UNIVERSIDAD NACIONAL AUTONOMA DE MEXICO

INSTITUTO DE ECOLOGIA,

EFECTOS DE LA ESTACIONALIDAD AMBIENTAL EN LA DENSIDAD, LA CONDUCTA DE AGRUPAMIENTO Y EL TAMAÑO DEL AREA DE ACTIVIDAD DEL COATI *(Nasua narica)* EN SELVAS TROPICALES CADUCIFOLIAS.

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DAVID VALENZUELA GALVAN

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"La Ciencia, muchacho, está formada de errores, pero de errores que conviene cometer, porqué conducen poco a poco a la verdad. *Errando deponitur error"*

Prof. Otto Lidenbrock, en Viaje al Centro de la Tierra, de Julio Verne.

"Hay una hora del día en que la llanura está por decir algo; nunca lo dice o tal vez lo dice infinitamente y no lo entendemos, o lo entendemos pero es intraducible como una música..."

De "El Fin" de Jorge Luis Borges

"La palabra trae luz para nuestro animal introspectivo..."

Benjamín Valdivia en "El Juego del Tiempo"

"Uno apenas es una cosa cierta
que se deja vivir, morir apenas,
y olvida cada instante, de tal modo
que cada instante, nuevo, lo sorprenda.

Uno es algo que vive,
algo que busca pero encuentra,
algo como hombre o como Dios o yerba
que en el duro saber lo de este mundo
halla el milagro en actitud primera"

de Uno es el Hombre de Jaime Sabines

"Every intellectual has a very special responsibility....he owes to his fellow men (or to society) to represent the results of his/her study as simply, clearly, and modestly as he/she can. The worst thing he/she can do -the cardinal sin- is to try to set themselves as great prophets vis-a-vis their fellow men and to impress them with puzzling philosophies. Anyone who cannot speak clearly should do nothing and continue to work until he/she can do so."

Karl Popper (against big words, 1956)

"This paper, by its very length, defends itself against the risk of being read"
-espero que este no sea el caso!!!-

Sir Winston Churchill

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A los tejones, la salsa y el son.

INDICE

RESUMEN

Estudié la relación del coatí o tejón (*Nasua narica;* Procyonidae) con su entorno, la selva tropical seca de la Reserva de la Biosfera de Chámela-Cuixmala (RBCC), en la costa de Jalisco, México, para obtener respuestas a tres preguntas generales. Por una parte, obtuve información básica sobre la historia natural del tejón en este sitio, pues es el carnívoro más abundante ahí, el único carnívoro social que habita selvas secas neotropicales y sólo se había estudiado en los extremos de su área de distribución geográfica. Por tanto el presente trabajo es el primero en su tipo que se realiza en México y aporta información sobre la especie en la porción media de su rango de distribución.

Por otra parte, me interesó responder algunas interrogantes acerca de como vive este mamífero en un ambiente tan estacional; que respuestas o adaptaciones presenta para enfrentar las limitantes ambientales que ocurren cada año durante la estación seca. Finalmente, me interesó explorar el efecto de la estacionalidad ambiental, en la densidad, el tamaño grupal y el tamaño de las áreas de actividad de los tejones en la RBCC. Para esto exploré las predicciones de la Hipótesis de la Dispersión de Recursos (HDR). La HDR propone que en hábitats con una distribución de recursos agregada (espacial y temporalmente) el tamaño de los grupos y el tamaño de las áreas de actividad de un carnívoro social, dependen, de la abundancia y dispersión de los recursos limitantes.

Obtuve información sobre densidad, tamaño de grupo, diversidad trófica, hábitos alimentarios, carga de ectoparásitos, factores de mortalidad y aspectos reproductivos de los tejones en la RBCC. La densidad promedio estimada de 42.9 ± 16.9 ind. / km^2, confirma el patrón de variación latitudinal esperado con base en la literatura (mayor en el sur y menor en el norte de su distribución), pero varió notablemente entre dos zonas dentro de la reserva, que difieren en la intensidad de los efectos de la estacionalidad climática. El 85 % de la dieta de los tejones en la RBCC consistió en artrópodos y fruta, pero presentaron la mayor diversidad trófica reportada para la especie y esta cambió estacionalmente.

Los tejones parecen enfrentar los intensos cambios ambientales que ocurren durante la estación seca, con un juego de conductas que incluyen cambios en los patrones de actividad y en el tamaño de sus áreas de actividad. Esto les permite un uso más eficiente de los recursos escasos (e.g. alimento y agua) y seleccionar los hábitats con mayor disponibilidad de recursos. Esto varió entre sexos, las hembras en grupos, a diferencia de los machos, presentaron mayor actividad en la época seca que en la de lluvias e incluyeron en sus áreas de actividad una proporción, mayor a la esperada por azar, de hábitats ricos en recursos. Encontré también, que el tamaño de las áreas de actividad varió entre zonas con diferente dispersión y abundancia de recursos. Esta variación no se relacionó con la riqueza de recursos y si con la dispersión de las fuentes de agua durante la estación seca, lo que apoya parcialmente las predicciones de la HDR. Además hice un experimento modificando la disponibilidad de fuentes de agua, cuyos resultados sugieren que la relación entre el tamaño de las áreas de actividad del tejón y la dispersión de las fuentes de agua, no es tan directa como se puede interpretar en una primera aproximación.

La información generada en esta investigación permite predecir que tácticas generales pueden presentar los coatíes (y tal vez otros carnívoros) para enfrentar la estacionalidad ambiental presente en otras selvas secas de México y Centro América. Esto es importante para el diseño de estrategias de manejo, administración y conservación de la biodiversidad de la RBCC y en otras zonas de selva seca.

ABSTRACT

I studied the relation of the White-nosed Coati (*Nasua narica;* Procyonidae) with its environment in the tropical dry forests of the Chamela-Cuixmala Biosphere Reserve (CCBR), in the coast of Jalisco, Mexico, to obtain answers for three general research questions. On the one hand, I wanted to obtain basic information about natural history of the Coati in this site, because it is the most abundant carnivore in the CCBR, the only social carnivore inhabiting neotropical dry forests and it have been studied only in the extremes of its geographical distribution range. Hence present work it is the first of its kind that had been done in Mexico and it gives information about the species in the middle portion of its distribution range.

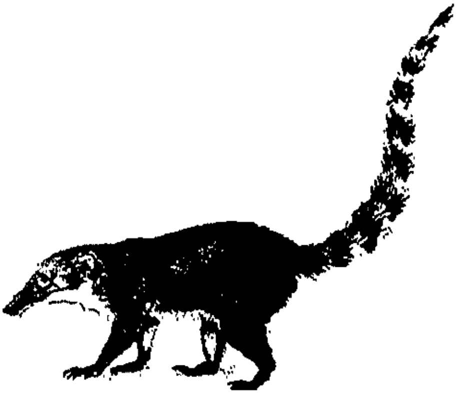
On the other hand, I was interested in understand how could this mammal live in such a seasonal environment, what type of answers or adaptations presents to cope with the environmental limitations that occurs each year during the dry season. Finally, it interested me to explore the effects of the environmental seasonality, on density, group size and home range size of the coatis in the CCBR. I did this by exploring the predictions of the Resource Dispersion Hypothesis (RDH), that proposes that in an habitat with an aggregated (in space and time) resource distribution, the pattern of resource dispersion will determine size of home ranges, while the number of individuals on groups will be determined by resource richness.

I obtained information about density, group size, diet diversity and feeding habits, ectoparasite load, mortality factors and aspects of the reproductive behavior of coatis at the CCBR. The average coati density estimated in the CCBR of 42.9 ± 16.9 ind. / km^2, confirms the expected pattern of latitudinal variation (higher in the southern and lower in the northern portion of its distribution), but it varies notably between two zones inside the reserve that differs in the intensity of the effects of the climatic seasonality. The 85 % of coati diet in the CCBR was arthropods and fruit, but presented the highest feeding diversity reported for the species and this varied seasonally.

Coatis seems to cope with the intense environmental changes during the dry season, with a set of behavioral responses that included changes in the patterns of activity and home range sizes, to attain a more efficient use of sparse resources (e.g. food and water) and to select habitats with more resource availability. There were, however, important differences among sexes, females in groups, in contrast with males, presented greater activity in the dry season than in the wet season and include inside its home ranges, a higher proportion than expected by chance of the habitats with more resources. Also, I have found, that home range size varied between zones with different dispersion and richness of resources, and that this variability it did not correlate with resource richness but it did so with dispersion of water sources during the dry season, a result that partially supports predictions of the RDH. Finally I have done an experiment by changing the dispersion of water sources. The results obtained suggests that the relation between home range size and dispersion of water source is not as direct as could be interpreted from a first approximation.

The information obtained in this research permits to predict what general traits could be used by coatis (and maybe by other carnivores) to cope with the environmental seasonality of other dry forests in Mexico and Central America. This is important when designing management and conservation strategies to protect the biodiversity in the CCBR and in other areas of dry forests..

INTRODUCCIÓN GENERAL



INTRODUCCION GENERAL

Estacionalidad y sociabilidad en Carnívoros

La estacionalidad ambiental, entendida como los cambios periódicos en los factores abióticos particularmente en la temperatura y la precipitación (Krebs, 1985; Wolda, 1988), tiene un gran efecto en la abundancia y la distribución de los seres vivos ya que afecta los parámetros poblacionales de plantas y animales, así como la estructura y el funcionamiento de las comunidades y los ecosistemas (August, 1983; Clutton-Brock y Harvey, 1978; Frankie *et al.*, 1974; Wolda 1988) y es una fuerza de selección importante (Andrewartha y Birch, 1954; MacArthur, 1972; Begon *et al.*, 1986; Lominicki, 1988; Wiens, 1986). En general, la estacionalidad climática significa, para los organismos, una variación en la disponibilidad de recursos, principalmente agua y alimento. Variación que puede imponer serias limitantes para el establecimiento, permanencia y reproducción de un organismo dado en un lugar y que por su carácter cíclico puede promover respuestas adaptativas en sus poblaciones.

En el caso de los organismos animales, estos enfrentan tales limitantes mediante una gran variedad de respuestas morfológicas, fisiológicas y conductuales (Ceballos, 1995; Leigh *et al.*, 1982). Identificar estas respuestas y considerar las distintas habilidades de los organismos, para explotar o tener acceso a los recursos limitados, no solo tiene importancia a nivel poblacional, además facilita el entendimiento de los mecanismos de organización de las comunidades. Aquellas respuestas de los individuos a la variabilidad ambiental, que aumenten la probabilidad de adquirir esos recursos y su eficiencia para utilizarlos, pueden ser favorecidas por la selección natural convirtiéndose en una adaptación. Con mucha frecuencia estas adaptaciones se manifiestan conductualmente (Real y Levin, 1991).

Una de estas respuestas puede ser la formación de grupos de individuos, de los que pueden distinguirse cuatro tipos: 1) grupos poblacionales, formados por individuos que comparten permanentemente un área de actividad común; 2) grupos de alimentación, que se forman por individuos que comparten el mismo recurso alimenticio en un tiempo dado; 3) grupos de forrajeo, que son que se agrupan al buscar comida o cazar; y 4) grupos reproductivos, formados por individuos que conforman una unidad reproductiva (Gittleman, 1989). Esta conducta se presenta en taxa muy diferentes, entre ellos los carnívoros, que muestran una gran variación intra e interespecífica en la formación de estos grupos y en la conducta de los individuos en ellos (Bekoff *et al.*, 1984). En el caso de los carnívoros, la mayoría viven en parejas o son solitarios. Se estima que solamente entre el 10 y 15 % forman grupos fuera de los periodos reproductivos (Gittleman, 1989).

El origen y mantenimiento de la conducta social en carnívoros se ha explicado como el resultado del balance entre los costos y beneficios de la sociabilidad (Krebs y Davies, 1987; Pulliam y Caraco, 1984). Las ventajas o desventajas de vivir en grupo equivalen, respectivamente, a un aumento o un decremento en la adecuación de los individuos (Krebs y Davies, 1987). Esto es, cuando el vivir en grupo aumenta la adecuación de los individuos que lo integran, se favorece el surgimiento de conductas de agregación y la sociabilidad (Pulliam y Caraco, 1984).

Algunas de las ventajas evolutivas asociadas a la sociabilidad en carnívoros son: a) mejor y más eficiente vigilancia y defensa contra depredadores (Clark y Mangel, 1986; Grier, 1984; Krebs y Davies, 1987), b) incremento en la eficiencia de búsqueda y captura de presas, c) mayor capacidad competitiva de los individuos para obtener alimento (Clark y Mangel, 1986; Gittleman, 1989), d) acceso a miembros del sexo opuesto, e) facilita la cooperación en el cuidado y protección de las crías y f) favorece el aprendizaje de algunas conductas de alimentación y de escape a depredadores (Gittleman, 1989; Krebs y Davies, 1987). Las desventajas del agrupamiento intraespecífico son numerosas., incluyen: a) mayor probabilidad de detección por competidores y depredadores, b) mayor competencia entre los individuos de un grupo, c) aumento en los encuentros agonísticos intragrupales, d) mayor probabilidad de transmisión de enfermedades, ectoparásitos y epizootias, y e) menos alimento disponible para cada individuo (Bekoff *et al.*, 1984; Kruuk y Macdonald, 1985; Pulliam y Caraco, 1984).

Los principales factores asociados con la conducta social de carnívoros son la forma de explotación de recursos alimenticios y las características del hábitat. Se han encontrado correlaciones entre la sociabilidad de los carnívoros y la disponibilidad de recursos. Por ejemplo, el tamaño del grupo aumenta con el incremento en el tamaño de la presa y con la visibilidad del hábitat, es decir, el tamaño de grupo es mayor en especies que viven en hábitats abiertos. Aunque también se ha encontrado que el tamaño corporal del carnívoro no afecta el tamaño de los grupos en las diferentes especies de carnívoros sociales (Bekoff, *et al.* 1984; Gittlemann, 1989).

Para entender la evolución de la sociabilidad en carnívoros, es necesaria la aproximación comparativa en la cual se obtiene información sobre la variación en la organización social de diferentes especies y poblaciones de carnívoros y se relaciona con los factores ambientales (Kruuk y Macdonald, 1985). La Hipótesis de la Dispersión de Recursos (HDR; Macdonald, 1983) considera este enfoque y propone que los patrones de la abundancia y disponibilidad de los recursos más limitantes (e.g. alimento y agua), en condiciones de heterogeneidad ambiental fueron, presumiblemente, el factor ecológico inicial que determinó la evolución de la sociabilidad en carnívoros, misma que se ve afectada por los beneficios y desventajas de esta conducta. La HDR establece las condiciones teóricas que explican la variación en el tamaño de los grupos y el tamaño de las áreas mínimas requeridas para mantener grupos de diferentes tamaños, como una función de la abundancia y dispersión de los recursos limitantes.

La regulación de la variación en el tamaño de los grupos y el tamaño de las áreas de actividad en los carnívoros sociales se da por diversos mecanismos, pero dos estrategias en particular se han observado con frecuencia: estrategias expansionista y contraccionista (Kruuk y Macdonald, 1985). En la primera, el número de individuos en el grupo aumenta al aumentar los recursos disponibles, lo que causa un incremento paralelo en el área que el grupo puede usar. Por el contrario si disminuye la disponibilidad de recursos, el tamaño del grupo disminuye también y, en consecuencia, el espacio que ocupa. Este modelo asume una distribución homogénea de los recursos. En la estrategia contraccionista no existe una correlación entre el número de individuos en los grupos y el área que utilizan, ya que se argumenta que estos parámetros son determinados en forma independiente por la abundancia de recursos y por la dispersión que tengan esos recursos, respectivamente. La estrategia contraccionista se presenta más comúnmente en sitios donde la disponibilidad del recurso limitante (generalmente el alimento) ocurre en parches, aunque puede también presentarse cuando hay variación temporal en la disponibilidad de estos recursos o en el patrón de renovación de los mismos (Kruuk y Macdonald, 1985). Esta estrategia se relaciona directamente con lo que predice la HDR.

Varios trabajos con carnívoros sociales han aportado en alguna medida apoyo a las predicciones de la HDR. Macdonald (1981) encontró que para la zorra roja (*Vulpes vulpes*) en una zona rural de Inglaterra, en donde los recursos alimenticios presentaban una distribución en parches, no había una correlación entre el tamaño de sus grupos y el de sus áreas de actividad y que al parecer la configuración de estas áreas estaba determinada por la dispersión de estos parches. En el caso del tejón euroasiático (*Meles meles*), se ha encontrado que el tamaño de sus territorios estaba estrechamente relacionado con la distancia entre parches de alimentación (Kruuk y Parish, 1982) y también por la distribución espacial de los sitios en los que les es posible excavar sus madrigueras subterráneas (Doncaster y Woodroffe, 1993). Para la zorra de Blanford (*Vulpes cana*), se encontró que la variabilidad en el tamaño de sus áreas de actividad, se explicaba mejor por la distancia media a los parches de mayor riqueza de recursos alimenticios (Geffen *et al.*, 1992). Y para la zorra ártica (*Alopex lagopus*) y la mangosta enana (*Helogale parvula*) no se ha encontrado una relación entre la variabilidad en el tamaño de sus territorios y el de sus grupos (Hersteinsson y Macdonald, 1982; Rood, 1983). Finalmente para la hiena moteada (*Crocuta crocuta*), la distancia media a la que sus grupos perseguían a las presas se relacionó en forma positiva con el tamaño de sus territorios (Kruuk & Macdonald, 1985).

Además, se han publicado trabajos teóricos alrededor de la RDH que han generado modelos matemáticos para explorar, explícitamente, los supuestos y predicciones de esta hipótesis respecto a la variación en los parámetros sociales y su relación con la disponibilidad de recursos limitantes (Carr y Macdonald, 1986; Bacon *et al.* 1991a y 1991b; Doncaster y Macdonald, 1992; Macdonald y Carr, 1989).

En este proyecto analice experimental y teóricamente las predicciones de la HDR respecto a la relación de la disponibilidad de recursos con el tamaño de los grupos y el tamaño de las áreas de actividad. Para estos análisis utilicé como modelo a la población coatí o tejón (*Nasua narica*; Procyonidae; Linnaeus, 1766) de una selva tropical seca, en la costa de Jalisco, México. El tejón es el único carnívoro social en el neotrópico y es el más abundante de los carnívoros en el sitio de estudio, caracterizado por una marcada estacionalidad en la precipitación pluvial. Existen pocos estudios que hayan trabajado el tema en situaciones de campo (e.g. Geffen *et al.*, 1992) y ninguno en selva seca. Por esto la información que aquí se presenta, contribuye a entender, cual es el papel que la variabilidad en la disponibilidad de recursos tiene en el surgimiento y mantenimiento de la sociabilidad en carnívoros.

Historia natural del coatí o tejón

Este prociónido se ha estudiado fundamentalmente en los extremos de su distribución geográfica, al sur, en la Isla Barro Colorado, Panamá (Gompper, 1996 y 1997; Kaufmann, 1962; Russell, 1981 y 1982; Smythe, 1970) y en Costa Rica (Saénz, 1994) y al norte, en Arizona, Estados Unidos (Hass, 1997; Kaufmann *et al.*, 1976; Ratnayeke *et al.* 1994; Risser, 1969; Wallmo y Gallizioli, 1954). En México solo se han realizado dos investigaciones enfocadas, al menos parcialmente, a la ecología del tejón, en los estados de Tamaulipas (Caso, 1994) y Durango (Delibes *et al.*, 1989). Gompper (1995) y Valenzuela (en prensa) presentan compilaciones de la información sobre la especie.

