

## SPATIAL AND TEMPORAL INTERACTIONS OF SYMPATRIC JAGUARS (*PANTHERA ONCA*) AND PUMAS (*PUMA CONCOLOR*) IN A NEOTROPICAL FOREST

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We used extensive camera-trap surveys to study interindividual interactions among individually recognizable jaguars (*Panthera onca*) and plain-colored pumas (*Puma concolor*). Timed location data from a network of 119 trap stations in the Cockscomb Basin of Belize provide the 1st evidence of interspecific avoidance calibrated against intraspecific interactions among jaguars. Camera trapping has advantages over radiotelemetry in its potential to provide data on the complete array of individuals within the study area. The 23 individually identified male jaguars showed high levels of overlap in ranges, with up to 5 different males captured at the same location in the same month. Low levels of avoidance between individuals and a high flux of individuals contributed to low consistency in home-range ownership over the long term (3 months to 2 years). Jaguars and pumas had similar nocturnal activity schedules. Both species used similar habitats within the Cockscomb Basin, indicated by a high correlation in capture rates per location between species. Apart from their overall spatial similarities, jaguars and pumas avoided using the same location at the same time. This interspecific segregation was detectable over and above the spatial and temporal segregation of individual jaguars.

Key words: avoidance, camera trapping, jaguar, puma, social interaction, territoriality

Felid social systems have been characterized as solitary with exclusive territories within the sexes (Sunquist and Sunquist 2002). Females generally occupy a range that encompasses enough prey for themselves and their dependents, whereas ranges of males are defined by maximizing access to females while maintaining enough food for individual survival (e.g., leopards [*Panthera pardus*—Mizutani and Jewell 1998], tigers [*Panthera tigris*—Sunquist 1981], and jaguars [*Panthera onca*—Schaller and Crawshaw 1980; Scognamiglio et al. 2002]). Deviations from this standard system, with same-sex individuals having overlapping ranges, have been noted for several species of large cats (pumas [*Puma concolor*—Hopkins et al. 1986; Núñez et al. 2002; Seidensticker et al. 1973], leopards [Muckenhirn and Eisenberg 1973], and jaguars [Núñez et al. 2002; Rabinowitz and Nottingham 1986]). It has been suggested that females

maintain stable and evenly distributed exclusive ranges when prey are abundant, and overlapping ranges when prey are scarce, seasonal, or clumped (Sandell 1989; Sunquist and Sunquist 2002). Núñez et al. (2002) and Muckenhirn and Eisenberg (1973) inferred that the high level of overlap found for female jaguars, pumas, and leopards was influenced by seasonally clumped distributions of prey species around permanent water holes. Seidensticker et al. (1973) suggested that ranges of female pumas overlapped in response to the migratory movement of deer between seasons. Among large cats in general, higher densities of females with small and stable ranges are associated with exclusive home ranges of males for dominant individuals, presumably maximizing the number of monitored females. Conversely, lower densities of females with larger and less-stable ranges are associated with overlapping ranges of dominant males, in this case roaming presumably becomes a more effective mate-acquisition strategy (Sandell 1989; Sunquist and Sunquist 2002).

These generic patterns are not observed in all field studies. Ranges of males overlap for jaguars, pumas, and leopards in areas where densities of females are high and ranges are overlapping (Muckenhirn and Eisenberg 1973; Núñez et al.

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2002). In this case, it seems likely that males as well as females are responding to clumped distributions of prey, and dominance hierarchies may be expressed in other ways than exclusive territories. If distribution patterns of males are dictated by the strategy that maximizes the number of mating opportunities for the dominant males (Sandell 1989), subordinates may be more focused on finding food and consequently have similar land-tenure strategies as females. In a study of jaguars in Belize, Rabinowitz and Nottingham (1986) found high overlap of males within an area of high overall population density sustained by abundant and easy-to-catch nine-banded armadillos (*Dasypus novemcinctus*). Although little was known about ranges of females, this pattern contrasts with the expectation that abundant prey would give rise to small, exclusive ranges for females and larger, exclusive ranges for males. These authors hypothesized that the overlap in ranges of males was driven by a scarcity of adequate travel routes, characteristic of the thick jungles of Central America, forcing all males to share the few logging roads in the study area. Camera-trap data have since indicated that it is mainly male jaguars that use the larger roads (Harmsen 2006). Prey and female jaguars are detected infrequently on large roads, suggesting that the use of roads by males is not principally for hunting or for monitoring female activity (Harmsen 2006).

Hypotheses for explaining ranging behavior as a function of investment in resource and mate acquisition are difficult to test on large cats in the field because of the need for adequate sample sizes of males and females. Tests require estimating densities of males and females, and evaluating their land-tenure systems in relation to each other and to prey availability and distribution. The information on males must include land tenure in relation to dominance status. Meta-analyses of sparse data from different areas are unsatisfactory because large samples are needed from each area to understand dominance hierarchies and the causal links between ranging behavior and distributions of prey and mates.

