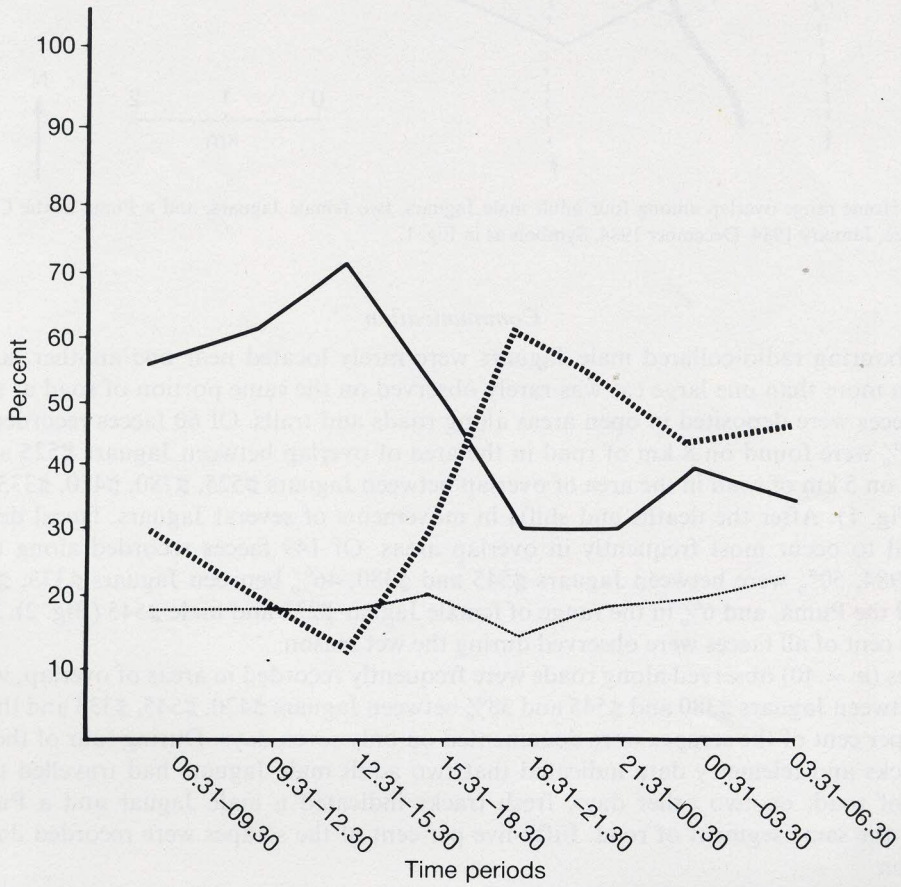

FIG. 3. Activity patterns of four collared male Jaguars ($n = 3274$ activity readings) in the Cockscomb Basin, Belize, 1983–1984. ——— Resting; ▪▪▪▪ travelling; ····· locally active.

active during the dry season ($\chi^2 = 10{\cdot}4$, *d.f.* = 1, $P = 0{\cdot}013$) than wet season; Jaguar ♯420 showed no seasonal differences ($\chi^2 = 1{\cdot}39$, *d.f.* = 1, $P = 0{\cdot}24$).

After leaving the basin, the translocated female Jaguar travelled an area that included both a cattle pasture and adjacent forest ($n = 224$ activity readings). When located in the forest, her activity was similar to that of the male Jaguars, travelling most between 18.30–00.30 h and resting between 09.30–12.30 h. When over a cattle kill, her behaviour was more diurnal, travelling most between 09.30–12.30 h, and resting between 15.30–21.30 h. Overall, she was active 60% of the time.

Food habits and feeding behaviour

Fresh jaguar faeces consisted of four to six pieces, each 8·0 cm long (4·0–15 cm, S.D. = 3·0 cm, $n = 40$) and 3·2 cm in diameter (2·5–3·8 cm, S.D. = 0·4 cm, $n = 62$). Remains in the faeces showed that small prey items (or young of larger prey) were often completely consumed. Exceptions included species such as armadillo and turtles, where only the carapace was left intact. Large body fragments in Jaguar faeces included peccary (*Tayassua* spp.) and brocket deer (*Mazama americana*) hooves, 2·4–3·5 cm long, armadillo and anteater (*Tamandua mexicana*) claws, 1·4–1·8 cm long, and a bone piece measuring 4·4 cm long by 1·2 cm wide. Sharp bone pieces in the faeces were matted with large clumps of hair.