El tejón es un animal de hábitos fundamentalmente diurnos y terrestres aunque presenta, como todos los prociónidos, adaptaciones anatómicas que le permiten trepar fácilmente a los árboles. El tejón es un omnívoro colector que se alimenta principalmente de fruta e invertebrados de la hojarasca, aunque puede consumir pequeños vertebrados terrestres en menor proporción (Gompper, 1996; Kauffmann, 1962; Russell, 1982; Sáenz, 1994; Smythe, 1970). El periodo de apareamiento es de una o dos semanas al año, ocurre entre enero y abril dependiendo de la latitud y es seguido de un periodo de gestación de entre 10 y 11 semanas. En casi todas las localidades estudiadas existe un solo periodo reproductivo, lo cual parece estar asociado con ciclos de abundancia de artrópodos de la hojarasca y de fructificación de varias especies de árboles (Russell, 1983; Smythe, 1970). En Nancite, Costa Rica, se ha detectado un segundo pico reproductivo que parece ser una respuesta a una alta presión de depredación por monos capuchinos (*Cebus capucinus*; Sáenz *et al.*, 1994).

Una característica notable del tejón es su conducta gregaria, pues forma grupos de hasta 25 individuos (aunque ocasionalmente se han reportado grupos mucho mayores) compuestos de hembras adultas e individuos juveniles, de ambos sexos. Los machos de tejón permanecen en los grupos hasta cerca de los dos años de edad, después de los cuales son excluidos de los mismos, por lo que son solitarios y sólo se reúnen con las hembras durante los breves periodos reproductivos anuales (Gompper, 1997; Kauffman, 1962). Tanto los grupos de tejones como los machos solitarios, pasan la mayor parte del tiempo en busca de alimento entre la hojarasca o en los arboles con fruta, aunque los machos solitarios pueden desplazarse mayores distancias, ser más activos en la noche e incluir un mayor porcentaje de vertebrados en su dieta que los grupos de hembras y juveniles (Russell, 1983; Smythe, 1970).

En Barro Colorado, Panamá, en particular, el coatí presenta a lo largo del año cambios en sus patrones de actividad, lo cual parece estar asociado a cambios estacionales en la abundancia de recursos alimenticios. En este sitio, los individuos de coatí se desplazan mayores distancias conforme decrece la disponibilidad de alimento a lo largo del año; en tanto que durante el periodo de mayor abundancia de recursos alimenticios, aumentan los periodos de descanso diurno y reducen sus áreas de actividad (Russell, 1983; Smythe, 1970).

La densidad de algunas poblaciones de tejón es mayor y el tamaño de las áreas de actividad de sus grupos tiende a ser menor, en los trópicos al sur de su distribución que en zonas semiáridas al norte de su distribución. En la isla de Barro Colorado se han reportado densidades de entre 24 y 51 individuos por kilómetro cuadrado y áreas de actividad de entre 30 y 50 hectáreas por grupo (Glanz, 1982; Gompper, 1997; Kaufmann, 1962). En Los Tuxtlas, Veracruz, México, las densidades son de 33 individuos por kilómetro cuadrado (Coates-Estrada y Estrada, 1986) y en Santa Rosa, Costa Rica el tamaño de las áreas de actividad varia entre 200 y 500 hectáreas (Sáenz, 1994). En Arizona, Estados Unidos, se reportan densidades entre 1.2 y 2 individuos por kilómetro cuadrado y áreas de actividad entre 300 y 1,900 hectáreas (Hass, 1997; Lanning, 1976; Ratnayeke *et al.* 1994). En el sitio de estudio del presente trabajo se considera al coatí como uno de los carnívoros con mayor abundancia (Ceballos y Miranda, 1986). Las densidades de esta especie pueden variar mucho de un año a otro por causa de enfermedades o variaciones en la disponibilidad de alimento (Kauffman, 1962; Risser, 1963).

Los tejones pueden ser depredados por jaguares (*Panthera onca*), pumas (*Puma concolor*), ocelotes (*Leopardus pardalis*), boas (*Boa constrictor*), hálcones cola roja (*Buteo jamaicensis*), águilas (*Aquila chrysaetos* y *Harpia harpyja*), monos capuchinos (*Cebus capucinus*), osos negros (*Ursus americanus*) y humanos (Aranda, 1993; Fedigan, 1990; Gilbert, 1973; Gompper, 1995; Hass, 1997; Janzen, 1970; Janzen y Wilson, 1983; Kaufmann, 1962; Newcomer y DeFarcy, 1985; Nuñez, 1999). Las crías y juveniles de coatí son más vulnerables al ataque de depredadores. Los tejones son susceptibles a enfermedades contagiosas como la rabia y al moquillo y presentan numerosos endo y ectoparásitos, como céstodos, larvas de moscas y garrapatas (Gompper, 1995). Los tejones son capturados con frecuencia para conservarlos como mascota y en algunos lugares se les caza para aprovechar su piel y carne (Aranda, 1991).

Sitio de Estudio

El área de estudio se ubica en el municipio de la Huerta, en la costa oeste del estado de Jalisco, México, entre los 19° 22 '- 19° 35'N y 104° 56' - 105° 03'W, limitando al sur con el Río Cuixmala y al norte con el arroyo Chámela. La Reserva de la Biosfera de Chámela-Cuixmala

(RBCC) tiene una extensión de 13,142 hectáreas y una topografía de lomeríos con algunas planicies (altitud de 0 a 400 msnm). La vegetación predominante es selva tropical caducifolia o selva seca. La RBCC constituye una de las últimas porciones no perturbadas de este tipo de selva en México y fue creada específicamente para proteger en particular este importante tipo de vegetación (Ceballos y García, 1995; SEMARNAP, 1995).

La característica más importante de la región es su marcada estacionalidad climática, con un período de lluvias concentrado de junio a octubre y un periodo largo de sequía de noviembre a mayo. La precipitación anual varía entre 700 y 1000 mm y la temperatura media anual oscila alrededor de los 25 °C (Bullock, 1986). La RBCC protege nueve tipos de vegetación que incluyen más de 1,100 especies de plantas vasculares (Lott, 1993), 19 especies de anfibios, 68 especies de reptiles, 270 de aves y 72 de mamíferos (SEMARNAP, 1995). Alrededor del 28 % de las especies de plantas y cerca de 81 especies de vertebrados son endémicas de México (Ceballos y García, 1995; Lott, 1983). Los dos tipos de vegetación más abundantes en la CCBR son la selva seca y la selva mediana. La selva seca se caracteriza porque durante la estación seca, cerca del 95 % de sus especies pierden las hojas (Lott, 1993). En contraste, se ha encontrado que la selva mediana presenta, en este mismo periodo, una mayor cobertura de dosel, más humedad del suelo y hojarasca y una mayor abundancia de artrópodos de la hojarasca, que las áreas de selva seca adyacentes (Janzen y Schoener, 1968; Martinez-Yrizar y Sarukhan, 1990; Pearson y Derr, 1986). También, la temperatura al mediodía, puede ser hasta 3° C menor en los arroyos que en la selva seca (K. Renton, com. pers.). Excluyendo la zona de humedales, aproximadamente un 90 % de la superficie de la RBCC esta cubierto por selva seca y un 8 % por selva mediana (A. Miranda, com. pers.). La selva mediana se localiza en parches en áreas con mayor humedad, como valles, o a lo largo del cauce de los arroyos. En este trabajo se considera selva de arroyo a la selva mediana distribuida a lo largo del cauce de los arroyos dentro de la RBCC.

Dentro de la reserva se eligieron dos zonas de trabajo, denominadas Cumbres y Cuixmala, separadas alrededor de 10 kilómetros y con características contrastantes. Cumbres es la zona central de la reserva, de topografía muy irregular con lomeríos y valles, entre 100 y 400 msnm. La vegetación dominante es selva seca pero también hay selva de arroyo a lo largo del cauce de los arroyos y manchones de selva mediana en áreas de mayor humedad. No hay fuentes permanentes de agua y su disponibilidad se ve severamente limitada durante la estación seca. Las actividades humanas son mínimas allí. Cuixmala es la porción sureste de la reserva y está conformada por la planicie costera del río Cuixmala. La selva seca también es dominante pero hay además áreas importantes de vegetación asociada a humedales (e.g. manglar, manzanillar, carrizal). Cuixmala presenta más actividad humana y hay grandes extensiones dedicadas a agricultura, palmares y varios cultivos frutales. Tiene además, disponibilidad de agua permanentemente en lagunas naturales y artificiales, canales de riego y en el mismo río Cuixmala.

Objetivos Generales

El objetivo central de este trabajo fue determinar si las limitantes impuestas por la estacionalidad climática en la RBCC, afectan la densidad, la conducta de agrupamiento y el tamaño de las áreas de actividad del coatí.

Objetivos particulares

1. -Obtener información sobre, diversidad trófica, hábitos alimentarios, carga de ectoparásitos, factores de mortalidad, tamaño de camada, fechas del periodo reproductivo de los tejones en la RBCC y compararlos con datos obtenidos en otros sitios.
2. Estimar la densidad poblacional, el tamaño de los grupos y las áreas de actividad que utilizan los tejones en el sitio de estudio, si cambian entre sitios y estaciones y su relación con la abundancia y dispersión de agua, fruta y artrópodos de la hojarasca.
3. Determinar los patrones de actividad y uso de hábitat de grupos y machos solitarios de coatí y si esto difiere estacionalmente.
4. Poner a prueba las predicciones de la HDR respecto a la relación del tamaño de grupo de los tejones y sus áreas de actividad con la disponibilidad de recursos limitantes.

En particular se esperaba que el tamaño de las áreas de actividad estuviera relacionado con la dispersión del (los) recurso(s) limitante(s), mientras que el tamaño de los grupos debería estar relacionado, con la abundancia de tales recursos. Por tanto se esperaba que las áreas de actividad fueran mayores en la zona con mayor dispersión de recursos y que una manipulación experimental de la dispersión del o los recursos limitantes provocara cambios en el tamaño de las áreas de actividad.

5. Utilizar los resultados de este trabajo para recomendaciones de conservación del tejón y de las selva seca en la RBCC y en otras zonas del país.

Estructura de la tesis

Este trabajo se divide en cinco capítulos y un apéndice. Los capítulos I, II, III y el Apéndice I, están escritos en inglés y redactados conforme los formatos de diferentes revistas. En el capítulo

I se presenta la información de la historia natural del coatí en la Reserva de la Biosfera de Chámela-Cuixmala, Jalisco, México. En el capítulo II se presentan los resultados del estudio de los patrones de actividad, el uso y selección de hábitats y las áreas de actividad usadas por los coatíes en esta región como un conjunto de estrategias conductuales para enfrentar la estacionalidad ambiental del sitio de estudio. En el capítulo III se presentan los resultados del análisis de las predicciones de la HDR al comparar los datos de las áreas de actividad de los coatíes entre Cuixmala y Cumbres y relacionar esto con las diferencias entre estos sitios, en dispersión y abundancia de recursos. El capítulo IV está escrito en español y presenta resultados de un experimento de modificación en la dispersión de agua y una revisión de los modelos matemáticos existentes acerca de la HDR. En el capítulo V se presentan las conclusiones generales del trabajo y sus implicaciones para manejo y conservación de la población de coatí y de la biodiversidad en general de la RBCC. Finalmente, en el Apéndice I se presentan resultados de las acciones realizadas para controlar la epizootia de sarna que se detectó en la población de coatíes.

CAPITULO I

NATURAL HISTORY OF THE WHITE-NOSED COATI, *Nasua narica* IN A TROPICAL DRY FOREST OF WESTERN MEXICO

(Escrito en el formato de la Revista Mexicana de Mastozoología)

NATURAL HISTORY OF THE WHITE-NOSED COATI , Nasua narica IN A TROPICAL DRY FOREST OF WESTERN MEXICO

DAVID VALENZUELA

Instituto de Ecología, UNAM, A.P. 70-270, Ciudad Universitaria, México, D.F.; C.P. 04510, Fax (5) 22-9004 y Fundación Ecológica de Cuixmala, A.C., A.P. 161, San Patricio Melaque, Jalisco, C.P. 48980, Fax (335) 1-00-40. E-mail: dgalvan@miranda.ecologia.unam.mx

ABSTRACT.- From November 1994 to March 1997, I studied the ecology of the White-nosed coati (Nasua narica; Procyonidae) in the central portion of its geographical range, in the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve (CCBR), Jalisco, Mexico. Here, I present information about population density, group size, trophic diversity, feeding habits, ectoparasite load, mortality factors and reproduction. The estimated average density was 42.94 ± 16.88 ind. / km^2 ($\bar{X}$ ± 95 % CI) and the average group size was 6.1 ± 0.49 (n = 142). Fecal analysis showed a trophic niche breadth value of 2.674 with 85.11 % of the diet consisting of fruit and arthropods, two resources whose spatio-temporal availability is strongly affected by seasonality. Results are compared with available data and discussed in the context of seasonality effects on the ecology of this species.

Título abreviado: Natural history of coatis in a tropical dry forest

RESUMEN.- De noviembre de 1994 a marzo de 1997, estudié aspectos de la ecología del coatí (Nasua narica; Procyonidae) en la porción media de su distribución geográfica, en la selva baja caducifolia de la Reserva de la Biosfera de Chamela - Cuixmala, Jalisco, México. Presento aquí, información sobre su densidad, el tamaño de sus grupos, la diversidad de su dieta y sus hábitos alimentarios, la carga de ectoparásitos, algunos factores de mortalidad y algunos aspectos reproductivos. El promedio de las estimaciones de densidad fue 42.94 ± 16.88 ind. / km^2 ($\bar{X}$ ± IC al 95%) y el tamaño promedio de grupo fue de 6.1 ± 0.49 (n = 142). De el análisis de heces fecales se encontró un valor de amplitud de nicho trófico de 2.674 y que el 85.11 % de la dieta consistió de frutas y artrópodos, dos recursos cuya disponibilidad espacio-temporal es fuertemente afectada por la estacionalidad climática. Los resultados se discuten en el contexto de los efectos de un ambiente estacional en la ecología de esta especie.

Key words: Climatic seasonality; Carnivore; Jalisco, México; Nasua narica; Tropical Dry Forest.

INTRODUCTION

The distribution range of the White-nosed Coati (Nasua narica; Procyonidae) extends from Central America to the South-western United States (Gompper, 1995). In México, the species occurs throughout the country, except in the Baja California Peninsula and the central highlands, and is most common in the coastal slopes of the Pacific Ocean and the Gulf of México. The White-nosed coati is one of the most abundant carnivore species by both density and biomass in the neotropical forests, as is the case in the study site (Ceballos and Miranda, 1986) and is the only truly social carnivore species inhabiting this environment.

The species has been studied mainly in the extremes of its distribution range (Gompper, 1994, 1996; C. Hass, in litt.; Kaufmann, 1962; Kaufmann et al., 1976; Ratnayeke et al. 1994; Risser, 1963; Russell, 1982; Saenz , 1994). In México, two comparative studies of the coati and other carnivores have been previously conducted. The first one analyzed the food habits of Coyote (Canis latrans), Gray fox (Urocyon cinereoargenteus) and coati in the western Sierra Madre (Delibes et al., 1989). The other, determined the home range size and the habitat use patterns of coati in northeastern México (Caso, 1994).

Basic ecological patterns related to resource availability seem to emerge from these studies: coatis depend heavily on fruit and litter arthropods. The variability in density, group sizes, home ranges and activity patterns of coatis is related to the spatio-temporal fluctuations in abundance of both resources (Gompper, 1995; Ratnayake et al., 1994; Russell, 1982). Data from the latitudinal extremes of its distribution range indicates that in the southern wet forests, where resources are more abundant and less dispersed, coati densities are higher and home ranges are smaller than in the northern semiarid zones, where resources are less available (Gompper, 1997; Haas, 1997). Data on group size do not show a clear tendency, but indicate a high intrapopulation fluctuation from year to year in relation to food abundance (Gommper, 1995, 1997). Besides, it has been reported that daily activity and home range size increases as dispersion of resources increases and resource abundance decreases during the progression from the rainy season to the dry season (Russell, 1982; Saenz, 1994). Also it has been observed that reproductive events are timed with the period of maximum food availability (Russell, 1982; Smythe, 1970).

Here, I present information about the natural history of the coati in the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve (CCBR) on the Western coast of México. This location is in the central part of its geographical range. Asides, whitin the reserve, two sites with contrasting resource (e.g. water and food) abundance were selected in order to explore at a local scale the relation of resource availability with coati density and other ecological traits of this species. Considering the latitudinal and ecological pattern previously observed, I expected to find *in this area: i) an intermediate* population density between Panama and Arizona that supports the latitudinal pattern related to changes in resource availability, ii) similar feeding habits to those found at other studied sites but with a higher trophic diversity than in tropical forests in the south of species distribution, because in the CCBR is expected a lower abundance of food resources than in the wet forests in Panama, and iii) differences in density between the two study sites that differ in resource abundance, being higher in the site with more abundance of resources.

STUDY SITE AND METHODS

Study site

The CCBR is located in western México on the coast of Jalisco, 140 kilometers south of Puerto Vallarta and 100 km north of Manzanillo, between 19° 22' 03" and 19° 35' 11" N and 104° 56' 13" and 105° 03' 25" W (Figure 1). The reserve extends over 13,141 hectares with a topography of hills and coastal plains with an altitude interval from sea level up to 400 meters above sea level. Excluding the coastal plains, the dominant vegetation type is the tropical dry forest (TDF) that covers roughly 90 % of the area and there is also semideciduous forest (SF) that covers around 8 % (A. Miranda, pers. comm.). The SF is found in small patches in areas with increased humidity or forming a band along main water drainages, that in this study will be named distinguished as arroyo forest (AF). In the coastal plain there are some wetland vegetation types near coastal lagoons (Ceballos and García, 1995).

A marked climatic feature of this area is the sharp rainfall seasonality, with rain concentrated in five months from June to October, followed by a seven month dry season from November to May. Annual average rainfall varies between 700 mm and 1000 mm, and annual average temperature is around 25 °C (Bullock, 1986). A detailed description of the area and the reserve is given elsewhere (Ceballos and García, 1995).

Within the reserve, the study was conducted at two sites with contrasting resource abundance and dispersion, and different levels of human activity: Cumbres and Cuixmala (Figure 1). Cumbres is the main portion of the reserve, with peaks and valleys ranging between 100 to 400 meters above the sea level. The dominant vegetation type is the TDF with occasional areas of SF and AF along the edges of seasonal streams. Human activity at Cumbres is minimum and there are no permanent water sources. The second study site, Cuixmala, is in the southeastern portion of the reserve and includes wetlands on the coastal plain of the Cuixmala River. Dominant vegetation is also TDF, but there are 8 other vegetation types associated with the wetlands. This site also contains agricultural land with permanent water sources in the form of natural and artificial lagoons, channels, and the Cuixmala River.

Methods

The field work was conducted between August 1994 and September 1997. To study the Coati, individuals were captured using Tomahawk live traps baited with sardines. Trap were set where coatis or evidence of their presence (e.g. tracks, scats) were observed regularly. Trapping periods were distributed in four periods of approximately three months: November 1994 to January 1995; late March to early June 1995; October to December 1995; and late March to early June 1996. Fifteen traps were set at each trapping site for 4 to 8 days or until there were no captures for 3 consecutive days. In Cuixmala, traps were set in 17 different sites distributed throughout the area. In Cumbres, trapping started during the second trimester and was carried out at 24 different sites, mostly in the arroyos close to water sources.

All captured animals were sedated with Ketamine in an optimal dose of 16 mg by kilogram of body weight, which gives a 4 -7 minutes induction time and 40-60 minutes of recovering time. Once tranquilized, standard morphometric data were obtained and each coati individual was marked with colored and numbered plastic eartags (Nasco Rototags). Each captured animal was sexed, assigned to a general age category (young, juvenile or adult), and examined to determine ectoparasite load (e.g. mites, fleas, chiggers) on a relative scale from 0 to 5, by inspecting head, back, belly, anterior and posterior legs. A value of zero denotes no ectoparasites, and a value of five means that ectoparasites were detected in all areas of the body, independently of the number of parasites by corporal area.