To date, telemetry studies on jaguar populations have had limited interpretability because of low sample sizes of 3–8 individuals, with only 2 or 3 tracked simultaneously (Ceballos et al. 2002; Crawshaw and Quigley 1991; Cullen et al. 2005; Núñez et al. 2002; Rabinowitz and Nottingham 1986; Scognamillo et al. 2003; Soisalo and Cavalcanti 2006). These studies all suffer from an absence of information on untagged cohabitants other than that revealed by unvalidated and potentially biased spoor tracking. In one of the few studies to use telemetry and camera trapping simultaneously, Soisalo and Cavalcanti (2006) photographed an additional 24 individual jaguars among the 8 radiocollared individuals. Nothing is known about dominance hierarchies of the tagged male jaguars when captured, making it difficult to interpret motivations behind movement patterns. Large sample sizes of males are needed to ensure the inclusion of both subordinate and dominant individuals.

A similar problem of inadequate sample sizes and unknown number of individuals is apparent in studies of coexistence between species, which is often explained for carnivores by

differentiation of prey selection, activity patterns, or habitat. However, the mechanisms of sympatric coexistence of jaguars and pumas elude such distinctions. Diet studies have shown overlap in food selection across their range, making them potential competitors (Crawshaw and Quigley 2002; Emmons 1987; Leite and Galvão 2002; Novack et al. 2005; Núñez et al. 2000; Scognamillo et al. 2003; Taber et al. 1997). Despite the dietary overlap, no evidence has been found of differentiated patterns of habitat use or activity (Scognamillo et al. 2003). Camera-trap studies have compared jaguar and puma densities between multiple sites in Bolivia and Belize, showing that both cats thrive in similar habitat types across their range (Noss et al. 2006). These are excellent model species for exploring mechanisms of coexistence between larger sympatric carnivores, given their similar sizes and comparable ability to take most of the available prey in the Neotropics (up to the 40-kg white-lipped peccary [*Tayassu pecari*]).

Here we analyze interactions within and between populations of jaguars and pumas in the broadleaf forest of the Cockscomb Basin in Belize. To date, only Scognamillo et al. (2003) have reported jaguar–puma interactions, from telemetry data on 4 jaguars and 5 pumas in the Venezuelan Llanos area. They found evidence of jaguars and pumas using the same habitat but avoiding each other temporally. Their sample sizes were too small to calibrate interspecific avoidance against intraspecific interactions, which is a prerequisite to inferences about niche separation between species.

In this study, we tackled the fundamental issue of small sample sizes in studies of large cats by deploying an extensive network of camera traps to capture timed locations of jaguars and pumas. The unique spot pattern of jaguars allows individual recognition from camera-trap photographs (Silver et al. 2004). Although recognition of individual pumas may be possible under certain circumstances (Kelly et al. 2008), in the present study individual pumas could not be identified with certainty over the long term because of their plain brown coat pattern (Harmsen 2006).

Camera traps have previously been used mainly for studies of dynamics at the population level (Maffei et al. 2005; Noss et al. 2006). Maffei et al. (2004) were the 1st to use them to compare ranges of jaguars within Bolivia in 3 different areas. Although residency could not be quantified from only 2 or 3 individuals per location, high overlap was apparent between 2 male individuals at 1 location and between 2 female individuals at another.

Here we analyze temporal and spatial interactions between a uniquely large sample of individuals to tackle 2 fundamental questions about the function of jaguar movements in resource exploitation: Does spatial overlap of ranges of males depend on hierarchies of residence? Are temporal interactions of jaguars with pumas distinguishable from conspecific interactions? These components of behavior were sampled more representatively than is possible with telemetry by using an array of more than 100 camera stations. Camera traps were placed on established and newly opened trails traversing the dense forest matrix. These trails are the major corridors of

travel for both jaguars and pumas, and individuals present within the immediate area of a camera are reliably caught on camera (Harmsen 2006; Maffei et al. 2004; Rabinowitz and Nottingham 1986). Additional high-density camera arrays sampling small areas (10 km<sup>2</sup>) on and off trails showed that off-trail photographs of jaguars were accompanied in 95% of the instances by on-trail photographs of the same individuals on the same day (Harmsen 2006). We were therefore able to use the time interval between individual captures at a camera location as an index of presence in an area, with longer intervals between recaptures of the same individual indicating that it had traveled farther away. This format permitted testing interspecific interactions of jaguars with pumas in relation to intraspecific interactions among individual jaguars. Interaction can be interpreted from a frequency distribution through time that is more regular than random, indicating mutual avoidance, or more aggregated than random, indicating mutual attraction.