From 228 faecal samples, 185 prey items of 17 species were identified (Table II). Fifteen

TABLE II

Percent occurrence of prey species in Jaguar faeces (n = 185 identified prey items) and along forest transects (n = 210 individuals) in Cockscomb Basin, Belize, 1983–1984*

	Per cent occurrence	
Prey species	Faeces	Transects
Armadillo (*Dasypus novemcinctus*)	54·0	53·0
Paca (*Agouti paca*)	9·3	30·0
Collared anteater (*Tamandua mexicana*)	9·3	0·5
Red brocket deer (*Mazama americana*)	6·5	11·0
Peccary (*Tayassua* spp.)	5·4	0·5
Agouti (*Dasyprocta punctata*)	4·3	4·0
Opossum (*Didelphis marsupialis*)	3·2	—
Iguana (*Iguana iguana*)	1·5	—
Coati (*Nasua nasua*)	1·0	0·5
River turtle (unknown species)	1·0	—
Small rodent (unknown species)	1·0	—
Four-eyed opossum (*Philander opossum*)	1·0	—
Skunk (*Spilogale putorius* or *Conepatus semistriatus*)	0·5	—
Kinkajou (*Potos flavus*)	0·5	—
Domestic rooster (from trap)	0·5	—
Snake (unknown species)	0·5	—
Bird (unknown species)	0·5	—
Tapir (*Tapirus bairdi*)	—	0·5

* Number of times a species was identified as a percentage of all prey items identified

percent of the faeces had no identifiable remains, while 14% contained more than one prey item. Armadillo comprised 54% of the identified remains, while Paca and anteater comprised 9·3% each. There were no significant seasonal differences ($\chi^2 = 7{\cdot}2$, $d.f. = 5$, $P = 0{\cdot}18$) between the frequencies of the six most common prey found in the faeces. Twenty-seven per cent of the faeces contained grass. Only three confirmed Puma faeces were found; these contained the remains of at least one small rodent and one Four-eyed opossum (*Philander opossum*).

In 27 km of transects, 210 individuals of eight prey species were noted. The percentage occurrence of different species generally followed the same pattern as their occurrence in faecal remains (Table II). Armadillo, Paca, and brocket deer accounted for 94% of the identified terrestrial prey, while comprising 70% of the identified prey in the faeces. Small prey, non-terrestrial, and semi-arboreal species were under-represented or not accounted for. Peccary trails were noted as a single sign because it was difficult to estimate numbers reliably, and Jaguars normally cannot kill more than one animal before the group scatters. This treatment may have underestimated the relative abundance of this species.

Discussion

Home ranges and land tenure among Jaguars in Cockscomb varied considerably from that of other large solitary cats. Jaguars in the Pantanal of Brazil had home ranges twice as large as those in this study (Schaller & Crawshaw, 1980). Sunquist (1981) showed that male Tigers in Nepal occupied minimum ranges of 60–72 km^2, while females occupied ranges of 16–20 km^2. Male Pumas in Idaho ranged within areas of at least 453 km^2, and females within 170–375 km^2 (Seidensticker, Hornocker, Wiles & Messick, 1973). Leopards moved within areas of only 10–19 km^2 in Rhodesia (Smith, 1978) or 40–60 km^2 in the Serengeti (Schaller, 1972). In all of these studies, resident adult males maintained exclusive ranges showing little overlap with adjacent resident males. This is the most commonly observed pattern among solitary felids (Sunquist, 1981).

Adult male Jaguars in Cockscomb travelled over areas of 28–40 km^2, while females moved over minimum areas of 10 km^2, within the ranges of males. Adjacent males showed overlapping ranges. Part of the range overlap may have been a result of the road system. Roads and trails are limited resources and have been shown to be used extensively by large cats for travel and hunting (Schaller, 1967; Sunquist, 1981). Two Jaguar deaths and subsequent shifts in Jaguar movements during the study left no area vacant for more than six weeks. This indicated a dynamic equilibrium among a relatively dense population whereby home ranges were actively maintained among resident adult males.

If density and distribution of prey are favourable, it is reasonable that large solitary felids can share limited areas. Sharing of territorial space when resources are abundant can be an economically efficient strategy (Davies & Houston, 1984) if encounters leading to physical aggression are avoided. Avoidance behaviour is an active endeavour among other adult male felids such as Pumas (Seidensticker *et al.*, 1973) and Tigers (Schaller, 1967; Sunquist, 1981). Although overlapping ranges increases the probability of such encounters, it was rare for adjacent adult males to be found in close proximity to each other. Evidence of physical aggression was virtually nonexistent.