In order to estimate the coati relative density, visual counts on diurnal walks, were carried out the first week of September, last week of November and first of December 1994; and the first week of March 1995, March 1996 and February 1997. Walks were carried out in rainless days, during periods of maximum coati activity (between 0700 and 1100 hrs and between 1600 and 1900 hrs). Due to the dense vegetation cover in the reserve, walking routes for visual counts, were selected over existing dirt roads and trails in the reserve, choosing the longest sections with less curves. Routes average length was 4 km, and were walked at a speed of 3-4 km / hour.

The following information was recorded for each coati encounter: time, location in route, sex and age category (when possible), angle and distance from the animal to the observer, and perpendicular distance from the animal at first sight to the center of the route. For each observed group, the distance to the closest individual and the number of individuals were recorded. A metric tape and a compass were used to obtain distances and angles. Binoculars were used to obtain ancillary information. Flushing behavior was observed carefully to diminish the possibility of double counting, and all individuals or groups suspected to be a double count were not recorded.

King estimator, with modifications suggested by Glanz (1982, 1990) and by Wright *et al.* (1994), was used to estimate density. This method was selected in order to facilitate the comparison with previous coati density estimates (Wright *et al.*, 1994). King's estimator was calculated as follows: $D = N/ (2\,L\,R)$, where D is the estimation of density of groups or solitary individuals, N is the total numbers of groups or solitary males observed on each walk, L is the route length, and R is the mean distance between animal (or group) and the observer at the moment of encounter. Density of coati groups was obtained and multiplied by mean number of individuals per sighted group to obtain an estimate of coati individuals in group that was combined with the density of solitary animals. Average observed group size was estimated from the diurnal walks data and from occasional observations.

Feeding habits were determined from analysis of faeces collected monthly during the study. Additionally, direct feeding observations were collected and are presented. Faeces were collected in paper bags, dated and marked, then sun dried. Analysis was done in the laboratory by dissecting each sample and inspecting it to identify remains of 5 trophic categories: fruit, arthropods, reptiles, mammals and birds. Diet composition was estimated as the percentage of occurrence of each trophic category. This value is obtained as the number of faeces where the trophic category occurs multiplied by 100 and divided by the number of total occurrences, of all trophic categories for all analyzed faeces.

Two measurements of trophic diversity was estimated, one using Levins (1968) formula for niche breadth: $B = 1/\sum pi^2$, where pi *is the proportion of* each trophic category. The other estimator was the Shannon Diversity Index (Zar, 1984): $H' = (n \log n - \sum fi \log fi)/n$. In wich the number of total occurrences of all trophic categories in all examined faeces was considered as n, therefore the number of faeces where the *ith* category occurs was fi and the logarithm of fi was $\log fi$. Values of B are between 1 and the number of trophic categories considered, values of H' are between 0 (no diversity) to the log of the categories considered (five in this case). Diet composition and trophic diversity values were obtained for all faeces and pooling faeces by season and site. In order to compare this results to other geographical regions, B and H' values were calculated from reported data for Panama (Gompper, 1996), Costa Rica (Sáenz, 1994), Durango, México (Delibes *et al.* 1989), and Arizona, USA (C. Hass in litt.), considering the five trophic categories used in this study.

During all the study period, information about reproduction was obtained by determining reproductive status of captured females (e.g. nulliparous, pregnant, lactating) from occasional field observations (e.g. females with youngs, number of youngs observed, nesting sites and dates, litter size). Information about mortality of coatis, was obtained whenever a dead coati was found, recording date and site of encounter, sex and age category (if feasible), possible cause of death, and all circumstantial evidence for determine it. Published information from other study areas was reviewed, but only data obtained using similar methodology was compared. The Normal approximation to the Mann-Whitney test ($\underline{Z}$ critical value; two tailed, $\underline{\alpha}_{0.05}$) was used to test differences between sexes and between sites in morphometric measurements, ectoparasite load and average observed group size. A Mann-Whitney test ($\underline{U}$ critical value; one tailed, $\underline{\alpha}_{0.05}$) was used to test differences in density estimates between sites. The latitudinal pattern for density was tested using Pearson correlation analysis, as well as the relation of density with precipitation rates at each locality, as an exploration of a possible explanation for the latitudinal trend. Differences between $\underline{H'}$ trophic diversity values were compared with $\underline{t}$-tests modified by Hutchinson (Zar, 1984).

RESULTS

Capture success and morphometrics

From both study sites, excluding recaptures, a total of 146 animals were captured in 4,107 trap-days, with a total capture success of 3.6 %. From those 146 captured animals, 32 were captured at Cumbres in 3,215 trap-days, with an overall capture success of 1 %, and 114 animals were captured at Cuixmala in 892 trap-days with a total capture success of 12.8%.

Adult males were, on average, almost 30% heavier than adult females (Z = 5.545, P=0.000; Males = 5404.1 ± 406.4 g, n = 24; Females = 4185.7 ± 155,1 g, n = 42; data is $\bar{X}$ ± 95 % CI) and nearly 8% larger (total length) than adult females (Z = 5.612, P=0.000; Males = 1200. 6 ± 24.4 mm, n =24; Females = 1102.0 ± 14.9 mm , n = 42).

Density and group size

A total of 314 km of walks were conducted, 165.8 km in the Cuixmala site and 148.8 in the Cumbres site. For each sampling period, density estimates were obtained considering the sum of all routes covered as a sample. Average density was higher in Cuixmala than in Cumbres ($U_{0.05\,(1),\,3,\,4} = 12$; P = 0.05; Table 1). Averaging all estimates, the density value for the reserve as a whole during the study period was 42.9 ± 16.9 ind. / km^2 (Table 1). Density values decreased over the study period in both sites (Table 1).

A correlation analysis between density and latitude, including present estimates and previous reports, yielded a significant negative correlation (r = -0.8458; t = -3.170; P = 0.0296). By using the density value for Cuixmala site alone, the correlation was not significant (r = -0.7833; t = -2.520; P = 0.0594) but when using only the density value obtained for Cumbres, it produced a better adjustment (r = -0.8751; t = -3.616; P = 0.0247). However, due to small sample size (n = 6), power of the two significant correlations was low ($Zb_{(1)}$ = 0.4247 and 0.3520, respectively). Density values do not correlate significantly with precipitation rates, reported for each locality. Nor either using the average value for the CCBR (r = 0.4461; t = 0.9969; P =

0.3752), the value for Cuixmala ($r = 0.3399$; $t = 0.7227$; $P = 0.5098$), or the value for Cumbres ($r = 0.5497$; $t = 1.316$; $P = 0.2584$).

Overall, average group size observed at the reserve was 6.1 ± 0.47 ind. ($n = 165$ sights). Average group size observed did not differ significantly between sites ($Z = 0.712$; $P = 0.4764$; Cumbres = 5.76 ± 0.7 ind., $n = 55$ sights; Cuixmala 6.28 ± 0.6 ind., $n = 110$ sights).

Feeding habits

A total of 130 faeces were collected and analyzed. Collection of faeces was more difficult during the wet season than during the dry season and also in Cumbres than in Cuixmala. Of the identified remains in all faeces, 46.05 % were of fruit, 39.07 % of arthropods, and 14.88 % of vertebrates (6.98 % mammals, 6.51 % reptiles, 1.39 % birds). The most important arthropod remains were from insects of the orders Coleoptera and Orthoptera, while the identified plant remains in the faeces were from *Ficus sp.*, *Guazuma ulmifolia*, *Jacquinia pungens*, *Randia armata*, *Acacia hindsii*, and other legume species (Tables 3 and 4).

Trophic diversity values obtained were $B = 2.674$ and $H' = 1.147$ (Table 4). Inspecting data by season revealed that trophic diversity index (H') was significantly higher during the dry than during the wet season ($t = -2.778$, $v = 56.39$; $P < 0.01$; Table 4). Litter arthropods represented the highest proportion of the Coati diet during the wet season, while fruit was so at the end of the dry season. Vertebrates were much less consumed during the wet season than during the dry season (Table 4).

Due to reduced number of faeces collected in the wet season, differences in diet composition between sites were explored only for the dry season. In Cumbres there was a higher proportion of vertebrates in diet than in Cuixmala during this period (Table 4), but trophic diversity values H' did not differ ($t = 1.951, v = 146; P > 0.05$).

In observation of feeding events, the fruits most commonly consumed were from *Jacquinia pungens*, *Brosimum alicastrum*, *Rechia mexicana*, *Spondias purpurea*, *Jacaratia mexicana*, *Ficus sp.*, *Morisonia americana* and *Guazuma ulmifolia*. Cultivated fruits were also commonly consumed, in particular papaya (*Carica papaya*), coconut (*Cocos nucifera*), banana (*Musa paradisiaca*), mango (*Mangifera indica*), grapefruit (*Citrus paradisi*) and watermelon (*Citrullus vulgaris*; Table 3).

Trophic niche breadth (B) estimated for the CCBR was higher than estimated values for other areas (Table 5). Trophic diversity estimated (H') in the CCBR was higher than estimated values for Panama ($t = 8.643, v = 300.38; P = 0.000$), Costa Rica ($t = 5.70, v = 398.4; P = 0.000$) and Arizona ($t = 4.688, v = 366; P = 0.000$) but similar to the estimated value for Durango ($t = 0.905, v = 157.52; P>0.05$; Table 5).

Reproduction

One arboreal copulation event was observed in early April 1995. From a total of 77 adult females captures (including recaptures) in different months (except February, July and September), only five pregnant females were caught, all in the month of May.

The nest of one female was located in a tree, it gave birth to four kits around the last week of July. Another female, nested two consecutive years in a big flowerpot of a house in Cuixmala. The first year gave birth in late July to three kits and the second year gave birth to four kits in the first week of July.

One of the captured pregnant female was kept in captivity to observe gestation and early growth processes of offspring. Three kits were born in the first week of July, with their eyes closed. At birth, the cubs weighed 100-120 gr, and averaged a total length of 280 mm. After the first week, the kits weighed 195 gr, measured 350 mm in length and opened the eyes. By the fourth week, the young were able to walk and teeth eruption started, the weight was 400 gr and length was 430 mm. By the sixth week, weight was 750 gr and length was 540 mm. The youngs and the mother were released by week 12, weighing 1,100 gr, and measuring 700 mm in length. Based on recapture data, the juveniles reached 2 kg by the first year of age. From a total of 31 youngs captured, only six weighted 2 kg or more and all were trapped between late April and early June, when they are nearly one year of age.

From 13 adult lactating females captured, 10 were captured in late November and early December. Young coatis captured with those lactating females, averaged 1,411 ± 66 g ($\underline{\bar{X}}$ ± 95 % *CI*; $n = 14$). Based on Risser (1963) data on weight gain of captive coatis, a weight of 1,400-1,500 g is achieved around 100 days of age, hence, birth date for captured young coatis of this weight, could be estimated around mid August.

Ectoparasites and some mortality factors

Ectoparasite load differed significantly between sites (Z=2.312; P = 0.0208), with a higher average load rating (1.05 ± 0.192, n= 78 individuals; $\underline{\bar{X}}$ ± 95 % *CI*) in Cuixmala site, than in Cumbres site (0.434 ± 0.286, n= 23 individuals). Overall, the average ectoparasite load (0.91 ±

0.203; n = 101 individuals) was relatively low with respect to maximum possible value (5). As expected, ectoparasite load was higher in Cuixmala, where estimated density was also higher.

A total of 31 death coatis were recorded, 13 in Cuixmala, 15 in Cumbres and three in the main road. Twenty eight were found in the dry season months. Ten could be attributable to diseases, eight to predation, three were animals killed by vehicles in the main road on the eastern limit of the reserve, and 10 were of unknown causes. Of those animals whose death was attributable to diseases, seven showed a severe scabies infestation, with almost no fur present, and a general thinning. The remaining three animals were captured presenting low locomotion coordination, irritated eyes with signs of infection, a weak appearance and no alert behavior in response to human presence; they died closely after capture. A veterinarian inspected them, and suggested that it could be canine distemper, but laboratory confirmation could not be obtained.

Of the eighth animals killed by predators, three were so by unidentified predators and five by jaguars. All these five animals were marked with radio-transmitters and hence their radios and their remains: a pile of hair, no skull remnants or only very small pieces, and in one case half mandible and a portion of the tail, could be found. Nine out of 10 of the coatis that died because of diseases were recorded in Cuixmala, while seven out of eight of the coati predation events occurred in Cumbres.

DISCUSSION

Capture success and morphometrics

Lower capture success in Cumbres can be explained by the lower coati in this site. Weight and total length of coatis in this study are similar to average values reported for Panama (males: 5100 g and 1142 mm, n = 51; females = 3700 g and 1037 mm, n = 37; Gompper, 1996) and Arizona (males: 4800 g and 1256 mm, n = 15; females: 4000 g and 1199 mm, n = 30; C. Hass in litt.) in the southern and northern extremes of its distribution, respectively. This suggests that latitudinal variation in body measures is not very marked. The largest weight recorded was 9000 g for a male captured in Cuixmala. This male was seen repeatedly in a zone near the beach where sea turtle eggs is a temporally abundant resource (rich in protein and fat) available for the Cuixmala coatis.

Density and group size

Density estimates in the CCBR support the initial prediction, density was lower than in Panama (Gompper, 1997) and greater than in Arizona (C. Hass in litt.). However, it is necessary to point out that a limitation of present estimates is the small sample size, that increased variation in density estimates. The proposed inverse relationship between coati density and latitude was supported here with the results of the correlation analysis. A proposed explanation for this pattern is that is related to differences in precipitation rates, which in turn influence resource abundance, particularly food. However, precipitation alone does not seems to explain properly the latitudinal pattern. This requires more detailed information about coati densities and the spatio-temporal abundance of food resources, as well as information about other ecological factors (as predation rates for example), throughout distribution range of the species.

Interestingly, in the Cuixmala site, where food and water abundance is higher and spatio temporally less dispersed (e.g., there are nearly 130 hectares of fruit plantations and several permanent lagoons), estimated density is similar to values from the southern range of the species.

Also, as expected, is higher than at the Cumbres site, where food and water are severely limited during the dry season. This reflects, on a smaller scale, the expected pattern. The higher density in Cuixmala could also be an effect of food supplementing, a common practice of local inhabitants before the reserve was established, in order to attract the coati groups for touristic activities. There are reports of feeding congregations of more than 70 coatis in the sites where food was provided.

High coati density fluctuations have been reported as a result of changes in food availability (Kaufmann, 1962) or diseases (Risser, 1963). In this study, the decline in density over the study period could be explained partially by the impact of the 1994 -1995 dry season, and by the effects of the outbreak of scabies detected in Cuixmala (Valenzuela, 1999).

Feeding habits

Results from the faeces analysis showed that coatis at the CCBR consumed predominantly fruit (46.05 %) and litter arthropods (39.07%). This is similar to what has been reported in other sites, using the same methodology, but there are differences in the percentage of those resources in the diet and in the trophic diversity values. Fruit plus litter arthropods were 100 % of the diet (63.3% and 36.7% respectively; n = 86 scats) in Panama (estimated from Gompper, 1996); 97% (46.8 % and 50.2 %; n= 194 scats) in Costa Rica (Sáenz, 1994); 88.1% (37 % and 51.1%; n = 87) in Durango, México (Delibes et al., 1989); and 97.5 % (53.1% and 44.37%; n = 92) in Arizona, USA (estimated from C. Hass in litt.).

Trophic diversity at the CCBR reserve was higher than for other regions. This might be related to the high climatic seasonality at the reserve that affects the predictability and availability of food resources. Litter arthropods are as much as three times more abundant in the wet season than in the dry season (Lister and García, 1992; Valenzuela, 1999), and a fruiting peak is reported in the CCBR during the dry season (Bullock and Solís-Magallanes, 1990). Although, differences between sites were found, and fruit was more abundant in the dry season, only in Cuixmala (Valenzuela, 1999).

Theory on feeding strategies predicts that food niche breadth will increase as the absolute abundance of food decreases (Schoener, 1971). This seems to be the case in the reserve, where trophic diversity was lower during the wet season and increased as the dry seasons progressed, reaching the highest value at the end of the dry season (Table 4). While vertebrates represented less than 10 % of the diet during the wet season, by the end of the dry season this percentage rises to nearly 20 %. Aside from this, consumption of litter arthropods decreased, and consumption of fruit increased during the dry season, compared to the wet season values (Table 4). This seasonal changes in diet may be explained by the seasonal differences in food availability explained above.

Reproduction

Gestation period in coatis is 70-77 days (Gompper, 1995), hence, based on all this observations, breeding seems to occur between late March and late April, with births occurring between late June and the middle of August, during the early wet season. This it is similar to reported data for Arizona, where most of the births occurred by late June (C. Hass in litt.) and for Chihuahua, Sinaloa and Guerrero in México, where births have been observed between June and September (Leopold, 1959). In Panama and Costa Rica, births occurred between April and early May (Gompper, 1995) and parturition coincided with the period of higher availability of fruit (Russell, 1982; Smythe, 1970). In the present study, parturition coincided with the onset of the wet season, where water is not limited and arthropods availability reaches its maximum level (Lister and García, 1992). This is a common strategy of many other vertebrates in seasonal environments in order to increase the survival probabilities of newborns (Ceballos, 1996; Wolda, 1988).

Ectoparasites and some mortality factors

In the case of coati diseases in the area, some individuals carrying rabies antibodies were identified in both study sites, indicating that this coati population has been exposed to the disease (J.A. Montaño, in litt.). Also, some of the recorded deaths of coatis could be attributable to canine distemper, a disease that has caused population decreases in other areas (Risser, 1963).

Pathogens and parasites could become a density dependent factor of mortality and a management and conservation problem (Aguirre and Starkey, 1994; Holmes, 1996; May, 1988). The dispersion of a disease or parasite is determined by a combination of factors, that includes: individual susceptibility, how many individuals are affected and how intensely, and the rate of contact between vectors (Holmes, 1996). In the present study the estimated ectoparasite load was greater and more animals that died by diseases were detected at Cuixmala, where estimated density was also higher.

On the other hand, in Cumbres, where estimated density was lower, ectoparasite load was also lower. Only one out of eight death animals found there, was attributed to a disease, and the other seven were classified as killed by predators. This suggests a higher predation rate in Cumbres, something that is under further exploration but that receives some support from an ongoing jaguar an puma research in the CCBR. This research on cats revealed from scat analyses, that in Cumbres, up to 20 % of jaguar's diet consisted in coati (Núñez, 1999). A high jaguar or puma predation on coatis had been reported for other sites (C. Hass in litt.; Aranda, 1993).

Most of the death records of coati were from dry season months, a period of food and water shortage that should impose severe constraints for the organisms survival. This could be even worse in drier years, as it was 1994, with an atypical wet season (in which rainfall was less than half of the annual average), followed by the 1994 -1995 extremely dry season. More than half of the total death records of coatis, were found during this period. In Panama, the peak of mortality of adult and sub-adult coatis was during the dry season and it was attributable to predation and declining food availability (Russell, 1982; Milton, 1990).

The present study supports the latitudinal trend in density values, however it also showed that density could differ substantially even between two sites in the same latitudinal area. This variability in density could be attributable at least in part, to differences in resource availability, as seem to be the case for the difference between Cumbres and Cuixmala sites that mainly differ, precisely, in resource availability. Present results also showed that in the CCBR coatis have similar feeding habits and reproductive behavior to those reported in the edges of its distribution range.

Further research is required into the effect of climatic seasonality on the ecology of coatis in other sites of México, and in general on the impact of this environmental factor on the ecology of vertebrates. In the case of social carnivores, the study of this effect it is of particular interest because of the relation between resource dispersion and sociability, for this purpose the coati is an ideal species.

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LITERATURE CITED

Aguirre, A. A. and E. E. Starkey. 1994. Wildlife diseases in U.S. National parks: historical and coevolutionary perspectives. Conservation Biology 8: 654-661.