This study represents the largest camera-trap data set for neotropical cats collected to date from 1 site. The study site overlaps almost entirely with that of Rabinowitz and Nottingham (1986), allowing comparison between their telemetry data and our photographic data.

## MATERIALS AND METHODS

The Cockscomb Basin Wildlife Sanctuary encompasses 425 km<sup>2</sup> of broadleaf tropical forest with a mosaic of regenerating secondary forest at several stages of succession. The area was selectively logged until 1981, and has been formally protected since 1986. Many of the old logging roads are maintained as trails. A total of 119 different camera locations were active for continuous periods of 2–20 months between January 2003 and July 2005. The camera network spanned an area of about 200 km<sup>2</sup>, with neighboring cameras separated by 0.5–2 km, and a maximum distance between any cameras of 21.6 km ( $\bar{X}$  = 7.9 km  $\pm$  4.3 *SD* for all cameras).

Jaguars were individually identified from photographic captures. Cameras had an enforced 3-min delay between exposures to prevent wasting film on herd-forming species such as peccaries. Each photograph was stamped with the time and date, allowing calculation of time intervals between consecutive captures at the same camera location. To ensure spatiotemporal independence, simultaneously running camera stations were separated by >2 km. Any jaguar or puma captured at 2 stations on a single day was recorded for analysis at only 1 of the stations, chosen at random. Minitab version 14 (Minitab Ltd., Coventry, United Kingdom) was used for all statistical analyses.

*Jaguar ranging and overlap.*—The unit of analysis was the pooled data from a single camera-trap location for 1 calendar month, hereafter referred to as a location-month. The response variables were the number of individuals identified from photographic captures per location-month, or the number of captures of an individual per location-month.

Evidence for exclusivity in range use was sought by enumerating overlap in the distribution of individuals across camera locations throughout the study period. The data set

used only location-months with >2 captures of jaguars. Relative exclusivity of range occupancy was inferred from a high proportion of location-months with single individuals (either sex) and a low proportion with multiple individuals of the same sex.

Occupancy of the camera-trap vicinity was estimated from the capture frequency of each individual per location-month. The individual with the highest capture frequency per location-month was assigned the highest residency ranking. A relative score of residency was calculated from the excess number of captures of the individual with highest residency ranking over the individual with the next highest capture frequency per location-month. A high residency score indicated a single resident occupant, and other conspecifics of the same sex either passing in transit or using the area only in the brief absence of the resident. A low residency score indicated an absence of exclusive occupancy by any 1 individual, and multiple use of the local area by different individuals during the same month. The total capture frequency per location-month constrained the maximum possible score to 1 less than the total captures. Therefore, the data were presented separately as scores for 3, 4, and >4 total captures per location-month.

Because long-running cameras (maximum of 2 years continuously) contributed more location-months to the data set than short-running cameras, analyses of exclusivity also were performed on a sampling unit comprising the mean number of individuals and the mean residency scores of long-running cameras ( $n$  = 42 stations).

*Consistency of residency ranking through time.*—The maintenance of residency was quantified from the number of location-months over which a single individual maintained the highest number of captures. Changes in rank from 1 individual to another can occur when resident individuals are displaced or die and thus may be consistent with exclusive ranges. A rank reversal, whereby the individual with the highest residency rank loses it and then regains it in later months, is not consistent with exclusive ranges. The number of changes in top-ranking individual between location-months, and the number of reversals in top-ranking individual per location-month, were calculated for 21 long-running camera locations separated by >2 km (3–20 months;  $\bar{X}$  = 8.8 months  $\pm$  4.3 *SD*). All long-running cameras were separated by >2 km. The mean rate of change and reversal per month was then calculated for each of the 21 camera locations, to give an index of flux in occupancy through time.

*Intraspecific interactions between jaguars.*—The main unit of analysis was number of days between consecutive captures per camera location. For each camera location, time intervals were calculated between consecutive captures of “same male,” “male–male” (i.e., different individuals), and “male–female” (including female–male). Sample sizes of “same female” and “female–female” captures were too small for statistical analyses. All data were log<sub>10</sub>-transformed to approximate normal distributions. Student’s *t*-tests, adjusting for unequal variance, were used for all comparisons, except when stated otherwise.

If individual male jaguars occupy areas exclusively, with other males avoiding the area during that male's residency, then it was expected that the majority of consecutive captures would be recaptures of the same individual with consecutive captures between different individuals only happening when the resident departs the area. It was hypothesized that the number of pairs of consecutive recaptures of the same male per location would be larger than the number of pairs of consecutive captures of different males, indicating avoidance through time; and that the time intervals between same-male captures would be shorter than the interval between male-male captures. Consecutive captures of male jaguars at all locations were pooled into 2 groups (either same male or male-male) and the frequency and time interval between same-male captures were compared with those between different-male captures.