Avoidance usually necessitates some system of communication. In areas where small and isolated populations exist, Jaguars may simply avoid each other (Schaller & Crawshaw, 1980).

In Cockscomb, however, visual and olfactory cues in the form of faeces, urine and scraping were detected in open locations along roads. Similar marking has been documented with Tigers (Schaller, 1967; McDougal, 1977; Sunquist, 1981), Pumas (Hornocker, 1969; Seidensticker *et al.*, 1973), and Leopards (Eisenberg & Lockhart, 1972; Hamilton, 1976; Smith, 1978).

Faeces were often found where range overlap occurred between adjacent large cats. Such marking may have served to delineate boundaries between cats (Johnson, 1973), or provide spatial and temporal orientation between sexes and species. Scrapes were most frequently documented when more than one large cat, either adult male Jaguars or a Jaguar and a Puma, were in the same area at the same time. Such marking appeared to be event-specific. The suggestion that scrapes are an alternate form of marking during the wet season when faeces are quickly washed away (Schaller, 1967; Sunquist, 1981) is not supported in this study. Forty-five per cent of the observed scrapes occurred during the three-month dry season.

Male Jaguars often occupied small areas of 2·5 km^2 for approximately a week before shifting to other portions of their range. Almeida (1976) observed similar behaviour with Jaguars in Brazil. Such behaviour is made possible with abundant food resources, but can be limited by changes in prey availability over time (Charnov, Orions & Hyatt, 1976). Limited movements within these small transient feeding areas may facilitate avoidance and allow for a relatively dense Jaguar population.

One way to enhance prey availability and optimize foraging within an area is to be opportunistic. Although known to feed on large prey such as Capybara (*Hydrochoerus hydrochaeris*), tapir (*Tapirus terrestris*) and peccary (Schaller & Vasconcelos, 1978), Jaguars will eat what is available. In Cockscomb, Jaguars consumed at least 17 different species. However, 54% of the identified prey in the faeces consisted of armadillo.

Armadillo, Paca, and brocket deer accounted for 94% of the available terrestrial prey species, while comprising 70% of the identified prey remains in the faeces. Prey species of the Jaguar, such as armadillo (Layne & Glover, 1977), Agouti (Smythe, 1978), Paca (Smythe, 1970), and brocket deer (Eisenberg, O'Connell & August, 1979) can reach high densities and exhibit limited movements. Density estimates of these and other species indicated they were abundant and uniformly distributed within our study area (unpubl. data). The armadillo is a particularly vulnerable prey species due to its limited mobility, lack of defences, and muffled grunting that accompanies its nocturnal foraging (Kalmbach, 1943). Small prey were often completely consumed. This behaviour has been observed with other large felids such as Tigers (Schaller, 1967) and Pumas (Hornocker, 1970). Jaguars in Cockscomb are primarily nocturnal, as are most of their major prey species, such as armadillo (Kalmbach, 1943; Bider, 1962) and Paca (Smythe, 1970). However, Jaguars may be found active at any time of the day. This accounts for the presence of diurnal species in the faeces such as Agouti and brocket deer. Differences in activity patterns between male Jaguars may be a result of changes in prey availability within individual ranges. The diurnal activity of the collared female Jaguar when preying upon cattle indicated behavioural flexibility based on the prey. A similar activity pattern was observed with a female Jaguar feeding on cattle in the Pantanal (Schaller & Crawshaw, 1980).

Jaguars and Pumas exist sympatrically throughout Belize. Data from this study and sightings by locals indicate that Pumas are rarely observed where Jaguars are abundant; avoidance behaviour between these species was observed in the Pantanal (Schaller & Crawshaw, 1980). Pumas are capable of killing large prey items (Hornocker, 1970; Ackerman, Lindzey & Hemker, 1984) and are known to prey upon species similar to those preyed upon by Jaguars (Schaller & Crawshaw, 1980). Yet three Puma faeces contained small rodent and Four-eyed opossum

remains. These prey species comprised only 2% of species identified in Jaguar faeces. More data are needed, but it is possible that partitioning of prey size and type is a mechanism reducing competition in areas of overlap between these two large cats, a phenomenon observed by Seidensticker (1976) where Tigers and Leopards were sympatric.

The behavioural and ecological plasticity exhibited by the movements, activity patterns and feeding patterns observed in this study, and between this study and others, displays the adaptive capability of Jaguars. Such behavioural flexibility is crucial for an animal whose habitat is becoming increasingly threatened throughout its range.

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