Aranda, M. 1993. Hábitos alimentarios del jaguar (Panthera onca) en la Reserva de la Biosfera de Calakmul, Campeche. Pp. 231-238 in Avances en el estudio de los mamíferos de México. (R. Medellín, R. y G. Ceballos, eds.). Publicaciones Especiales, Vol. I, Asociación Mexicana de Mastozoología, A. C. México, D.F., México. 1: 1-464.

Bullock, S. H. 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of México. Archives for Meteorology, Geophysics, and Bioclimatology 36: 297-316.

Bullock, S. H. and J. A. Solis-Magallanes. 1990. Phenology of canopy trees of a tropical deciduous forest in México. Biotropica, 22 : 22-35.

Burger, J. and M. Gochfeld. 1992. Effect of group size on vigilance while drinking in the coati, Nasua narica in Costa Rica. Animal Behavior 44: 1053-1057.

Caso, A. 1994. Home range and habitat use of three neotropical carnivores in northeast México. Unpublished MS thesis. Texas A & M University, Kingsville. 86 pp.

Ceballos, G. 1996. Vertebrate diversity, ecology, and conservation in neotropical dry forests. Pp. 195-220. in Seasonally dry tropical forests (S.H. Bullock, H. A. Mooney and E. Medina, eds.). Cambridge University Press, Cambridge, UK. 450 pp.

-----. and A. García. 1995. Conserving neotropical biodiversity: the role of dry forests in western México. Conservation Biology 9: 1349-1356.

-----. and A. Miranda. 1986. Los Mamíferos de Chamela, Jalisco. Instituto de Biología, Universidad Nacional Autónoma de México. México, D. F. 436 pp.

Coates-Estrada, R. and A. Estrada. 1986. Manual de identificación de campo de los mamíferos de la Estación de Biología "Los Tuxtlas". Instituto de Biología, Universidad Nacional Autónoma de México, México, D. F., 151 pp.

Delibes, M., L. Hernández, and F. Hiraldo. 1989. Comparative food habits of three carnivores in Western Sierra Madre, México. Zeitschrift Säugetierkunde 54:107-110.

Estrada, A., G. Halffter, R. Coates-Estrada and D. A. Merritt. 1993. Dung beetles attracted to mammalian herbivore (Allouatta palliata) and omnivore (Nasua narica) dung in the tropical rain forest of Los Tuxtlas, México. Journal of Tropical Ecology 9: 45-54.

Glanz, W. E. 1982. The terrestrial mammal fauna of Barro Colorado Island: censuses and long-term changes. Pp. 455-468, in The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes (E.G. Leigh, A.S. Rand and D. S. Windsor, eds.) 2nd. Printing. Smithsonian Institution. Washington, D.C.

-----. 1990. Neotropical mammal densities: how unusual is the community on Barro Colorado Island, Panama?. Pp. 287-313, in Four Neotropical rainforests. (A.H. Gentry, ed.). Yale University Press. New Haven, CT, USA.

Gompper, M. 1994. The importance of ecology, behavior, and genetics in the maintenance of coati (Nasua narica) social structure. Ph D dissertation. Knoxville: University of Tennessee. 238 Pp.

-----. 1995. Nasua narica. Mammalian Species No. 487: 1-10

-----. 1996. Sociality and asociality in white-nosed coatis (Nasua narica): foraging costs and benefits. Behavioral Ecology 7: 254-263.

-----. 1997. Population ecology of the White-nosed coati (Nasua narica) on Barro Colorado Island, Panama. Journal of Zoology (London) 241: 441-455.

Holmes, J. C. 1996. Parasites as threats to biodiversity in shrinking ecosystems. Biodiversity and Conservation 5: 975-983.

Kaufmann, J. H. 1962. Ecology and social behavior of the coati, Nasua narica on Barro Colorado Island, Panama. University of California Publications, Zoology, 60: 95-222.

Kaufmann, J. H., D. V. Lanning and S. E. Poole. 1976. Current status and distribution of the coati in the United States. Journal of Mammalogy 57: 621-637.

Lanning, D. V. 1976. Density and movements of the coati in Arizona. Journal of Mammalogy 57: 609-611.

Leopold, S. A. 1959. Wildlife of México. University of California Press. Berkeley, California, USA. 568 pp.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princetown University Press, Princetown, USA. 120 pp.

Lister, B. C. and A. García. 1992. Seasonality, predation, and the behavior of a tropical mainland anole. Journal of Animal Ecology 61: 717-733

May, R. 1988. Conservation and disease. Conservation Biology 2: 28-30

Milton, K. 1990. Annual mortality patterns of a mammal community in central Panama. Journal of Tropical Ecology 6: 493-499.

Núñez, R. 1999. Hábitos alimentarios del jaguar (Panthera onca, Linnaeus 1758) y del puma (Puma concolor, Linnaeus 1771) en la Reserva de la Biosfera Chamela-Cuixmala, Jalisco, México. Bachelor Thesis, Universidad Michoacana de San Nicolas Hidalgo, Morelia, Michoacán, México.

Ratnayeke, S., A. Bixler and J. L. Gittleman. 1994. Home range movements of solitary, reproductive female coatis, Nasua narica, in south eastern Arizona. Journal of Zoology (London) 233: 322-326.

Risser, A. C. Jr. 1963. A study of the coatimundi (Nasua narica) in southern Arizona. M.S. Unpublished thesis, University of Arizona, Tucson. 77 pp.

Russell, J. K. 1982. Timing of reproduction by coatis (Nasua narica) in relation to fluctuations in food resources. Pp. 413-431, in The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes. (E. G. Leigh, A. S. Rand and D. S. Windsor, eds.). 2nd. Printing. Smithsonian Institution. Washington, D.C.

Sáenz, J. 1994. Ecología del pizote (Nasua narica) y su papel como dispersador de semillas en el bosque seco tropical, Costa Rica. Tesis de Maestría en Manejo de Vida Silvestre. Universidad Nacional, Costa Rica. 186 pp.

Schoener, T. W. 1971. Theory of feeding strategies. Annual review of Ecology and Systematics 2: 369-404.

Smythe, N. 1970. The adaptive value of the social organization of the coati (Nasua narica). Journal of Mammalogy, 51: 818-820.

Valenzuela, D. 1999. Efectos de la estacionalidad ambiental en la densidad, la conducta de agrupamiento y el tamaño del área de actividad del coati (Nasua narica) en selvas tropicales caducifolias. Tesis Doctoral. Instituto de Ecología, UNAM.

Vaughan, C. and M. McCoy, 1984. Estimación de las poblaciones de algunos mamíferos en el Parque Nacional Manuel Antonio, Costa Rica. Brenesia 22: 207-217.

Wolda, H. 1988. Seasonality and the community. Pp. 69-95. in The organization of communities (J. H. Gee and P. S. Giller, eds.). Blackwell Scientific Publications, Oxford, UK.

Wright, S. J., M. E. Gompper and B. DeLeon. 1994. Are large predators keystone species in Neotropical forests?: The evidence from Barro Colorado Island. Oikos 71: 279-294.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice Hall, New Jersey, USA. Pp. 717.

Table 1. Data obtained in transect lines for visual count of coatis to estimate its density. Transect length (L), total number of encounters of groups (NG) and solitary males (NM), group and male sighting rates per km (GSr and MSr), average distance between animal (or group) and the observer at the moment of encounter ®, density estimates (ind / km^2) for groups (DG) and for solitary males (DM) and total estimates (DT). Average observed group size used in density estimates was 6.1 individuals per group.

Site	Period	L (km)	NG	NM	GSr	MSr	R (m)	DG	DM	DT
Cuixmala	Sep-94	40	11	11	0.275	0.275	15	9.17	9.17	65.08
	Nov-Dec 94	45	14	5	0.311	0.111	15	10.37	3.70	66.96
	Mar-95	38.1	12	5	0.315	0.131	22	7.16	2.98	46.65
	Feb-97	42.7	7	2	0.164	0.047	12	6.83	1.95	43.62
Cumbres	Mar-95	79.1	11	1	0.139	0.013	14	4.97	0.45	30.75
	Mar-96	29	4	3	0.138	0.103	17	4.06	3.04	27.79
	Feb-97	40.7	5	0	0.123	0.000	27	3.23	0.00	19.72
Cuixmala	$\bar{X}$ ± 95% CI									55.58 ± 19.33
Cumbres	$\bar{X}$ ± 95% CI									26.85 ± 14.18
Reserve	Both sites $\bar{X}$ ± 95% CI									42.94 ± 16.88

Table 2. Published data on density and group sizes of the White-nosed coati. TRF = Tropical Rain Forest; TDF = Tropical dry forest; TSF = Tropical Semideciduous Forest; XS = Xerophitic Shrubland ; POF = Pine Oak Forest. Lat. = Latitude; D = density value as ind / km²; Group size is average number of individuals observed per group.

Site	Lat.	Rain (mm)	Vegetation	D	Group size	Reference
Barro Colorado Island, Panama	9° 9'	2,600	TRF	55.6	7.2	Wrigth et al., 1994
Manuel Antonio, Costa Rica	9° 45'	3,000	TRF	70	-	Vaughan and McCoy, 1984
Palo Verde, Costa Rica	10° 20'	1,750	TDF	-	5.4	Burger and Gochfeld, 1992
Santa Rosa, Costa Rica	10° 45'	1,600	TDF, TSF	-	-	Saenz, 1994
Tikal, Guatemala	15°	1,350	TRF	20	-	Glanz, 1990
Los Tuxtlas, México	18° 30'	4,900	TRF	33	22.5[1]	Coates-Estrada and Estrada, 1986
CCBR, México	19° 30'	780	TDF	42.4, 26.8, 55.6++	6.1	Present Study
Tamaulipas, México	23° 27'	927	XS	-	-	Caso, 1994
Durango, México	23° 27'	600	POF	-	-	Delibes et al., 1989
Arizona, USA	32°	466	XS / POF	1.2-2	-	Lanning, 1976
Arizona, USA	32°	466	XS / POF	1.7		C. Hass, in litt.

[1] Estrada et al., 1993

++These are the values on average for the reserve, for the Cumbres site and for the Cuixmala site, respectively.

Table 3. Food items of coatis in the Chamela-Cuixmala Biosphere Reserve based on occasional observations of feeding events. Cx = Cuixmala, Cm = Cumbres; TDF = Tropical dry forest, AF = Arroyo Forest, AL = Agriculture Land, SEF= Semi-Evergreen Forest.

1) Fruit (family and species)	Habitat	Site	# Obs.
Caricaceae			
Jacaratia mexicana	TDF, AF	Cm	1
Carica papaya	AL	Cx	9
Moraceae			
Ficus insipida	SEF	Cx	3
Ficus cotinifolia	TDF,SEF	Cx,Cm	12
Brosimum alicastrum	SEF,AF	Cm	6
Rosaceae			
Licania platypus	AL	Cx	4
Capparidaceae			
Morisonia americana	AF,TDF	Cx, Cm	5
Anacardiaceae			
Spondias purpurea	TDF	Cx, Cm	2
Mangifera indica	AL	Cx	7
Sterculiaceae			
Guazuma ulmifolia	TDF, AF	Cx, Cm	12
Simaroubaceae			
Rechia mexicana	TDF, AF	Cm	2
Theophrastaceae			
Jacquinia pungens	TDF, AF	Cm	6
Palmae			
Cocos nucifera	AL	Cx	20
Musaceae			
Musa paradisiaca	AL	Cx	6
Auraniaceae			
Citrus paradisi	AL	Cx	3
Cuccurbitaceae			
Citrullus vulgaris	AL	Cx	3

Table 3. Feeding habits of coatis…continues

2) Animals	Habitat	Site	# Obs.
Tarantulas	TDF	Cm	2
Scorpions	TDF	Cx, Cm	2
Grasshoppers, Crickets	SEF, AF	Cx, Cm	6
Crabs	TDF	Cm	3
Sea Turtle Eggs	Beach	Cx	8

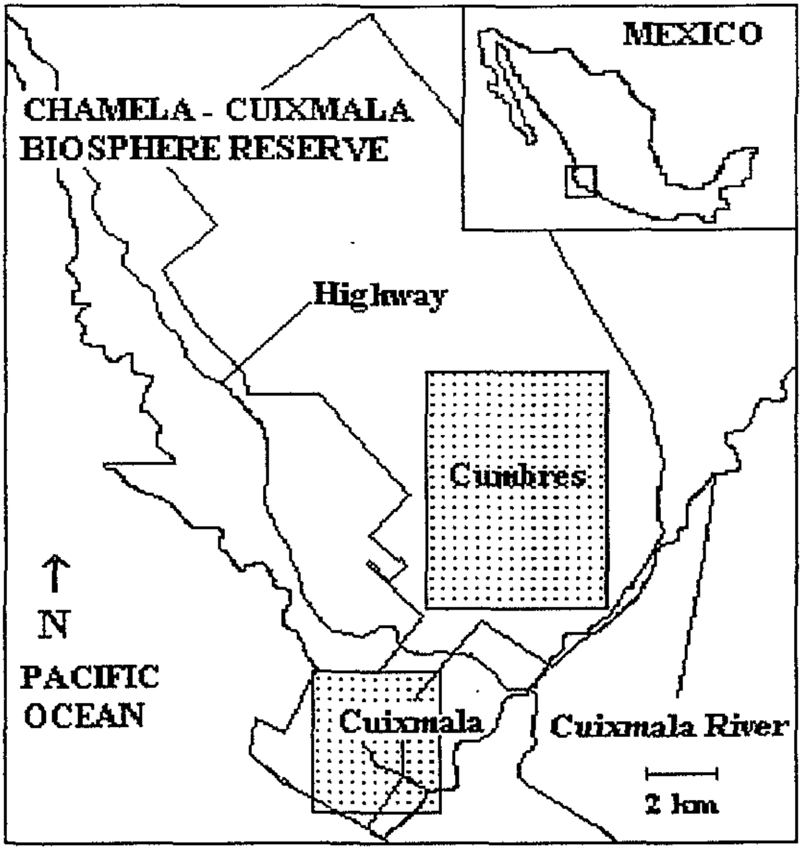
Table 4. Feeding habits of coatis in the Chamela-Cuixmala Biosphere Reserve based on analysis of 130 faeces collected over one year. Data is the percentage of occurrence = number of faeces where the ith trophic category (number in parenthesis) by 100 / sum of occurrences of all faeces. B is the trophic niche breadth and H'. is trophic diversity using Shannon Diversity Index. Faeces were pooled by seasons, sites and year (Total). Seasons are: wet season (July-October), dry season (November-June).

Food Category	Total (n = 130)	Wet season (n =19)	Dry season (n = 111)	Cuixmala Dry season (n = 74)	Cumbres Dry season (n = 37)
Fruit	46.05 (99)	41.94 (13)	46.74 (86)	47.54 (58)	45.16 (28)
Arthropods	39.07 (84)	51.61 (16)	36.96 (68)	40.98 (50)	29.03 (18)
Mammals	6.98 (15)	0 (0)	8.15 (15)	4.92 (6)	14.52 (9)
Reptiles	6.51 (14)	6.45 (2)	6.52 (12)	4.92 (6)	9.68 (6)
Birds	1.39 (3)	0 (0)	1.63 (3)	1.64 (2)	1.61 (1)
Sum	100 (215)	100 (31)	100 (184)	100 (122)	100 (62)
B	2.674	2.240	2.730	2.506	3.135
H'	1.1475	0.8826	1.1729	1.0828	1.2907

Table 5. Coati trophic diversity values based on scat analysis. B = Levin's trophic niche breadth (1968), H' = Shannon Diversity Index. Values for Panama (Gompper, 1996), Arizona (C. Hass, in litt.), Durango (Delibes et al., 1989), and Costa Rica (Saenz, 1994) were calculated from data presented by the authors, considering five trophic categories: fruit, arthropods, mammals, reptiles and birds.

Site	Dominant Vegetation	B	H'
Barro Colorado Island, Panama	tropical rain forest	1.868	0.6575
Santa Rosa, Costa Rica	mixture of disturbed and undisturbed tropical dry and semideciduous forests	2.063	0.7795
La Michilía, Durango, México	oak-pine forests	2.464	1.054
Arizona, USA	xerophitic shrubland and oak-pine forests	2.086	0.8143
This study	tropical dry and semideciduous forests	2.674	1.1475

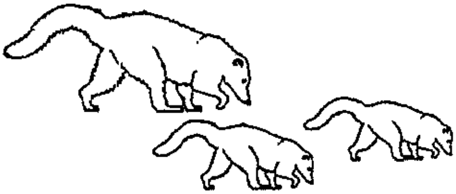
Figure 1. Localization of the Chamela-Cuixmala Biosphere Reserve and of the Cumbres and Cuixmala study sites.



CAPITULO II

HABITAT SELECTION, HOME RANGE AND ACTIVITY IN THE WHITE-NOSED COATI, *Nasua narica*, IN A MEXICAN TROPICAL DRY FOREST

(Escrito en el formato de Journal of Mammalogy)



HABITAT SELECTION, HOME RANGE AND ACTIVITY OF THE WHITE-NOSED COATI, *NASUA NARICA*, IN A MEXICAN TROPICAL DRY FOREST

[1]David Valenzuela and Gerardo Ceballos

Instituto de Ecología, UNAM, A. P. 70-270, Ciudad Universitaria,
México, D. F., C. P. 04510, MÉXICO *(DV, GC).*
Fundación Ecológica de Cuixmala, A. C., A. P. 161, San Patricio Melaque,
Jalisco, C. P. 48980, MÉXICO *(DV, GC)*

[1]Actual address: CEAMISH, UAEM, Av. Universidad No. 1001, Col. Chamilpa, CP 62210, Cuernavaca, Morelos, MÉXICO. E-mail: dvalen@buzon.uaem.mx

We investigated how white-nosed coatis (*Nasua narica*) cope with the extreme seasonality of a Mexican tropical dry forest by studying their activity, home ranges, and habitat selection in relation to climatic seasonality. From November 1994 to March 1997, we radio-tracked 7 solitary adult males and 11 bands of females and juveniles. Males extended their activity more into night hours, presented a higher intensity of activity in both the dry and the wet seasons, and traveled a greater daily distance during the wet season than bands. Average total home range was 383.0 ± 32.86 ha ($\overline{X} \pm SE$), and did not differ between sexes. Home ranges differed seasonally only in bands which used areas twice as large during the dry season than during the wet season. Three major habitats that differed in phenology were used by coatis. Both males and bands preferred arroyo forest to dry forest and semideciduous forests. These results illustrate the importance of the behavioral traits that permit coatis to have access to habitats where sparse resources (e. g. food and water) have a higher availability, as a mechanism to cope with climatic seasonality. Our study provided a basis to help the design of management and conservation strategies for the Chamela-Cuixmala biosphere reserve. This coati population may act as a model for predict the type of behavioral responses that other coati populations may present to cope with climatic seasonality other tropical dry forest throughout México and Central America.

Key words: coati; *Nasua narica*; México; activity, home ranges, habitat selection, tropical dry forest; climatic seasonality.

RUNNING HEAD: Habitat selection, home range, and activity in coati

Tropical dry forests of western México are among the most seasonal tropical environments. These forests experience a marked phenological seasonality mainly related to the amount of rainfall. During the dry season, which lasts from four to eight months, almost all plants shed their leaves, and many disperse their seeds (Bullock and Solis-Magallanes, 1990). The effects of such phenological changes on microclimatic conditions and availability of food resources are profound (Ceballos, 1995; Janzen and Schoener, 1968; Lister and García, 1992). Mammal species have different strategies to cope with environmental seasonality, that include local and regional movements, changes in activity patterns, shifts in diet, seasonal accumulation of fat or food resources, and physiological adaptations to cope with the lack of water (Ceballos, 1995; Ceballos and Miranda 1986; Fleming, 1977; Janzen and Wilson 1983; Wilson, 1971).