*Interspecific interactions between jaguars and pumas.*—Photographic records were analyzed for differences in daily activity schedules between the jaguars and pumas. The time of capture was used to create a 24-h activity pattern for both species. The number of photographs was summed within each hour for 0000–0059 h, 0100–0159 h, ..., etc. and converted to percentage of captures within an hour to facilitate comparisons between the 2 species. A Pearson's correlation on the arcsine-root-transformed percentages of jaguar and puma captures in each hour tested the hypothesis that jaguars and pumas have similar activity patterns.

Pearson correlations between the 2 species were calculated for the  $\log_{10}$ -transformed number of captures and for capture rates, at 2 spatial scales: 1) capture frequencies at each camera location over the study period, and 2) capture rates per location-month. Capture rates per location-month were calculated only for location-months with >25 trap nights. This analysis included all camera stations, because the correlations serve as indicators of travel and habitat use.

Correlation type 1 indicated the level of spatial overlap between the 2 species for the total period each camera was active (2–30 months); correlation type 2 indicated the level of spatial overlap for the shorter period of a calendar month. A difference between correlation types 1 and 2 indicated the level of attraction (positive value) or avoidance (negative value) throughout a calendar month. Because long-running camera locations contributed more data points (i.e., more location-months) to correlation type 2 than did short-running camera locations, the correlation was calculated separately for each location that had >2 months of data and compared to that for the complete data set to assess whether the contribution of the long-running cameras biased the results.

Temporal avoidance or attraction of jaguars and pumas was further analyzed by comparing the number of days between consecutive jaguar–jaguar captures, puma–puma captures, jaguar–puma captures, and puma–jaguar captures at a camera station. A general linear model was run on the response of capture interval, calculated between each capture and the next. These data were tested against cross factors “Capture1,” identifying the initial capture as either jaguar or puma, and

“Capture2,” identifying the subsequent capture as either jaguar or puma. Camera location was added to the model as a random block creating the following model:

$$\text{time interval} = \text{Capture1} \mid \text{Capture2} \mid \text{Location} + \varepsilon.$$

The response was  $\log_{10}$ -transformed to approximate a normal distribution of the residuals and equal variances. It was hypothesized that jaguars and pumas avoid (or attract) each other through time. A significant interaction effect would provide evidence of a longer (or shorter) interval between jaguar–puma and puma–jaguar captures than between jaguar–jaguar and puma–puma captures. No difference was expected in number of days between jaguar–jaguar captures and puma–puma captures (the main effects).

If jaguars and pumas avoid each other, then it was expected that captures of each species would be clustered in time. A nonparametric runs test was used to compare the distribution of male–male capture intervals against a random distribution, which is the expected outcome of negligible interaction. A single run consisted of all consecutive captures of the same species (jaguar or puma). The frequencies of runs of consecutive captures of the same and different species through time indicated to what extent the species attracted or avoided each other. A clustered distribution (few runs) occurred when each species had more consecutive captures than expected at random, indicating avoidance between the 2 species. A regular distribution (many short runs) occurred when the 2 species had fewer consecutive captures than expected at random, indicating attraction between species. Data were used only from camera locations with  $\geq 3$  captures per single species ( $n = 22$  camera stations). The runs test was performed on the pooled data set ( $n = 853$  cat captures). This analysis used only cameras separated by >2 km.

## RESULTS

*Residency and range overlap.*—Twenty-three male jaguars were uniquely identified from camera traps. The 119 camera stations each ran continuously for an average of  $101 \pm 137$  (mean  $\pm$  SD) days, with  $20 \pm 4$  stations simultaneously active. This trapping network of simultaneously running cameras triggered  $118 \pm 25$  captures of jaguars per 100 days of trapping (i.e., >1 capture per day on average), with  $6 \pm 4$  (maximum 16) captures per station per 100 days. The network caught  $23 \pm 8$  individually identified jaguars per 100 days, with  $2 \pm 2$  (maximum 11) individuals per station per 100 days.

Up to 5 different males were captured at the same location in the same month ( $n = 42$  camera stations; Fig. 1a). With only 24% of location-months containing a single individual, and a mode of 2 males per location-month, the data show a tendency for range sharing among conspecific males. The frequency distribution of the means of long-running cameras showed the same pattern (Fig. 1b), indicating a lack of bias in Fig. 1a from an uneven distribution of observations among stations.