In this paper we present data on habitat selection, activity patterns and home range size in the white-nosed coati (*Nasua narica*), to understand how this species respond behaviorally to the effects of climatic seasonality in a tropical dry forest in Western México. We choose to study this species because it is the most abundant carnivore in the region, it is diurnal, and it is the most social Neotropical carnivore. Adult females live in groups (hereafter called bands) of up to 30 individuals that include adult females and subadults of both sexes. Adult males are solitary. Coatis are omnivorous and eat mainly invertebrates and fruits (Gompper, 1995); in our study site fruits and arthropods represent 85 % of their diet (Valenzuela, in press). Home range size and activity of coatis are affected by seasonal changes in resource availability, and both parameters tend to increase where or when resources are sparse, such as during the dry season (Gompper, 1997; Hass, in litt.; Russell, 1982; Saenz, 1994). Previous studies in tropical forests have found that, home range sizes in males and bands do not differ, and they usually overlap considerably (Gompper, 1997; Kaufmann, 1962; Ratnayeke *et al.*, 1994; Saenz, 1994). Reproductive energetics could affect too movements and size of home ranges. Pregnant females leave bands temporarily to give birth and during nesting season they used smaller home ranges (Ratnayeke *et al.*, 1994). Also, it had been previously noted that males could be more active at night than females (Smythe, 1970).

In our study site we have defined three types of habitats. The dominant habitat, tropical dry forest and two more humid and more productive forests the semideciduous forests and the arroyo forests, which are distributed in small patches or stripes across the area. Humid habitats may be a key resource during the dry season when water availability is extremely limited. Based on the climatic and plant conditions of our study site we made several predictions. First, we expected to find seasonal differences in activity patterns, with larger daily distances traveled and higher intensity of activity in the dry season when compared with the wet (i.e. rainy) season. Second, we predicted that home range size would vary seasonally, with larger sizes during the dry than in the wet season, and no differences between sexes. We also anticipated an extensive home range overlap in both sexes. Finally, we expected that coatis should exhibit habitat selection, by including the humid habitats in their home ranges in a larger proportion than expected by chance.

METHODS

Study site

The Chamela-Cuixmala Biosphere Reserve is located on the coast of Jalisco, México, between 19°22' and 19°35' N, and 104°56' and 105°03' W (Fig. 1, in page 45). The reserve comprises 13,141 hectares, with topography of hills and coastal floodplains from sea level up to 400 m of elevation. Our study was done in the central part of the reserve, known as Cumbres (Fig. 1, in page 46), a hilly terrain where tropical dry forest is the dominant vegetation type. Climate is strongly seasonal with rainfall concentrated from late June to October, followed by a prolonged drought, with no rain at all, from November to early June. Annual average rainfall in the reserve varies between 700 mm and 1000 mm. Annual average temperature is 24.9 °C (Bullock, 1986). Ceballos and García (1995) give a detailed description of the reserve.

Capture and radio-tracking

Coatis were captured using Tomahawk live traps baited with sardines. Radio-transmitters (HLPM-2140; HLPM-2140A, with activity sensor; HLPM-3140; 164.000 MHz; Wildlife Materials, Inc.) were fitted to 11 adult females from equal number of bands (based on home ranges and distance between females in simultaneous locations), and to 7 adult solitary males. Radiotelemetry data was collected from November 1994 to March 1997. Signal of radio-collared animals were located at least twice a week and during 12 hr monitoring sessions, with the use of handheld radio-telemetry equipment and three fixed receiving stations (peak-null systems, with eleven element antennas; AVM, Inc.) located on the highest points of the reserve. Location error of these stations was determined to be on average < 2 degrees, and signals as far as 8 kilometers could be received clearly. The average error polygon of the radio-locations was 3.60 ± 0.26 ha ($\overline{X}$ ± 95 % *CI*; *n* = 1070). Coati activity patterns and locations were determined during 18 nocturnal (from 1900 hr to 0800 hr) and 18 diurnal (from 0800 hr to 2100 hr) monitoring sessions, carried out between January and November 1995, when we had 10 radio-collared individuals simultaneously. Every 30 minutes, during the monitoring sessions, we recorded the presence or absence of all the signals, the azimuths, and if the animal was active or inactive. A coati was considered active if the activity sensor indicated so, or in the case of transmitters without activity sensor, if the intensity of its signal varied constantly during a 30-second interval. Therefore, the active condition could indicate traveling on the ground as well as other activities without substantial displacement as grooming or movements in a tree. We analyzed the components of activity in three different ways: (1) *daily pattern*, determined from the frequency distribution of the proportion of individuals active per hour intervals, throughout the day (2) *intensity*, determined as the proportion of active locations over the total number of locations for each hour. (3) *daily distance traveled* by individual coatis, measured as the sum of all distances between consecutive points in a complete 12 hr diurnal session. Data were analyzed by sex, seasons, and for all tracking sessions considering as a sample each complete sequence of consecutive points.

Locations of the coatis were obtained by triangulation, plotted on a map of the area and scanned into a map file for use with telemetry software. Radio-telemetry data were processed with the TRITEL program (Biggins *et al.*, 1992) and analyzed with the TRACKER program (Camponotus, 1994) to calculate daily distance of movements and home ranges. Each individual sequence of points from complete 12 hr diurnal sessions was considered a sample to estimate the average daily distance. For home range calculations, we determined statistical independence of successive telemetry locations (Swihart and Slade, 1985) and it was achieved with 4-hour intervals. From each total point sequence, total home ranges were estimated using Minimum Convex Polygons (MCP; Mohr, 1947), removing the outer 5% locations to exclude possible outliners (White and Garrott, 1990). Because of its relevance for animal movements, we also estimated seasonal home ranges during the two climatic seasons and also in four biological periods: mating period (April), gestation period (May--June), nesting period (1 July--15 August), and non-reproductive period (16 August--31 March).

We evaluated habitat selection as the distribution of animal locations in each habitat type in relation to habitat availability, during certain periods of time. We defined our study area by plotting in a map of the area (1:50,000), all independent radio-locations for all coatis, and obtaining an MCP of these locations. Then we superimposed a 200 by 200-m cell grid on this map. A total of 744 cells were included inside the polygon or crossed by the polygon line and were assigned to habitat type. We considered the proportion of these 744 cells, classified on each habitat category, as the habitat availability in the study area. Based on vegetation maps of the area, three habitat types were defined: 1) the dominant tropical dry forest (TDF), that covered most of the area. 2) The semideciduous forest (SF) which was found in small patches in areas with relatively high humidity. 3) The arroyo forest (AF), a plant community very similar to SF but distributed as a stripe along main water drainages; we considered a 60-m width on average to define this particular plant community. A cell was assigned to TDF or SF habitats when more than half of the cell was covered by that vegetation and to AF when the band of that vegetation crossed the cell completely. The same procedure was used to estimate habitat availability in each home range but using the 95% MCP home range obtained from all the independent radio-locations of each studied animal. Habitat selection was evaluated at gross and fine scales or approximations (equivalent to the broad view of an animal's requirement and to the detailed view of resource use, respectively; Aebisher *et al.*, 1993). At a gross scale, we compared if home ranges included the three habitats in the same proportion of their availability in the whole study site. At a fine scale we estimated if locations of coatis were distributed among habitat types randomly, or if locations tended to be congregated in certain areas.

Differences between sexes and seasons in daily pattern of activity were evaluated with the Kolmogorov-Smirnov test, and differences in intensity of activity were evaluated using the Sign Test. Differences between sexes and seasons in daily distance traveled and in home range size were evaluated with *t*-tests and with analysis of variance. Selection of habitats was assessed with *G*-tests and Bonferroni simultaneous confidence intervals (Alldredge and Ratti, 1986; Byers *et al.* 1984; Neu *et al.*, 1974). All tests were two tailed at the 0.05 level of significance.

RESULTS

Activity

Of the 3,524 telemetry locations available for analysis of activity, 2,494 were for females and 1,030 for males. Coatis were mostly active during the day, with some activity at night (Fig. 2a). As expected, daily patterns of activity statistically differ between males and bands, because males exhibited more nocturnal activity (Kolmogorov-Smirnov test, $D = 0.08$, $P = 0.0004$; Fig. 2a). Daily pattern of activity in bands did not differ between seasons ($D = 0.03$, $P = 0.544$; Fig. 2b). Interestingly, males exhibited differences between seasons, and showed a higher concentration of activity during the day in the wet season ($D = 0.06$, $P = 0.0112$; Fig. 2c).

The intensity of activity (Sign Test; $P = 0.2706$; Fig. 2c), and the daily distance traveled (wet season: 4588 ± 693.24 m, $n = 6$; dry season: 4268 ± 450.8 m, $n = 11$; $t = 0.404$, *d.f.* = 15; P

= 0.6922) did not differ seasonally in males. In contrast, there were statistical seasonal lifferences in both parameters in bands. Intensity of activity decreased during the wet season (P = 0.008; Fig. 2b), when bands also traveled less distance by day than during the dry season (2299 ± 187.3 m *vs* 3912 ± 310.5 m, respectively; $t = 4.11$, *d. f.* = 42; $P = 0.0002$). When comparing nales and bands, there were clear differences because males exhibited a higher intensity of ctivity than bands in both seasons (wet season $P = 0.001$; dry season $P = 0.0113$; Figs. 2b an 2c). Males also traveled a greater daily distance than bands during the wet season (males = 4268 ± 450.8 m, $\bar{X} \pm SE$, $\underline{n} = 11$; bands = 2299 ± 187.3 m, $n = 19$; *t*-test; $t = -4.69$, *d. f.* = 28, $P = 0.0001$).

Home ranges

Home ranges averaged 383.0 ± 32.86 ha for all animals ($n = 17$; Table 1). As expected, no significant differences were found between average size of total home ranges for bands and males ($t = -0.0663$; *d. f.* = 15; $P = 0.948$; Table 1 and Fig. 3). A two-way analysis of variance for seasonal home ranges revealed no difference between sexes ($F_{1,\ 23} = 0.274$; $P = 0.6059$), a significant difference between seasons ($F_{1,\ 23} = 12.569$; $P = 0.0017$), and a no significant interaction of those factors ($F_{1,\ 23} = 0.626$; $P = 0.4368$). Home range size for males did not differ significantly between season. However, home range size for bands during the dry season was greater than both band and males' home range sizes during the wet season ($P < 0.05$).

Interestingly, the average area used during the dry season represented 90 % of the average otal home range. The spatial distribution of total home ranges overlapped extensively in both sexes (Fig. 3). Home range overlapping in bands occurred in 91% (82) dyads, and was on average around 35% of the total home range size. Home range overlapping in males occurred in

53% (16) dyads and was approximately 44 %. Average home range overlap did not differ between sexes (Mann-Whitney test with normal approximation; $Z_{82, 16} = -1.225$; $P = 0.222$).

Bands used on average 329 ± 46 ha ($n = 10$) outside the reproductive period, 218 ± 38 ha ($n = 10$) during gestation period, and 145 ± 19 ha ($n = 6$) during nesting season. A one way analysis of variance revealed a significant difference in areas used during these periods ($F_{2, 23} = 4.75$; $P = 0.01$), and a post-hoc comparison revealed that areas used during nesting season were significantly smaller than those used outside the reproductive period ($P<0.05$). The average area used by males outside reproductive period (336 ± 50 ha; $n = 5$) did not differ of those used by females during the same period ($t = -0.07$; $d.f. = 13$; $P = 0.9$).

Habitat selection

The most abundant vegetation type was TDF (62 %), followed by AF (31 %), and SF (Table 2). Habitat selection in bands and males showed interesting contrasts at different scales. On a gross scale, i.e. when considering habitat composition of home ranges in relation to habitat availability at the study site, bands showed habitat selection. Their home ranges included AF in a higher proportion and SF in a lower proportion than expected by chance; TDF was used in accordance to its availability. Males did not exhibit such pattern (Table 2). On a fine scale, i.e. when considering the distribution of activity in the habitats inside the home range, both bands and males exhibited habitat selection, showing seasonal variation (Table 3). Both males and bands showed habitat selection during the dry season, and used more the AF and less the TDF than expected. In contrast, such trend was observed exclusively in males during the wet season, because, although the G test for bands during the wet season suggests a differential habitat use, such trend could not be detected by the confidence intervals.

DISCUSSION

The marked climatic seasonality in the Chamela-Cuixmala reserve causes enormous spatial and temporal variability in the availability of resources for coatis. During the dry season water availability sharply decreases, and water becomes restricted to a few highly scattered small waterholes (Valenzuela, 1999). Litter arthropods are 2--3 fold times less abundant and 30 % more dispersed in the dry season than during the wet season (Lister and García, 1992). Resources strongly differ among habitats during this season. In general it has been found that during the dry season, in the arroyo forest, canopy cover, soil humidity and litter arthropod abundance are greater than in the adjacent dry forest (Janzen and Schoener, 1968; Martinez-Yrizar and Sarukhan, 1990; Pearson and Derr, 1986). Also, midday temperatures may be as much as 3°C cooler in arroyo than in dry forests (K. Renton, pers. comm), a trend similar to other dry forests in Central America (Janzen and Schoener, 1968).

In the Chamela-Cuixmala reserve coatis coped with the intense environmental dry season changes with a set of behavioral responses that included changes in the patterns of activity and home range sizes, that allowed them to have access to habitats where sparse resources (e. g. food and water) were more readily available. There were important differences between sexes. During the dry season bands exhibited larger home ranges sizes, traveled more distance daily, and presented a higher intensity of activity (distributed similarly in daylight hours) than during the wet season. Bands also showed habitat selection by including inside their home ranges more AF than expected by its availability. Arroyo forest had higher soil humidity, more food resources and the only available water sources (Valenzuela, 1999; see also Ceballos, 1989). In contrast, solitary males did not present significant seasonal changes in home ranges, a result that could be attributed in part to a small sample size. However, intensity of activity and distance traveled daily did not differ seasonally in males, suggesting that aside of small sample size, this was probably a real pattern.

Interestingly, males showed more nocturnal activity hours than bands, particularly during the dry season. This behavior has not been reported in other quantitative studies (Gompper, 1997; Saenz, 1994). Nonetheless, in areas where coatis are heavily hunted they tend to shift their activity to nocturnal hours (Gompper, 1995). In our study site, however, coatis are not hunted but we did observe consistently nocturnal activity, that sometimes included energetic demanding activities such as long distance travel. Detailed observations on the nocturnal activity will be helpful to understand its nature. Males did not show habitat selection at a gross scale but did so in a fine scale, spending more time in the AF, and using less TDF than expected during the dry season.

These differences in the behavioral responses of males and bands could be explained in terms of differences in energetic requirements and different resource limitations. Home range size is determined by an animal's energetic needs and by the availability and dispersion of resources in a given site (Bacon *et al.*, 1991; Kruuk and Macdonald, 1985; Mace *et al.*, 1984; Macdonald, 1983). Where or when resource availability decreases, animals must range more widely in order to obtain the same amount of energy. In general, a key factor determining home range size in females is access to food, while for males it is food resources outside the mating season and access to females during the mating period (Mace *et al.*, 1984; Sandell, 1989).

The difference in activity patterns between sexes could be attributed in part, to the larger size of solitary males (Gompper, 1996; Valenzuela, in press), which should have higher energetic requirements. Hence, as observed in the Chamela-Cuixmala forests, solitary males should have more hours of activity and less resting periods than bands of females, to attain energetic requirements. Similar seasonal changes in coati's activity which include increased activity and greater daily movement during the period of lower abundance of resources, and more nocturnal activity of males have been previously reported for Central American tropical (Kaufmann, 1962; Russell, 1982; Saenz, 1994; Smythe, 1970). Additionally, some differences in activity patterns between coati males and bands could arise from different foraging success. Solitary adult males have higher foraging success when feeding on fruit patches than females in bands. However, males may have lower foraging success, when foraging for litter arthropods between fruit patches (Gompper, 1996), or less success in finding fruit patches than bands, and hence need to wander more time in search of food resources. However, as stressed by Gompper (1996), detailed information on foraging success while traveling between resource patches is needed in order to give more support to this hypothesis.

The reproductive behavior of coatis could contribute to explain the difference between sexes in seasonal home ranges. The non-reproductive season comprises most of the year and during this period home ranges do not differ between sexes. During the wet season water and litter arthropods are more abundant, and is during this period when births occur and when the nesting season happens. It has been reported that during nesting season female coatis reduce notably their home ranges (Hass, in litt.; Kaufmann, 1962; Ratnayeke *et al.*, 1994; Russell, 1982). We found similar results in some females that presented significantly smaller home ranges during the nesting season than outside the reproductive period, a result that could explain partially the reduction in average home range size of bands during the wet season.

Differences in habitat selection between sexes could be related to differences in energetic requirements too. Adult males tend to leave natal bands and use a home range that overlaps their natal home range (Gompper, 1997; Gompper *et al.*, 1998). The extent of this overlap must be a compromise between the benefits of remaining in a familiar area with high competition for resources with individuals from the natal band or the cost of using unfamiliar or less productive areas. Our argument is that home ranges of males should include well-known and productive areas, were competition for resources with natal band should be higher, as well as unfamiliar areas with lower probability of resource competition. Therefore, at these gross scale there is no habitat selection, and home ranges of males may have and overall lower resource availability than home ranges of bands. This condition could be balanced by using intensely richer habitats inside their home ranges (e.g. fine scale habitat selection). Further studies on home range settlement of dispersing males and about resource availability are required to provide supporting evidence for this assumption.

Home range overlapping in solitary males of carnivores is expected if female density is low and they have an aggregated distribution (Sandell, 1989), as is the case for band-living female coatis. In accordance with this idea we found a relatively high overlap in males' home ranges. This is also the case for other sites (Gompper, 1997; Saenz, 1994). Latitude has been reported to be positively correlated with carnivore home range size (Gompper and Gittleman, 1991). Apparently, home range sizes of the coati also follow this trend. Home ranges estimated at CCBR were 12 times greater than those reported for Panama (Gompper, 1997), and 2 to 3 times smaller than those reported for Arizona (Hass, in litt.), and similar to those reported for Santa Rosa, a tropical dry forest in northwestern Costa Rica (Saenz, 1994).

The results presented here provide a general pattern of how coatis cope with seasonal changes in resource availability through behavioral plasticity, providing support to our initial predictions on spacing and activity patterns. Also, our study highlights the relevance of arroyo forests as a key habitat for the survival of white-nosed coatis in this highly seasonal forest.

Similar results have also been reported for other vertebrates in Chamela and other regions (e.g. Ceballos, 1995). We strongly recommend that this habitat should be given priority in management and conservation strategies for the Chamela-Cuixmala Biosphere Reserve in particular and the tropical dry forests of the coast of Jalisco in general. Finally, we consider that the Chamela-Cuixmala Biosphere Reserve coati population may act as a model for predict the type of behavioral responses of other coati populations to cope with climatic seasonality in other habitats throughout México and Central America.

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LITERATURE CITED

Aebisher, N. J., P. A. Robertson and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology, 74: 1313--1325.

Alldredge, J. R. and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management, 50: 157--165.

Bacon, P.J., F.G. Ball, and P.G. Blackwell. 1991. A model for territory and group formation in a heterogeneous habitat. Journal of Theoretical Biology, 148: 445--468.

Biggins, D. E., L. R. Hanebury and J. L. Godbey. 1992. Instructions for radio-tracking and using program TRITEL. U. S. Fish and Wildlife Service, National Ecology Research Center, Fort Collins, Colorado.

Bullock, S. H. 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of México. Archives for Meteorology, Geophysics, and Bioclimatology, 36: 297--316.

Bullock, S. H. and J. A. Solis-Magallanes. 1990. Phenology of canopy trees of a tropical deciduous forest in México. Biotropica, 22: 22--35.

Byers, C. R. and R. K. Steinhorst. 1984. Clarification of a technique for analysis of utilization - availability data. Journal of Wildlife Management, 48: 1050--1053.

Camponotus AB. 1994. Tracker version 1.1. Wildlife tracking and analysis software. User manual. Sweden.

Ceballos, G. 1989. Population and community structure of small mammals from tropical deciduous and arroyo forests in Western México. PhD dissertation, The University of Arizona, Tucson, Arizona.

---. 1995. Vertebrate diversity, ecology, and conservation in neotropical dry forests. Pp 195-220. in Seasonally dry tropical forests (S. H. Bullock, H. A. Mooney and E. Medina, eds.). Cambridge University Press, Cambridge, United Kingdom.

Ceballos, G. and A. García. 1995. Conserving neotropical biodiversity: the role of dry forests in western México. Conservation Biology, 9: 1349--1356.

Ceballos, G. and A. Miranda. 1986. Los Mamíferos de Chamela, Jalisco. Instituto de Biologia, Universidad Nacional Autónoma de México. México, D. F., México.

Fleming, T. H. 1977. Response of two species of tropical heteromyid rodents to reduced food and water availability. Journal of Mammalogy, 58: 102--106.

Gompper, M. 1995. *Nasua narica*. Mammalian Species No. 487 pp. 1-10.

---. 1996. Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. Behavioral Ecology, 7: 254--263.

---. 1997. Population ecology of the white-nosed coati (*Nasua narica*) on Barro Colorado Island, Panama. Journal of Zoology (London), 241: 441--455.

Gompper, M. and J. L. Gittleman. 1991. Home range scaling: intraspecific and comparative trends. Oecologia, 87: 343--348.

Gompper, M., J.L. Gittleman and R. K. Wayne. 1998. Dispersal, philopatry, and genetic relatedness in a social carnivore: comparing males and females. Molecular Ecology 7:157-165

Janzen, D. H. and T. W. Schoener. 1968. Differences in insect abundance and diversity between more humid and drier sites during a tropical dry season. Ecology, 49: 96--110.

Janzen, D.H. and D. E. Wilson. 1983. Mammals. Pp. 426--442. *in*: Costa Rican natural history (D. H. Janzen, ed.). University of Chicago Press, Chicago, Illinois.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, 6: 65--71.

Kaufmann, J. H. 1962. Ecology and social behavior of the coati, *Nasua narica* on Barro Colorado Island, Panama. University of California Publications, Zoology, 60: 95--222.

Kruuk, H. and D. Macdonald. 1985. Group territories of carnivores: empires and enclaves. Pp. 521-536. *in* Behavioral Ecology: Ecological Consequences of Adaptative Behaviour (R. M. Sibley and R. H. Smith, eds.). Blackwell Scientific Publications, Oxford, United Kingdom.

Lister, B. C. and A. García. 1992. Seasonality, predation, and the behaviour of a tropical mainland anole. Journal of Animal Ecology, 61: 717--733.

Mace, G. M., P. H. Harvey and T. H. Clutton-Brock. 1984. Vertebrate home-range size and energetic requirements. Pp.32--53. *in* The ecology of animal movement (I. R. Swingland and P. G. Greenwood, eds.). Clarendon Press, Oxford, United Kingdom.

Macdonald, D. 1983. The ecology of carnivore social behaviour. Nature, 301: 379--384.

MartÍnez-Yrizar, A. and J. SarukhÁn. 1990. Litterfall patterns in a tropical deciduous forest in México over a five-year period. Journal of Tropical Ecology, 6: 433--444.

Mohr, C. O. 1947. Table of equivalent populations of North American mammals. American Midland Naturalist, 37: 223--249.

Neu, C. W., C. R. Byers and J. M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management, 38: 541--545.

Orians, G. H. and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. The American Naturalist, 137: S29--S49.

Pearson, D. L. and J. A. Derr. 1986. Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. Biotropica, 18: 244--256.

Ratnayeke, S., A. Bixler and J. L. Gittleman. 1994. Home range movements of solitary, reproductive female coatis, *Nasua narica*, in south eastern Arizona. Journal of Zoology (London), 233: 322--326.

Russell, J. K. 1982. Timing of reproduction by coatis (*Nasua narica*) in relation to fluctuations in food resources. Pp. 413--431. *in:* The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes (E. G. Leigh, A. S. Rand and D. S. Windsor, eds.). 2nd. Printing. Smithsonian Institution, Washington, D. C.

Saénz, J. 1994. Ecología del pizote (*Nasua narica*) y su papel como dispersador de semillas en el bosque seco tropical, Costa Rica. M. S. thesis. Maestria en Manejo de Vida Silvestre. Universidad Nacional, San Jose, Costa Rica.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pp. 164--182. *in* Carnivore behavior, ecology, evolution (J. L. Gittleman, ed.). Chapman and Hall, London, United Kingdom.

Smythe, N. 1970. The adaptative value of the social organization of the coati (*Nasua narica*). Journal of Mammalogy, 51: 818--820.

Swihart R. K. and N. A. Slade. 1985. Testing for independence of observations in animal movements. Ecology, 66: 1176--1184.

Thomas, D. L. and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management, 54: 322--330.

Valenzuela, D. 1999. Efectos de la estacionalidad ambiental en la densidad, la conducta de agrupamiento y el tamaño del area de actividad del coati (*Nasua narica*) en selvas tropicales caducifolias. Tesis Doctoral. Instituto de Ecología, UNAM. México, D.F., México.

---. In press. Natural history of the white-nosed coati, *Nasua narica* in a tropical dry forest of western México. Revista Mexicana de Mastozoología 3.

White, G. C. and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic press, Inc., New York.

Wilson, D. E. 1971. Food habits of *Mycronycteris hirsuta* (Chiroptera: Phyllostomidae). Mammalia, 35: 107--110.

Table 1. Home ranges of coatis at the Chamela - Cuixmala Biosphere Reserve. Total and seasonal areas were estimated as the 95 % Minimum Convex Polygon (MCP).

Band	# Fixes	95% MCP (ha)	Dry 95% MCP (ha)	Wet 95% MCP (ha)	Observations
Alba	37	361.2	318.8	32.6	Radio lost
Aura	106	246.0	247.6	122.8	Died of unknown cause
Beba	82	329.7		329.7	
Karen	138	685.2	513.8	365.6	
Lore	90	556.7	480.7	311.9	
Luna	48	299.3	208.5	175.9	
Luna b	60	374.7	345.6	207.9	
Maga	56	349.7	340.0	117.8	Radio failure
Mar	58	362.5	350.3	26.3	Killed by Jaguar
Mili	46	245.8	245.8		Killed by Jaguar

Table 1. Home ranges of coatis…continues.

Males	# Fixes	95% MCP (ha)	Dry 95% MCP (ha)	Wet 95% MCP (ha)	Observations
Ares**	77	400.5	394.2	49.0	
Canelo	36	293.0	293.0		Killed by Jaguar
Che	71	594.4	594.4		
Italo	65	217.9	103.2	183.3	Radio lost
Moro	54	508.0	503.1	114.8	Killed by Jaguar
Nahual	50	451.2			Radio failure
Oso	23	234.5	234.5		Killed by Jaguar
Bands $\overline{X}$± *SE*		381.0 ± 43.58	339.0 ± 34.42	187.8 ± 42.99	
Males $\overline{X}$ ± *SE*		385.6 ± 54.04	353.7 ± 73.61	115.7 ± 38.77	
Total $\overline{X}$ ± *SE*		383.0 ± 32.86	344.9 ± 34.41	169.8 ± 33.45	

**this male was included only in the home range analysis because data was collected in the same period by C. Lopez in a carnivore ecology research in the CCBR.

Table 2. Gross scale habitat availability and selection by coatis. *G*-tests were used to determine significant habitat selection. Bonferroni simultaneous confidence intervals (BI) were used to detect particular habitat selection. Signs indicate a use greater (+), less than (–) or not different than expected from chance (0). Level of significance used is 0.05. AF = arroyo forest, TDF = tropical dry forest, SF = semideciduous forest.

Habitat	Proportions on Study Site (Availability)	Proportions on average home range of bands	BI	Proportions on average home range of males	BI
AF	0.309	0.424	+	0.358	0
TDF	0.617	0.548	0	0.571	0
SF	0.074	0.027	–	0.071	0
	G	32.601		4.24	
	P	< 0.001		> 0.05	

Table 3. Seasonal fine scale habitat selection by coatis. *G*-tests were used to determine significant habitat selection. Bonferroni simultaneous confidence intervals (BI) were used to detect particular habitat selection. Signs indicate a use greater (+), less than (–) or not different than expected from chance (0). Level of significance used is 0.05. AF = arroyo forest, TDF = tropical dry forest, SF = semideciduous forest.

Habitat	Proportions on average home range (Availability)	Average proportions of band locations	BI	Average proportions of male locations	BI
Wet season					
AF	0.400	0.455	0	0.432	+
TDF	0.557	0.498	0	0.549	0
SF	0.044	0.047	0	0.019	–
	G	7.349		26.948	
	P	< 0.05		< 0.001	
Dry season					
AF	0.400	0.482	0	0.478	+
TDF	0.557	0.482	0	0.461	–
SF	0.044	0.036	0	0.061	0
	G	7.088		23.329	
	P	< 0.05		< 0.001	

Figure 2. Daily pattern (frequency distribution of the proportion of individuals active per hour interval throughout the day) and intensity of activity (proportion of active locations on each hour category), (2a) annual pattern, (2b) seasonal patterns for bands and (2c) seasonal patterns for solitary males.

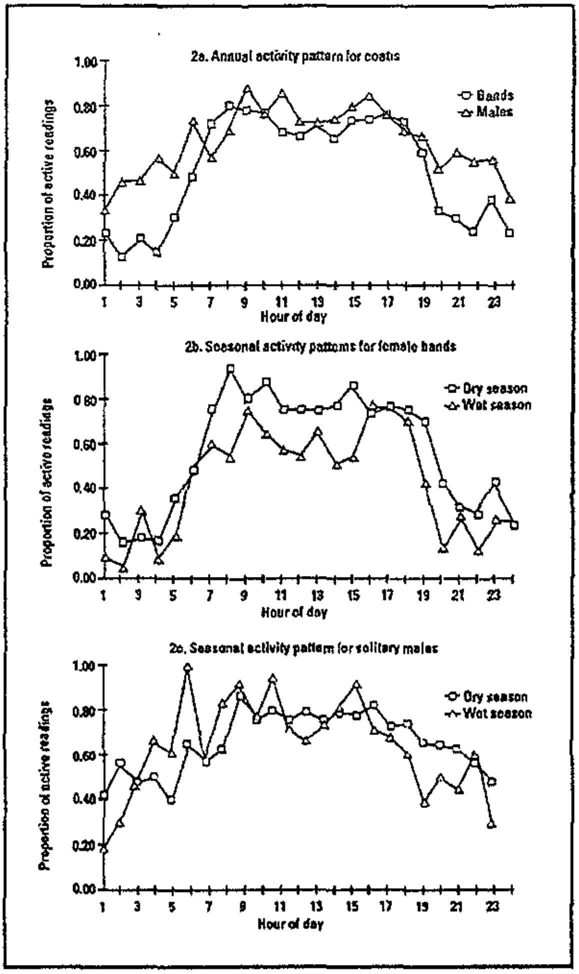
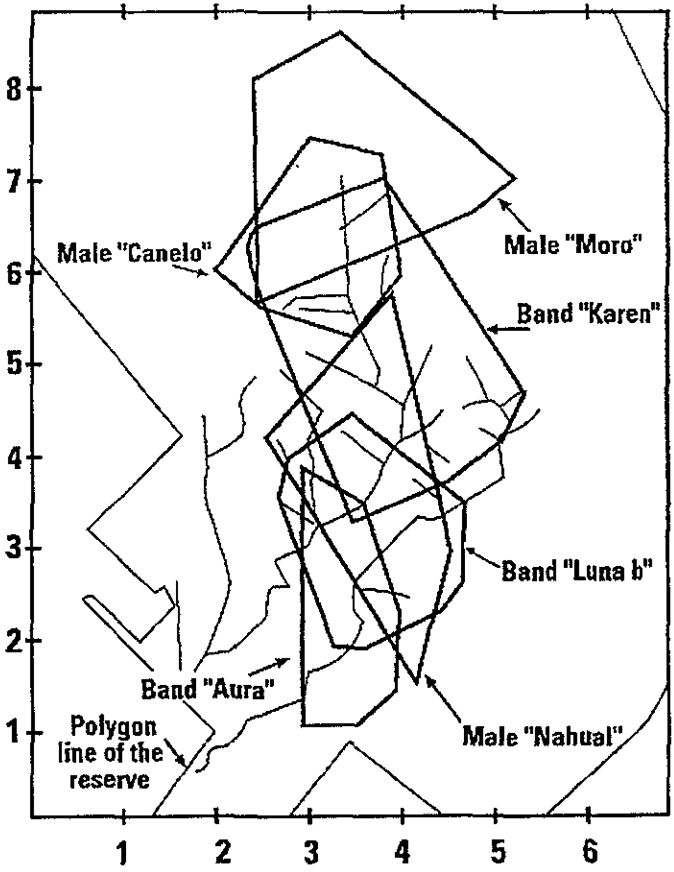


Figure 3. Total home ranges of three bands of females and three solitary males from the Chamela-Cuixmala Biosphere Reserve. X and Y-axes represent one km units east-west and north-south, respectively. The thin lines in the central part of the figure represents the temporal streams along which the arroyo forest is distributed in the study site.



CAPITULO III

DO COATIS KNOW THE RESOURCE DISPERSION HYPOTHESIS?: EVIDENCE FROM A NATURAL EXPERIMENT

(En formato para Journal of Animal Ecology)

DO COATIS KNOW THE RESOURCE DISPERSION HYPOTHESIS?: EVIDENCE FROM A NATURAL EXPERIMENT.

David Valenzuela

Instituto de Ecologia, UNAM, AP 70-275, Ciudad Universitaria, Mexico, D.F. C.P. 04510

e-mail: dgalvan@miranda.ecologia.unam.mx; Fax (52) (5) 622 9004

Summary

1. - The Resource Dispersion Hypothesis (RDH) proposes that in a spatially and temporally heterogeneous environment, territory or home range size of social carnivores increases as the dispersion of limited resources or key habitats increases, whereas group size is limited, independently, by the richness or abundance of those variables or key habitats.

2. - I examined the relationship of home range size and spatio-temporal availability of resources in the White-nosed Coati in tropical dry forests with seasonal rainfall.

3. - I compared home range size between two study sites, broadly similar but contrasting in environmental variables (e.g. resource abundance and dispersion).

4. - Home ranges estimated for seven White-nosed Coati bands varied between 45 and 362 hectares. The variation in home range size did not correlate with resource abundance and was better explained by the dispersion of water sources during the dry season.

5. - Average home range size was three times greater in the site where during the dry season, water sources were more dispersed. These results are in accordance with the prediction of the

RDH that home range size of social carnivores in a heterogeneous environment depends on dispersion of key resources.

Key words: Mexico, coati, *Nasua narica*, home ranges, dispersion of resources, social carnivore, tropical dry forest.

Introduction

Of the 271 carnivore species of the world (Wozencraft, 1993), only 10 -15 % form social groups outside the reproductive period (Gittleman, 1989). This suggests that conditions that favour this behaviour are limited. Grouping behaviour has been explained as the result of a compromise between costs and benefits of sociability. Sociability is favoured if it increases the fitness of individuals living in a group (Pulliam & Caraco, 1984; Krebs & Davies, 1993).

Resource availability is composed of two characteristics: one of which is abundance or richness, how much of a resource exists; and the second is dispersion, how a resource is distributed in space and time. For many social carnivores the availability of limited resources, particularly food, determines their patterns of spacial distribution and social organization, and hence on density and population dynamics (Bekoff, Daniels & Gittleman, 1984; Macdonald, 1983; Gittleman, 1989). These ideas were generalised as the Resource Dispersion Hypothesis (RDH; Macdonald, 1983, 1984; Carr & Macdonald, 1986; Macdonald & Carr, 1989). The RDH proposes that in spatially and temporally heterogeneous environments, the dispersion of patches of limited resources, or key habitats, determines territory or home range size, whereas richness of the resources limits group size.

The basic patterns of social organisation in carnivores (e.g. size of the groups and home range size) show considerable intra-specific variation, even in broadly similar habitats, and these differences could be related to changes in the availability of limited resources. Two general alternative strategies have been proposed for the adjustment of group and territories or home range sizes to the exploitation of limited resources by social carnivores (Kruuk & Macdonald, 1985). For an expansionist strategist, size of territory or home range depends on the relative strength of the defending group, and because group size will increase as resource abundance increases, an expansionist will tend also to increase its territory or home range area as abundance of resources increases. For a contractor strategist, group size will also depend on the resource abundance, but the area needed by that group will be adjusted independently to resource dispersion in a way that ensures sufficient resources for the group, even in years or seasons of resource scarcity. Therefore, territory or home range size will be greater when or where resource is more dispersed, adjusted to the most extreme scenario when dispersion it is the highest. Hence group size and the size of the area used by a group are related independently to different components of resource availability. The contractor strategy is compatible with the RDH but not the expansionist strategy.

Examples of both strategies are given in Kruuk & Macdonald (1985). The Coyote *Canis latrans* in Canada behave as expansionist. Coyote diets vary between summer and winter. During winter part of the coyote diet was mule deer that must be hunted in groups, and a significant correlation was found between group size and the percentage of mule deer in their diet. In addition, 87 % of the variation in home range size was explained by variation in group size. The Eurasian badger *Meles meles* in Scotland behaves as contractor. Eurasian badgers lives in groups or clans and feeds on earthworms, insects and fruits, which occurs in feeding patches with a very heterogeneous distribution. The size of territories is strongly correlated with the distance between feeding patches, while the number of badgers per clan is correlated with the biomass of resources per food patch. Clan size varied independently of territory size.

Testing predictions of the RDH is important for understanding how resource availability contributes to the variability in group and home range sizes in carnivores and allows predictions of the outcome of the management of carnivore populations (Kruuk & Macdonald, 1985).

I elected to test this hypothesis on the white-nosed coati *Nasua narica* (hereafter referred to as coati) because it shows a high variability in home range and band size across its geographical range (Gompper, 1995). Adult females form groups (bands) of up to 30 females and sub-adult males, while adult males are solitary individuals. The tropical dry forests in western Mexico, where I studied the coatis, present a marked seasonality in rainfall, and in the abundance and dispersion of fruit and litter arthropods (Bullock & Solis-Magallanes, 1990; Lister & Garcia, 1992). Both food resources form 85 % to 100 % of the coati diet (Gompper, 1996; Saenz, 1994; Delibes *et al.*, 1989; Hass, 1997; Valenzuela, in press).

I tested only the relation of resource availability with home range size. To explore this, I conducted a study in two sites within the Chamela-Cuixmala Biosphere Reserve (CCBR) which differ markedly in spatial and temporal distribution of these resources. One is Cuixmala, where food and water are abundant and little dispersed in space and time and the other is Cumbres, where water and food resources are expected to be less abundant and more dispersed spatiotemporally than in Cuixmala. The comparison between these sites was considered as a natural experiment (*sensu* Diamond, 1986).

In both sites, I estimated total and seasonal home ranges of bands as well as measured water and food availability inside each home range.. The RDH predicts that home range size will present little or no correlation with resource abundance, but a strong positive correlation with resource dispersion, and that size of home range should be adjusted to the most extreme scenario when dispersion it is the highest, as is the case for a contractor strategist. Hence, I predicted from the RDH: 1) that total home range sizes should correlate positively only with resource dispersion during the dry season, and 2) that total home ranges should be greater at Cumbres than at Cuixmala, because resource dispersion during the dry season is expected to be higher in the former site than in the later. Finally I predicted that differences in seasonal home ranges should be of greater intensity in Cumbres because in this site seasonal changes in availability of resources are expected to be greater than in Cuixmala.