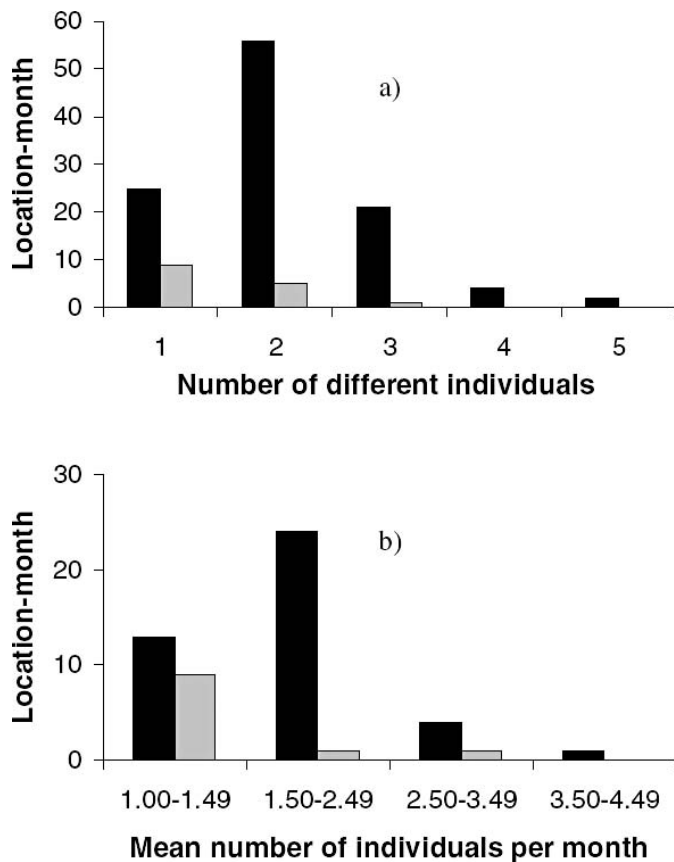


FIG. 1.—Shared occupancy of locations. a) Frequency distribution of individual jaguars (*Panthera onca*) photographed per location-month. Only location-months with >1 capture of either sex are included. Black bars show males ( $n = 108$  location-months), gray bars show females ( $n = 15$  location-months). b) Frequency distribution of means for the number of individuals per month (males:  $n = 42$  locations, females:  $n = 11$  locations).

Only 6 females were uniquely identified from camera traps. As many as 3 different females were captured at the same location in the same month (Fig. 1a). Although the sample size was small, locations more commonly had occupancy by a single female within a given month than occupancy by multiple females (Fig. 1b).

Sample sizes were sufficiently large to calculate residency scores for male jaguars only. The frequency distribution peaked at 1 excess capture of the highest ranking resident per location-month and rarely exceeded 2 excess captures (Fig. 2a). Likewise, the vast majority of locations had a mean of 1 excess capture per month for the highest ranking resident (Fig. 2b).

Only male jaguars had sufficiently large sample sizes to calculate rates of residency change and reversal. Of 21 long-running camera stations, 19 had changes in residency, and 14 had reversals throughout the time the cameras were active. Residency changed  $0.5 \pm 0.23$  times per month and reversed  $0.2 \pm 0.17$  times per month ( $n = 21$  months). Residency at a location could therefore be expected to change every 2 months, and to reverse every 5 months, but with substantial variation between locations. The high averages indicate a rapid flux of individuals per location through time. Sampling

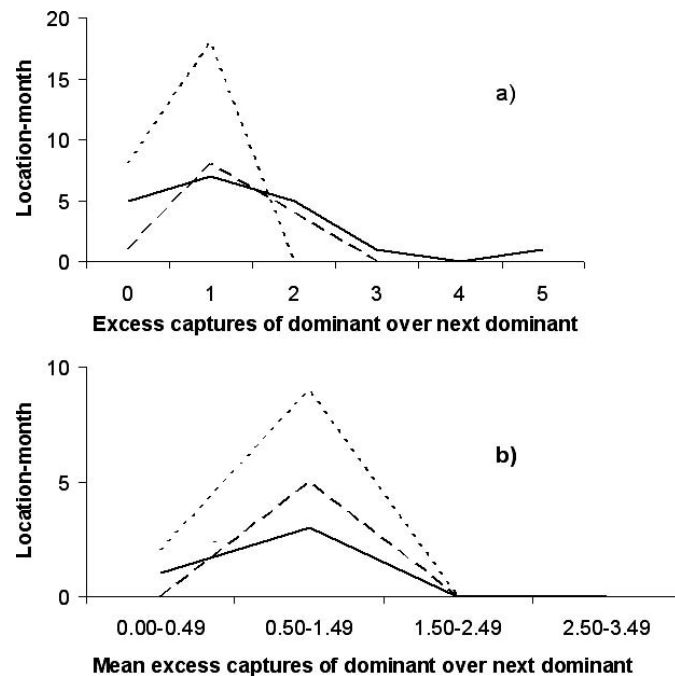


FIG. 2.—Residency of male jaguars (*Panthera onca*) at shared locations. a) Frequency distribution of residency scores ( $n = 108$  location-months). The 3 lines represent location-months with 3 (dotted), 4 (dashed), and >4 (continuous) total individuals captured. b) Frequency distribution of means for residency scores ( $n = 42$ ).

effort per location was correlated with reversals ( $r = 0.77$ ,  $P < 0.01$ ) but not with changes ( $r = 0.10$ ,  $P > 0.1$ ). The correlation with reversals was an expected consequence of the longer sampling effort required to detect these rarer events.