Materials and methods

STUDY SITES

The CCBR is located in western Mexico on the coast of Jalisco, between 19° 22' and 19° 35' northern latitude and 104° 56' and 105° 03' western longitude. The reserve comprises 13,141 hectares with a topography of hills and coastal plains reaching an altitude interval from sea level up to 400 meters above sea level. The dominant vegetation type is tropical dry deciduous forest, with semi-deciduous vegetation types along water-courses or arroyos in valleys. The most important ecological feature of this forest is the sharp climatic seasonality, with a rainy season concentrated from late June to October and a long dry season from November to late June. The annual average rainfall varies between 700 mm and 1000 mm, and annual average temperature is near 25°C (Bullock, 1986; Garcia-Oliva, Ezcurra & Galicia, 1991). Ceballos & Garcia (1995) give detailed description of the area and the reserve.

Two contrasting sites within the reserve were selected: Cumbres and Cuixmala. Cumbres, in the central portion of the reserve, is characterised by an irregular topography of peaks and valleys between 100 to 400 m elev., covered extensively by the dominant tropical dry forest with patches of semi-deciduous forest along the courses of seasonal arroyos, and with no permanent water sources. Cuixmala, in the south-eastern portion of the reserve, includes wetlands on the coastal floodplain of the Cuixmala River, with tropical dry forest and eight other vegetation types related to the wetlands. Cuixmala also contains agricultural land with permanent water sources in the form of natural and artificial lagoons, channels, and the Cuixmala River. Hence, food and water is expected to be more abundant and less dispersed in space and time in Cuixmala than in Cumbres.

CAPTURE AND RADIOTELEMETRY

Seven female coatis were captured using Tomahawk Live Traps baited with sardines. After capture, animals were sedated with Ketamine, then weighed, measured and marked with coloured and numbered plastic ear-tags (Nasco Rototags). A radio-collar was fitted to each animal. Animals were released after full recovery from sedation. Information about site of capture, home range overlap and distance between simultaneous locations was used to confirm that each individual female belonged to a different band, therefore movements of each female were considered as representative of movements of her band. Three females were captured in Cumbres, 10 km away from Cuixmala, where the other four females were captured. All females but two from Cuixmala (Cx2 and Cx4), were captured in trapping sites separated by more than 1-2 kilometers; trapping sites where females Cx2 and Cx4 were caught are 400 m apart.

Twice a week, from November 1994 through October 1995, each marked coati was located at a distance by triangulation from three fixed receiving stations (each one consists of two antennas of 11 elements and a Null / Peak switch box, AVM, Inc.). Animals were also located at closer range with hand-held antennas of three elements (Wildlife Materials, Inc.) and a Global Positioning System (Garmin) to determine the position of observed animals. Location points were plotted on scale maps of the area (1:50,000). The radio-telemetry data was processed with the TRITEL program (Biggins, Hanebury & Godbey, 1992) and analysed with the TRACKER program (ABS Systems) to estimate yearly and seasonal home range sizes.

The 95 % Minimum Convex Polygon (MCP), using all independent locations (Swihart & Slade, 1985) obtained for each animal during all study period was considered as the total home range of each band, while the 95% MCP using only locations obtained in each season was considered as the seasonal home range for each band. Therefore, seasonal home ranges are a portion of total home ranges. Average total home ranges and seasonal home ranges for each study site were obtained by pooling estimates for all bands on each site.

SPATIO-TEMPORAL VARIATION IN RESOURCE AVAILABILITY

The abundance and dispersion of water, litter arthropods, and fruit within each home range was monitored monthly during the tracking period. Water sources were identified, measured, located on maps and monitored monthly based on aerial photographs and field inspection of study sites. In Cuixmala, a permanent system of lagoons and channels of more than 50 hectares and four temporal water-holes were identified. In Cumbres, water sources, with the exception of a permanent pond of one hectare, varied seasonally. During the wet season, water runs along the main courses of the arroyos, forming a system of nearly 16 hectares (estimated as the sum of the length of all arroyos with an average width of 2 meters) where water could be easily obtained. However during the dry season, water was restricted to only 20 water-holes, of 2 to 16 square meters in size. The surface area of these water sources inside each home range was considered as a measure of water availability. The average distance of all radio-telemetry locations, of each tracked individual, to the nearest water source, was considered as a measure of water dispersion.

Fruit abundance in each home range was estimated with a modification of the method suggested by Chapman, Wrangham, & Chapman (1994). Within each home range, 10 phenology transects of 200 x 4 m were established randomly along existing trials and arroyo courses (five in tropical dry forest and five in semi-deciduous vegetation types). These transects were reviewed once a month to record every tree within 2 meters of each side of the transect, greater than 10 cm of diameter at breast height and producing fruits with a fleshy pulp or aril. Trees were identified to species level. The abundance of fruit on each tree was ranked from 1 to 5, corresponding to fruit numbers as follows: 1= 1-199 fruits; 2= 200-399; 3=400-599 fruits; 4=600-799 fruits; and 5= 800 -999 or more fruits. Ten samples of fruit were taken from each tree species to obtain average fruit weight. Finally, the medium value of each rank was multiplied by average weight of fruits of every tree recorded, and summed over all trees in the transect to obtain an estimate of fruit biomass per transect. Results were averaged over all transects to obtain monthly estimates of fruit abundance for each home range. Dispersion of fruit was estimated as the coefficient of variation (CV) of these monthly estimates. This value is considered one of the best and simplest measures of dispersion (Krebs, 1989). Values lower than one indicate a uniform dispersion, while a CV of one occurs if dispersion is random, and values above one indicate a clumped distribution.

To estimate abundance of litter arthropods in each home range , 20 litter samples of 0.1 m^2 (10 in tropical dry forest and 10 in semideciduous vegetation types) were taken randomly each month, from established phenology transects. Each sample was collected in plastic bags, between

07:00 and 11:00 hrs, then carefully inspected at the laboratory. All arthropods larger than 5 mm in length found in the debris were counted, identified to order level and stored in 70% alcohol. Abundance of litter arthropods for each home range was estimated as the average number of arthropods per square meter of litter, while dispersion was measured as the CV of these estimates.

Values for abundance and dispersion of water, fruit, and litter arthropods for each home range were pooled by site and season. Normality and equality of variances of all variables analysed were inspected and when possible all non-normal variables were log-transformed to meet criteria of parametric analysis, otherwise non- parametric tests were used. To confirm difference in abundance and dispersion of water, fruit and litter arthropods, between sites, seasons and home ranges nested ANOVA models were used, considering sites and seasons as factors and home ranges nested to site. If the interaction was significant, test of simple main effects were applied to explore the interaction (insert citation). When differences between home ranges in resource availability were found, a post - hoc approach using Newman-Keuls multiple comparison tests was applied to determine which home ranges differed. A t-test was used to compare total home ranges between sites and a two -way analysis of variance (ANOVA) was used to test if seasonal home ranges differed and if this differed between sites. Pearson correlation cnalyses were done to explore the relationship between size of total home ranges and seasonal values of abundance and dispersion of water, litter arthropods and fruit, on each home range.Home range values and those resource variables that were significantly correlated with them were fit to a linear regression model. All statistical tests were done with alpha = 0.05, except when indicated, using JPM (version 1.3.6.2.; SAS Institute, Inc.) and SIGMASTAT (version 1.0.; Jandel Corporation) analytical software.

Results

SPATIO-TEMPORAL AVAILABILITY OF RESOURCES

The model for water abundance was significant ($F_{(8,5)} = 139.99$; $P < 0.0001$). All factors were significant, sites ($F_{(1,5)} = 548.13$; $P < 0.0001$), seasons ($F_{(1,5)} = 247.48$; $P < 0.0001$) and home ranges inside each site ($F_{(5,5)} = 27.74$; $P = 0.0012$). But also, the interaction between seasons and sites ($F_{(1,5)} = 247.48$; $P < 0.0001$), hence, tests of simple main effects were applied to investigate the interaction. Seasonal differences in water abundance were explored for each site independently. Water abundance in Cuixmala did not differ seasonally seasonally ($t = 0.00$; $df = 6$; $P = 1.0$), while in Cumbres water differed significantly between seasons ($t = 9.04$; $df = 4$; $P = 0.0008$), being much less abundant during the dry season than during the wet season (Table 1 and Fig. 1a). Newman - Keuls multiple comparison tests were applied to explore differences in water abundance between home ranges on each site. It was found that in Cuixmala home range of band Cx1, contains more water than any other home range ($P < 0.05$), followed by home range of band Cx4 ($P < 0.05$), while in Cumbres there were no differences between home ranges in water abundance.

The model for water dispersion was significant ($F_{(8,5)} = 23.50$; $P = 0.0015$). Again all factors were significant, seasons ($F_{(1,5)} = 52.23$; $P = 0.0008$), sites ($F_{(1,5)} = 62.15$; $P = 0.0005$) and home ranges inside each site ($F_{(5,5)} = 7.67$; $P = 0.0216$), as well as the interaction of season by site ($F_{(1,5)} = 49.07$; $P = 0.0009$), hence tests of simple main effects were applied for comparing seasons within sites independently. Water dispersion did not differ seasonally in Cuixmala ($t = -0.451$; $df = 6$; $P = 0.6682$), while in Cumbres it was significantly greater in the dry season than in the wet season ($t = -3.59$; $df = 4$; $P = 0.0229$; Table 1 and Fig. 1b). Newman - Keuls multiple comparisons tests revealed that in Cuixmala water dispersion was significantly lower in the home range of group Cx1 ($P<0.05$) while in Cumbres water was more dispersed in home range of group Cm3 than in the other two ($P< 0.05$).

The model for litter arthropods abundance was significant ($F_{(8,75)}= 9.35$; $P<0.001$) and only the factor season was significant ($F_{(1,75)}= 63.69$; $P< 0.0001$). This resource was 2-3 times higher during the wet season than during the dry season (Table 1 and Fig. 1c). The model for fruit abundance was significant ($F_{(8,74)}= 5.74$; $P<0.001$), and the only significant factor was seasons ($F_{(1,74)}= 32.42$; $P < 0.0001$) but also the interaction of site and season was significant ($F_{(1,74)} = 5.65$; $P = 0.02$). To explore this interaction, simple main effects tests were applied. Fruit abundance in Cuixmala differed significantly ($t = 5.763$; $df = 46$; $P < 0.000$), being nearly five times more abundant in the dry season than in the wet season (Table 1 and Fig. 1e). In Cumbres fruit abundance was also higher in the dry season than in the wet season ($t = 2.415$; $df = 34$; $P = 0.0213$) but this difference is only one fold (Table 1 and Fig. 1e).

The model for litter arthropods dispersion was also significant ($F_{(8,75)}= 2.096$; $P = 0.046$) and only the factor season was significant ($F_{(1,75)}= 12.401$; $P =0.0007$). Dispersion of this resource was as 25-34 % higher in the dry season than during the wet season (Table 1; Fig. 1d). Model for fruit dispersion was marginally non-significant ($F_{(8,74)}= 2.0188$; $P = 0.0554$; Table 1 and Fig. 1f).

HOME RANGES

In Cuixmala only two bands (Cx2 and Cx4) presented overlap in home ranges and was 34 % (Fig. 2a). These two individual females were on average separated by 780 ± 89 m ($\bar{X} \pm SE$; $n = 12$) during simultaneous locations. Distance between the home ranges of these two bands and the remaining two (Cx1 and Cx3) was greater than 1 km, as well as distance between home ranges of band Cx1 and Cx3. In Cumbres average overlap between the home ranges of the three bands (Cm1, Cm2 and Cm3) was 28.71 ± 6.37 % ($\bar{X}$ ± SE; $n = 6$; Fig. 2b) and on average individual females were separated by 1594.45 ± 109.9 m ($\bar{X}$ ± SE; $n = 86$) during simultaneous locations.

home ranges overlapped extensively among seasons (Fig. 2c-d). In Cuixmala, the average overlap between seasonal home ranges in Cuixmala was 75.8 ± 6.08 % ($\bar{X}$ ± SE; $n = 8$), while in Cumbres was 44 ± 11.96 % ($\bar{X}$ ± SE; $n = 6$).

As expected, based on the RDH, average total home range was significantly greater (nearly five times) in Cumbres than in Cuixmala ($t = 11.7$; $df = 5$; $P < 0.001$; Table 2). An inspection of home ranges by site and season, revealed that both factors are significant, sites ($F_{(1,10)} = 17.68$; $P = 0.0018$) and seasons ($F_{(1,10)} = 10.93$; $P = 0.0079$), but also the interaction of site by season ($F_{(1,10)} = 9.999$; $P = 0.0101$). A t - test revealed that in Cuixmala seasonal home ranges did not differ ($t = -0.359$; $df = 6$; $P = 0.7322$), while in Cumbres on average, home ranges during the dry season were greater than during the wet season ($t = -2.785$; $df = 4$; $P = 0.049$). Interestingly, dry season home ranges represented between 63 and 96 % (on average 76.6 %) of the total home ranges (Table 2). Therefore the correlation of total home ranges with seasonal home ranges was also explored.

HOME RANGE CORRELATIONS WITH RESOURCES

A total of 38 correlations was done, 36 between three home range values (total, wet and dry) with two seasonal values for resource abundance and dispersion (water, litter arthropods and fruit). Total home range values were also correlated with seasonal home range values. Because of the number of correlations performed, α was set as 0.001 in order to lessen the probability of committing a type one error. Only 2 out of the 38 correlations were found to be significant. Total home range was significantly correlated with dry season home range ($\underline{r} = 0.9522$; $\underline{n} = 7$; $\underline{P} < 0.001$). Dry season home range was significantly correlated with dispersion of water in the same season ($\underline{r} = 0.9620$; $\underline{n} = 7$; $\underline{P} < 0.001$).

Based on these results, two linear regression analyses were run and two significant models were obtained. The first one explains variability among bands in total home range as a function of the area used by bands during the dry season ($\underline{r}^2 = 0.888$; $\underline{n} = 7$; $\underline{P} = 0.0009$; Fig. 3a), with the following equation:

Total home range = 20.9 + 1.16 x dry season home range

And the second one explains variability among bands in dry season home ranges as a function of water dispersion on each home range in this period ($\underline{r}^2 = 0.9106$; $\underline{n} = 7$; $\underline{P} = 0.0005$; Fig. 3b) with the following equation:

Dry season home range = -38.874 + 0.4731 x water dispersion during dry season

Discussion

Results confirmed a high seasonal fluctuation in the availability of resources that varied between the study sites. For water, the dry season is the period of lowest abundance and highest dispersion only in Cumbres. For litter arthropods, the wet season is the period of highest abundance and lowest dispersion in both sites. The dry season is the period of highest abundance of fruit only in Cuixmala. And fruit dispersion did not differs between sites, seasons or home ranges inside each home range. Similar results have been previously reported for the CCBR. Lister & Garcia (1992) reports a 2-3 fold increase in litter arthropods numbers between the dry and the wet season and Bullock & Solis-Magallanes (1990) reports a peak in fruiting events during the dry season for the majority of plant species, although not sharply defined.

Similarly in Barro Colorado Island, Panama, where coatis have been studied, fruit and litter arthropods presented clear seasonal peaks in abundance (Foster, 1982; Levings & Windsor, 1982; Smythe, 1970). Specifically it has been reported that the litter fauna in this place become less evenly distributed during the dry season as local differences in moisture, due to differences in drainage, become more pronounced.These changes in abundance of litter arthropods affect coati movements (Russell, 1982).

Seasonality is a common and important feature of tropical ecosystems (Wolda, 1988), particularly in the tropical dry forests where the seasonal fluctuation in water availability is a key ecological feature directly or indirectly affecting abundance of other important resources (Murphy & Lugo, 1986; Janzen, 1988; Ceballos, 1996). However this ecological feature appears to be experienced differently by the animals inhabiting each site. In Cuixmala there are no seasonal differences in availability and dispersion of water, while in Cumbres water abundance and dispersion differ seasonally, being extremely limited and highly dispersed during the dry season. These differences are reflected in home ranges. Average home range in Cuixmala was nearly five times smaller than in Cumbres and did not differ seasonally, meanwhile in Cumbres, the average area used by bands during the dry season was three times greater than during the wet season.

The prediction that total home ranges will correlate positively only with resource dispersion during the dry season was confirmed partially. Total home ranges do not correlate with any value of resource availability but were strongly and positively correlated with dry season home ranges, which in turn were, highly and positively correlated with water dispersion during the dry season. The prediction that total home ranges should be greater in Cumbres than in Cuixmala was confirmed. Finally, the last prediction was also confirmed, not only seasonal variation in home ranges was greater in Cumbres than in Cuixmala, it occured only in Cumbres These result supports the RDH predictions about home range size and the assumption that coatis behave as contractors in this highly seasonal area, adjusting the maximum size of their home range to the spatial dispersion of the more limited resource during the bottleneck period of the year (Macdonald, 1984; von Schantz, 1984; Kruuk & Macdonald, 1985).

Similar results have been found with other species. The territory sizes of European Badgers, *Meles meles*, were found to be closely correlated with the distance between feeding patches (Kruuk & Parish, 1982), as well as influenced by the spatial distribution of dens (Doncaster & Woodroffe, 1993). For Blanford's Foxes, *Vulpes cana*, variability in home range sizes was best explained by the mean distance to the patches of high resource abundance (Geffen et al., 1992). Finally, for Spotted Hyaenas, *Crocuta crocuta*, average distance over their chase preys determined territory sizes (Kruuk & Macdonald, 1985).

A major limitation in present results is that only one control and one experimental site were considered. This could be ameliorated by confirming observed results with some formal experiments, as those suggested by Kruuk & Macdonald (1985), by altering number of individuals in bands, resource abundance or resource dispersion, or by removing patches of key resources. The relation of resource dispersion and the basic parameters of the social organisation of coatis require further exploration in other sites of the geographical range of the species, to add evidence for the assumption that behaves as a contractor strategist does.

Additional evidence for the RDH comes from data on habitat selection by coatis in Cumbres, where it was determined that on average, coati home ranges included more area of arroyo forest, than expected from its availability (Valenzuela & Ceballos, unpublished). Based on the RDH, it could be predicted that home ranges should be configured to encompass patches of key habitats and hence, dispersion of these habitats should determine size of home range (Geffen et al., 1992). The arroyo forest it is a key habitat for vertebrates in the CCBR. Water sources are restricted to this habitat during the stressful period of the year. During the dry season, this forest retains approximately25 % of leaf cover, is 3° C cooler at midday (K. Renton, pers. comm.) and has greater soil humidity and more litter arthropods than the adjacent matrix of tropical dry forest (Janzen & Schoener, 1968; Martinez-Yrizar & Sarukhan, 1990; Pearson & Derr, 1986).

Is coati behavior consistent with the Resource Dispersion Hypothesis? Based on present results on the relation of water dispersion and size of coati home ranges in the CCBR the answer appears to be affirmative. More detailed information on size of coati bands and how this parameter is related to resource availability and to size of home ranges is needed in order to give full answer to this question.

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References

Bekoff, M., T. J. Daniels & J. L. Gittleman. 1984. Life history patterns and the comparative social ecology of carnivores. *Annual Review of Ecology and Systematics* 15:191-232.

Biggins, D. E., L. R. Hanebury & J. L. Godbey. 1992. *Instructions for radio-tracking and using program TRITEL*. U. S. Fish and Wildlife Service, National Ecology Research Center, Fort Collins, Colorado, USA.

Bullock, S. H. 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. Archives for Meteorology, Geophysics, and Bioclimatology 36: 297-316.

----- & J. A. Solis-Magallanes. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22 : 22-35.

Carr, G. & D. W. Macdonald. 1986. The sociality of solitary foragers: a model based on resource dispersion. *Animal Behaviour* 34: 1540-1549.

Ceballos, G. 1996. Vertebrate diversity, ecology, and conservation in neotropical dry forests. *Seasonally dry tropical forests* (eds S. H. Bullock, H. A. Mooney & E. Medina), pp 195-220. Cambridge University Press, Cambridge.