*Intraspecific interactions between jaguars.*—The number of consecutive pairs of recaptures of the same individual was significantly smaller than the number of consecutive pairs of captures of 2 different individuals ( $\bar{X} = 3.8$  pairs and 6.3 pairs, respectively;  $t = -2.44$ ,  $P < 0.05$  on  $\log_{10}$ -transformed numbers of pairs,  $n = 39$  locations). The time interval between consecutive captures of different males was significantly shorter than the interval between consecutive captures of the same male ( $\bar{X} = 7.2$  days from  $n = 248$  pairs,  $\bar{X} = 8.6$  days from  $n = 151$  pairs;  $t = 1.97$ ,  $df = 318$ ,  $P < 0.05$  on  $\log_{10}$ -transformed intervals). Thus, there was no evidence of mutual avoidance between male jaguars.

*Interspecific interactions between jaguars and pumas.*—Jaguars and pumas had overlapping activity with a similar hourly distribution pattern (Fig. 3;  $r = 0.69$ ,  $P < 0.01$  on arcsine-transformed percentages).

Capture frequency of jaguars and pumas was positively correlated at each camera location ( $r = 0.65$  between  $\log_{10}$  captures,  $P < 0.01$ ,  $n = 93$ ) indicating that both species used the same areas (Fig. 4a). However, jaguars and pumas did not appear to use the same areas at the same time: capture rates of jaguars and pumas were never simultaneously high at the same location within the same month (Fig. 4b; Pearson correlation between  $\log_{10}$  nonzero captures,  $r = 0.09$ ,  $P = 0.17$ ,  $n = 258$ ). This suggests the possibility of an inverse relationship of the sort jaguar  $\times$  puma = constant. However,  $\log_{10}(\text{month}/\text{jaguar})$

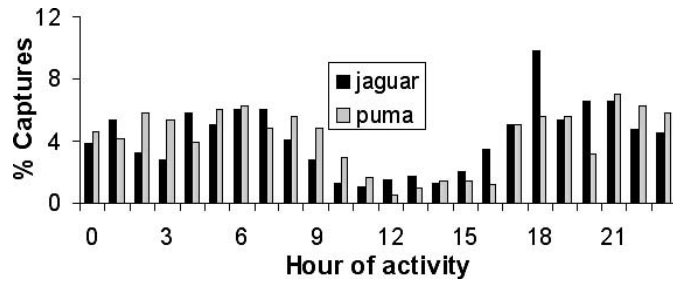


FIG. 3.—Frequency distribution of hourly activity for jaguars (*Panthera onca*; based on 397 captures) and pumas (*Puma concolor*; based on 413 captures).

was not correlated with  $\log_{10}(\text{puma/month})$  ( $r = 0.08$ ,  $P = 0.35$ ). The capture rates per location-month thus were uncorrelated but not simultaneously high in general. No single location biased the pattern in Fig. 4b, with correlations for individual camera locations of  $-0.8 < r < +0.5$ , indicating no fixed relation between capture rates at any given location.

The interval between consecutive jaguar captures did not differ significantly from that between consecutive puma captures (Table 1). The intervals between jaguar–puma captures and puma–jaguar captures were significantly longer than those between consecutive same-species captures (Table 1; Fig. 5). This interaction indicates that interspecific temporal avoidance exceeded temporal avoidance between conspecifics.

The order in which jaguars and pumas were captured through time differed significantly from random (373 runs of consecutive puma or consecutive jaguar captures observed, 427 expected, average  $K = 0.52$ ,  $P < 0.01$ ). The lower number of observed than expected runs indicated a clustering of conspecifics and therefore a tendency for conspecifics to be closer together in time than different species.

## DISCUSSION

Male jaguars in Cockscomb have highly overlapping ranges, with some locations visited by up to 5 males within

TABLE 1.—Balanced analysis of variance on time interval between consecutive captures (with jaguar and puma as the 2 factor levels) using camera location as a block. Responses were determined from totals of 278 jaguar–jaguar captures, 258 puma–puma captures, 166 jaguar–puma captures, and 173 puma–jaguar captures. SS = sum of squares, MS = mean square,  $P < 0.05$  values are shown in bold.

	<i>df.</i>	SS	MS	<i>F</i>	<i>P</i>
Location	15	681.14	45.41	6.04	<0.01
Capture1	1	6.42	6.42	0.50	0.49
Capture2	1	11.49	11.49	1.49	0.24
Location × Capture1	15	193.29	12.89	1.71	0.15
Location × Capture2	15	115.79	7.72	1.03	0.48
Capture1 × Capture2	1	45.42	45.42	6.04	<b>0.03</b>
Error	15	112.77	7.52		
Total	63	1,166.32			

a single month. Although the same males are often captured within the same locality, there seems to be little consistency in residency of ranges across time, with several different males occupying the same area simultaneously and no evidence of spatial avoidance. We have 5 records of different males captured at the same location within 10 min of each other, indicating that male jaguars can come into close proximity (an average walking speed of 0.05 km/min would put them <0.5 km apart). From the total data set of 697 captures of 23 individual male jaguars, only 3 photographs suggested serious flesh wounds or scars that could have been inflicted by a conspecific. This indicates low levels of aggression when males encounter one another, as hypothesized by Rabinowitz and Nottingham (1986) from their telemetry study of 4 males. Our study of a large sample of individuals extends theirs by revealing the larger number of males that can occupy an area at any time, with a high frequency of changes in residency over time. Although range size cannot be estimated from the camera-trap data set, the fluctuating presence and absence of males across our camera network over periods of up to 36 months indicates that males can shift ranges across large areas. It seems likely that the high density of jaguars in Cockscomb

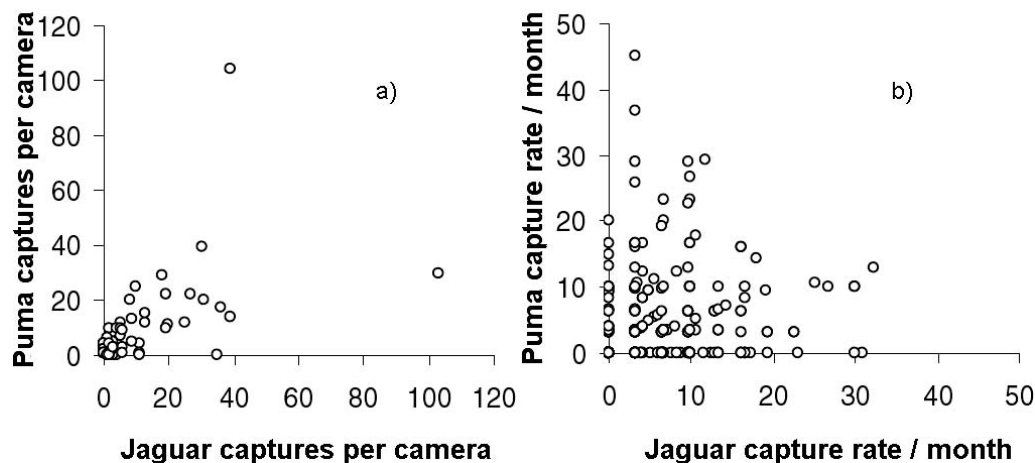


FIG. 4.—Relationships between pumas (*Puma concolor*) and jaguars (*Panthera onca*) regarding a) total captures per camera location ( $r_{91} = +0.65$  on  $\log_{10}$  nonzero data,  $P < 0.01$ ), and b) rate per location-month ( $r_{256} = +0.09$  on  $\log_{10}$  nonzero data,  $P = 0.17$ ).

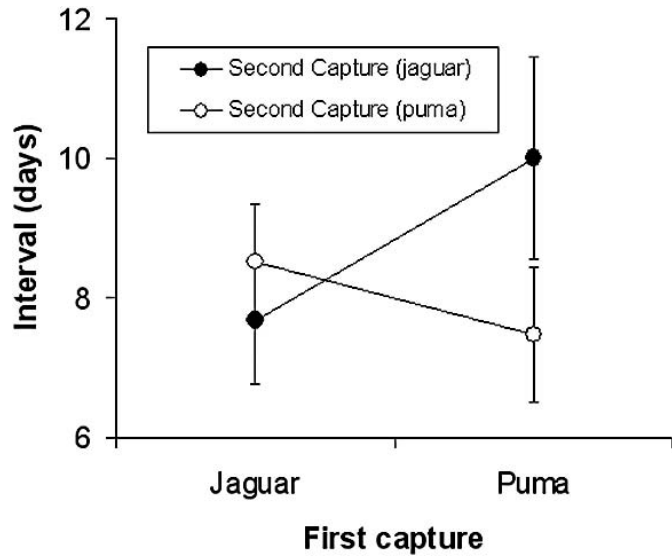


FIG. 5.—Mean  $\pm$  SE of time interval between consecutive captures per camera. The distribution of time intervals is given for all 4 combinations of 1st capture to 2nd capture (jaguar–jaguar, jaguar–puma, puma–jaguar, and puma–puma).

(estimated over the years to be  $\sim 10$  jaguars/100 km<sup>2</sup> [Harmsen 2006]) can only be sustained by a tolerant social system. The low average weight of jaguar prey, with almost 50% of the diet comprised of the abundant and solitary armadillo with small home ranges (Foster 2008; Rabinowitz and Nottingham 1986), may encourage foraging by different jaguars in relatively close proximity. The functional links between diet, density, and range overlap of jaguars need further study by regional comparison across different habitats.

Female jaguars were most commonly photographed as single individuals in any 1 location-month. It is not clear whether this reflects exclusive female ranges or whether it is simply an artifact of the small sample size resulting from a male bias in the survey method. It is likely that the high frequency of multiple, overlapping males creates conditions for infanticide, which has been recorded for jaguars (Soares et al. 2006). Females may therefore avoid the male-dominated travel routes (larger trails) that were the main locations with extremely high capture success. However, extensive camera trapping off trail, using small streams, game trails, and landscape features, did not reveal any habitat characteristics associated with higher capture rates of females (Harmsen 2006).

Although male jaguars showed little evidence of mutual avoidance, we found evidence of temporal avoidance between jaguars and pumas. The avoidance is active rather than passive, because it does not arise from differences in habitat use or activity schedules. Both species used the same locations and schedules, but avoided coincident times. Although examination of the data cannot reveal whether avoidance was mutual, it is likely that the physically smaller pumas avoid jaguars. Anecdotal evidence from Mexico indicates that pumas are occasionally eaten by jaguars (Brian Miller, Denver Zoo, pers. comm.). Scognamiglio et al. (2003) likewise never

found jaguars and pumas in close proximity in the Venezuelan Llanos despite similar habitat use and activity schedules, but this was not calibrated against intraspecific avoidance. Our results show for the 1st time that jaguars and pumas avoid one another more than they avoid conspecifics, indicating interspecific competition. The mechanisms that allow the 2 cats to coexist are subtle and need further study at multiple sites with different ratios of jaguars and pumas.

Camera trapping has proven to be a useful complement to telemetry as a method of studying social interactions by more fully sampling the complete array of individuals within an area. Although camera trapping cannot be used to estimate home-range size, it is well suited for testing temporal components of direct interactions by shifting the unit of analysis toward temporal changes of individuals per point location. Such a unit of analysis can be used as a standard, allowing comparisons between studies at multiple sites. Camera grids collect data on all jaguars walking within the vicinity of the cameras, a prerequisite for studies of social interactions, which is rarely logistically or financially viable with livetrapping and telemetry. The large number of camera-trap data sets already collected for abundance estimates of elusive large cats around the world could be used productively to study patterns of social behavior, especially shared use of space in relation to population density and diet. Camera trapping can augment the detail of telemetry data on individual movement schedules by sampling across the spatiotemporal patterns of multiple individuals simultaneously. Combinations of camera trapping and telemetry will provide the most detailed and powerful data sets for testing hypotheses about land-tenure systems of this highly elusive group of carnivores.

## RESUMEN

Usamos muestreos intensivos de cámaras-trampa para estudiar las interacciones inter-individuales entre individuos identificados de jaguar (*Panthera onca*) y puma (*Puma concolor*). Datos de ubicaciones temporales de una red de 119 estaciones de trapeo en la cuenca del Cockscomb en Belice proporcionó la primera evidencia de que ambas especies se evitan espacialmente, datos que fueron calibrados con la información de las interacciones intraespecíficas de los jaguares. El uso de cámaras-trampa tiene ventajas sobre a radio-telemetría para proveer de datos de un conjunto de individuos de una área de estudio. Los 23 jaguares identificados individualmente mostraron un alto grado de sobreposición de sus áreas de actividad, con hasta 5 individuos fotografiados en el mismo sitio en un mes. Registramos baja consistencia en las áreas de actividad ("home ranges") en períodos de 3 meses a dos años, con bajos niveles de separación espacial entre individuos pero con un alto flujo de individuos. Los patrones de actividad nocturna de jaguares y pumas fueron similares. Ambas especies usaron hábitats similares en la cuenca del Cockscomb, indicado por una alta correlación en las tasas de captura por sitio entre las especies. A pesar de estos patrones, los jaguares y pumas evitaron usar

el mismo sitio al mismo tiempo. Esta segregación inter-específica fue detectada sobre la segregación espacial y temporal de los individuos de jaguar.

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