Ceballos, G. & A. Garcia. 1995. Conserving neotropical biodiversity: the role of dry forests in western Mexico. *Conservation Biology* 9: 1349-1356.

Ceballos, G. & A. Miranda. 1986. *Los Mamiferos de Chamela, Jalisco.* Instituto de Biologia, Universidad Nacional Autonoma de Mexico. Mexico, D. F.

Chapman, C. A., R. Wrangham, & L J. Chapman 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica*, 26(2):160-171

Delibes, M., L. Hernandez, & F. Hiraldo. 1989. Comparative food habits of three carnivores in Western Sierra Madre, Mexico. Zeitschrift Säugetierkunde 54:107-110.

Diamond, J. 1986. Overview: laboratory experiments, field experiments and natural experiments. *Community Ecology* (eds J. Diamond & T. J. Case), pp. 3-22. Harper and Row Publishers Inc., NY, USA.

Doncaster, C. P. & R. Woodroffe. 1993. Den site can determine shape and size of badger territories: implications for group-living. *Oikos* 66: 88-93.

Foster, R. B. 1982. The seasonal rhythm of fruitfall in Barro Colorado Island. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes.* (eds E. G. Leigh, A. S. Rand & D. S. Windsor), pp. 151-172. 2nd. Printing. Smithsonian Institution. Washington, D.C.

García-Oliva, F., E. Ezcurra. & L. Galicia. 1991. Pattern of rainfall distribution in the central Pacific coast of Mexico. Geografiska Annaler 73 A (3-4): 179-186.

Geffen, E., R. Hefner, D. W. Macdonald & M. Ucko. 1992. Habitat selection and home range in the Blanford's fox, *Vulpes cana*: compatibility with the resource dispersion hypothesis. *Oecologia* 91: 75-81.

Gittleman, J. L. 1989. Carnivore group living: comparative trends. *Carnivore Behaviour, Ecology, and Evolution.* (ed J. L. Gittleman), pp. 183-207. Chapman and Hall, London.

Gompper, M. 1995. Nasua narica. *Mammalian Species* 487: 1-10

-----. 1996. Sociality and asociality in white-nosed coatis (Nasua narica): foraging costs and benefits. Behavioral Ecology 7: 254-263.

Hass, C. C. 1997. Ecology of the White -nosed coatis in the Huachuca Mountains, Arizona. Unpublished report, Arizona Game & Fish Department, Phoenix, Arizona. Pp. 52.

Janzen, D. H. & T. W. Schoener. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49 : 97-110.

Janzen, D. H. 1988. Tropical dry forests: the most endangered major tropical ecosystem. *Biodiversity* (ed E. O. Wilson), pp. 130-137. National Academy Press, Washington.

Krebs, Ch. J. 1989. *Ecological Methodology*. Harper Collins, New York.

Krebs, J. R. & N. B. Davies. 1987. *An Introduction to Behavioural Ecology*. Second Edition. Blackwell Scientific Publications, Oxford.

Kruuk, H. & D. W. Macdonald. 1985. Group territories of carnivores: empires and enclaves. *Behavioural Ecology: Ecological Consequences of Adaptative Behaviour* (eds R. M. Sibley & R. H. Smith), pp. 521-536. Blackwell Scientific Publications Oxford.

Kruuk, H. & T. Parish. 1982. Factors affecting population density, group size and territory size of the European badger *Meles meles*. *Journal of Zoology, London* 196: 31-39.

Levings, S. C. & D. M. Windsor. 1982. Seasonal and annual variation in litter arthropods populations. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes*. (eds E. G. Leigh, A. S. Rand & D. S. Windsor), pp. 355-388. 2nd. Printing. Smithsonian Institution. Washington, D.C.

Lister, B. C. & A. Garcia. 1992. Seasonality, predation, and the behaviour of a tropical mainland anole. *Journal of Animal Ecology* 61: 717-733.

Macdonald, D. W. 1983. The ecology of carnivore social behaviour. *Nature* 301: 379-384.

Macdonald, D. W. 1984. Reply to von Schantz. *Nature* 307: 390.

Macdonald, D. W. & G. Carr. 1989. Food security and the rewards of tolerance. *Comparative Socioecology: The behavioural ecology of humans and other mammals.* (eds V. Standen & R. A. Foley), pp. 75-99. Blackwell Scientific Publications, Oxford.

Martinez-Yrizar, A. & J. Sarukhan, 1990. Litterfall patterns in a tropical deciduous forest in Mexico over a five-year period. *Journal of Tropical Ecology* 6: 433-444.

Murphy, P. G. & A. E. Lugo. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67-88.

Pearson, D. L. & J. A. Derr. 1986. Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. *Biotropica* 18: 244-256.

Pulliam, H. R. & T. Caraco. 1984. Living in groups: is there an optimal group size?. *Behavioural Ecology: An Evolutionary Approach* (eds J. R. Krebs y N. B. Davies), pp. 122-147. Second Edition. Sinauer Associated, Inc. Sunderland.

Russell, J.K. 1982. Timing of reproduction by coatis (Nasua narica) in relation to fluctuations in food resources. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes.* (eds E. G. Leigh, A. S. Rand & D. S. Windsor), pp. 151-172. 2nd. Printing. Smithsonian Institution. Washington, D.C.

Sáenz, J. 1994. Ecología del pizote (Nasua narica) y su papel como dispersador de semillas en el bosque seco tropical, Costa Rica. Tesis de Maestría en Manejo de Vida Silvestre. Universidad Nacional, Costa Rica. 186 pp.

von Schantz T. 1984. Carnivore social behavior - does it need patches?. *Nature* 307: 389-390.

Smythe, N. 1970. The adaptative value of the social organisation of the coati (Nasua narica). *Journal of Mammalogy* 51 : 818-820.

Swihart R. K. and Slade N. A. 1985. Testing for independence of observations in animal movements. *Ecology* **66**: 1176-1184.

Valenzuela, D. in press. Natural history of the White-nosed coati , *Nasua narica* in the tropical dry forests of western Mexico. *Revista Mexicana de Mastozoologia*.

Wozencraft, W. Ch. 1993. Carnivores. *Mammal species of the world. A taxonomic and geographic reference.* (eds D. E. Wilson & D. M. Reeder), pp. 279-344. Second Edition. Smithsonian Institution Press. Washington, DC, USA.

Wolda, H. 1988. Seasonality and the community. *The Organisation of Communities* (eds J. H. R. Gee, & P.S. Giller), pp. 69-95. Blackwell Scientific Publications, Oxford.

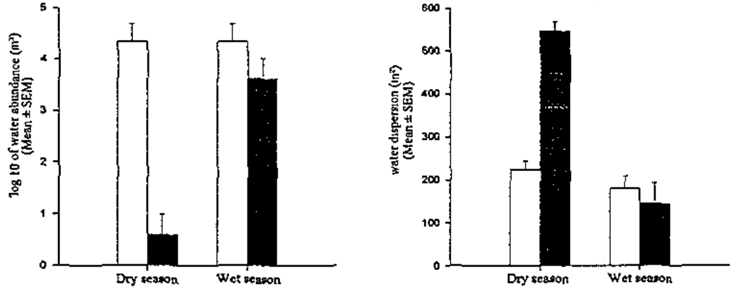
Table 1. Seasonal average abundance and dispersion of water, litter arthropods and fruit inside home range of each band and on average by site. Cm = Cumbres site; Cx = Cuixmala site. Average data by site is the mean ± standard error. CV = coefficient of variation.

Dry Season	Abundance			Dispersion		
Band	Water (m^2)	Arthropods (ind. / m^2)	Fruit (g / m^2)	Water (m)	Arthropods (CV)	Fruit (CV)
Cm1	8.00	9.35	1.67	460.54	1.61	1.09
Cm2	2.00	10.02	2.19	589.87	1.51	1.31
Cm3	4.00	7.11	2.38	801.43	2.05	1.35
Cx1	257,205.00	6.96	2.42	93.14	1.75	1.59
Cx2	6,260.00	10.05	5.30	256.90	1.69	1.25
Cx3	3,586.00	7.68	4.48	246.75	1.68	1.32
Cx4	45,056.00	9.55	3.32	234.65	1.55	1.14
Cumbres average	4.66 ± 1.76	8.83 ± 1.08	2.08 ± 0.26	546.79 ± 32.01	1.72 ± 0.13	1.25 ± 0.09
Cuixmala average	7.80E +04 ± 6.04E +04	8.56 ± 0.78	3.83 ± 0.55	222.74 ± 12.4	1.67 ± 0.08	1.33 ± 0.09
Wet Season	Abundance			Dispersion		
Band	Water (m^2)	Arthropods (ind. / m^2)	Fruit (gr / m^2)	Water (m)	Arthropods (CV)	Fruit (CV)
Cm1	3,000.00	14.03	1.54	155.89	1.23	1.14
Cm2	4,400.00	24.33	1.22	95.17	1.14	1.45
Cm3	5,400.00	24.03	0.33	315.90	1.05	1.60
Cx1	257,205.00	22.17	1.80	84.75	1.57	1.64
Cx2	6,260.00	27.67	0.89	250.87	1.01	2.43
Cx3	3,586.00	21.83	0.09	248.67	1.24	1.89
Cx4	45,056.00	30,17	0.29	146,11	1,20	1,90
Cumbres average	4,266.6 ± 696.02	20.80 ± 3.89	1.03 ± 0.38	145.09 ± 22.05	1.14 ± 0.09	1.40 ± 0.10
Cuixmala average	7.803E +04 ± 1.209E +05	25.46 ±3.18	0.77 ± 0.32	179.12 ± 17.32	1.25 ± 0.13	1.97 ± 0.17

Table 2. Home ranges of coati bands in Cuixmala (Cx) and Cumbres (Cm). Average data by site is the mean ± standard error.

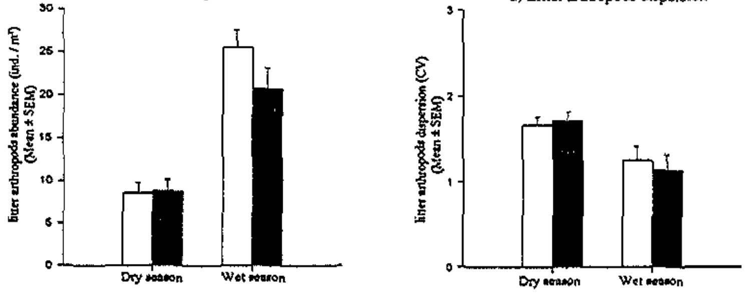
Band	No. Locations	Total home range (ha)	Dry season home range (ha)	Wet season home range (ha)
Cm1	37	361.20	227.74	32.66
Cm2	48	299.63	208.45	175.90
Cm3	58	362.48	350.30	26.30
Cx1	58	44.70	39.69	40.30
Cx2	44	101.50	80.56	59.15
Cx3	62	53.54	40.17	36.00
Cx4	69	79.65	50.52	59.15
Cumbres Average		341.10 (± 20.7)	262.16 (± 44.4)	78.29 (± 48.8)
Cuixmala Average		69.85 (± 12.9)	52.74 (± 9.6)	48.65 (± 6.1)

Figure 1 (a-f). Average abundance and dispersion of resources on each season and site. Bars represent mean values showing standard error of mean, clear bars represent Cuixmala and shaded bars Cumbres.



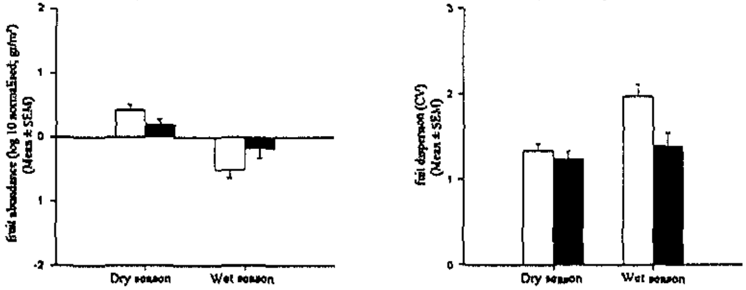
a) Water abundance

b) Water dispersion



c) Litter arthropods abundance

d) Litter arthropods dispersion



e) Fruit abundance

f) Fruit dispersion

Figure 2. Map of home ranges (95% MCP) of tracked animals. Total home ranges and range overlap in Cuixmala (a) and Cumbres (b). Seasonal home ranges and its overlap in (c) Cuixmala and (d) Cumbres. In (c) and (d) gross lines represent dry season home ranges and thin lines, wet season ranges.

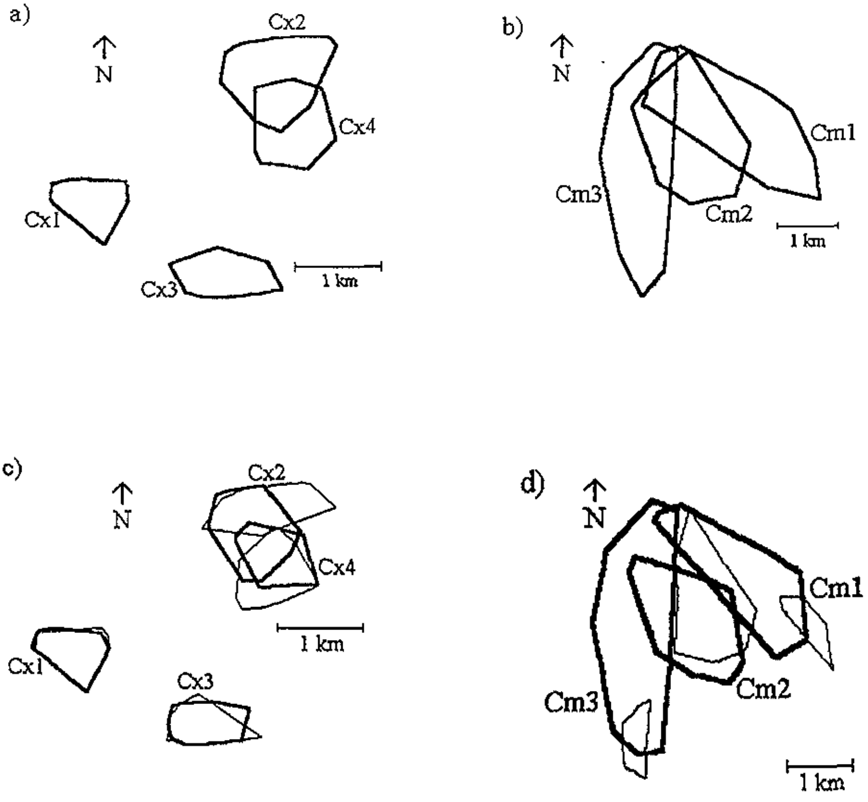
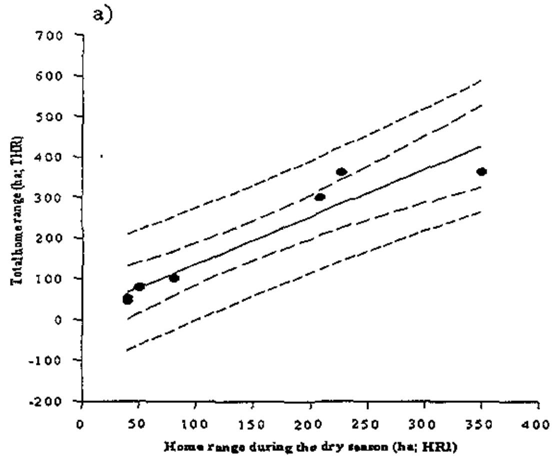
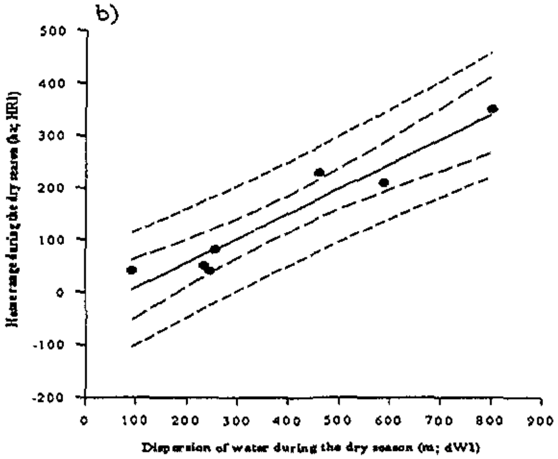


Figure 3. a) Total home range as function of dry season home range; b) dry season home range as function of dispersion of water during the same period.



THR = 20,9 + 1.16 x HR1; Adj r^2 = 0,888, P = 0.0009



HR1 = -38.874 + 0.4731 x dW1, Adj r^2 = 0,9106, P = 0.0005

CAPITULO IV

EXPERIMENTO DE MANIPULACION DE LA DISPERSION DE LAS FUENTES DE AGUA

EXPERIMENTO DE MANIPULACIÓN DE LA DISPERSIÓN DE LAS FUENTES DE AGUA

INTRODUCCIÓN

En el estudio de la evolución de la sociabilidad en carnívoros, se ha propuesto que el surgimiento de esta conducta en una especie de carnívoro, es el resultado de un balance entre las ventajas y desventajas asociadas al vivir en grupo, lo que resulta en un aumento en la adecuación de los individuos que conforman los grupos (Pulliam y Caraco, 1986). En particular se ha propuesto que en carnívoros la conducta social evolucionó como una respuesta contra la depredación o por razones de forrajeo (Clark y Mangel, 1985; Gittleman, 1989; .Rood, 1986). Además, se ha encontrado que la dispersión y abundancia de recursos limitantes es un factor fundamental para el uso de espacio y la estructura de las sociedades de carnívoros. Incluso se ha considerado que ciertos patrones en la disponibilidad de recursos pudieron haber permitido el surgimiento de la sociabilidad en carnívoros (Macdonald, 1983) y que posteriormente tal conducta se vería reforzada por las ventajas inherentes a la misma. La Hipótesis de la Dispersión de Recursos (HDR; Macdonald, 1983) formaliza esto y propone condiciones teóricas que explican en que forma la variación en el tamaño de los grupos y en el espacio mínimo requerido para mantener diferentes tamaños de grupo, se ven afectados por la abundancia y dispersión de recursos, respectivamente.

A la propuesta de la HDR inicial, siguió el desarrollo de un modelo matemático para explorar la HDR (Carr y Macdonald, 1986), que dio pauta a una serie de publicaciones en las que se que revisó este modelo inicial para proponer modificaciones y alternativas.

Carr y Macdonald (1986) desarrollaron su modelo bajo cuatro premisas: 1) que el área disponible en un ambiente se reparte en territorios exclusivos, cuyos ocupantes primarios son la unidad social mínima, viable reproductivamente, de la especie bajo estudio, 2) que el tiempo puede dividirse en una serie de periodos de alimentación (e.g. noches o días) y consideran a un animal capaz de visitar todo su territorio durante un periodo de alimentación, 3) que durante ese periodo de alimentación un animal tiene una cierta necesidad básica de alimento que puede variar entre individuos, 4) que para poder mantenerse, un individuo debe cubrir su necesidades de alimentación durante un número determinado de periodos de alimentación. Es decir, para cada periodo debe existir cierta probabilidad de cubrir tal requerimiento. Estos autores definen esta probabilidad como *probabilidad critica* (*Cp*) y a la probabilidad de que el alimento esté disponible en el área de actividad o territorio de un animal, la denominan la *seguridad de alimento* de un animal. Todo el desarrollo matemático posterior se basa, sobre todo, en la explicación de cómo diferentes condiciones de dispersión espacio-temporal de los recursos, resultan en diferentes valores de *seguridad de alimentación* para cada territorio, permitiendo por tanto cubrir las necesidades alimentarias de los ocupantes primarios (aquellos que inicialmente llegan al sitio) del territorio y de uno o más ocupantes secundarios. Esto determina que el área requerida por los ocupantes primarios deba ajustarse a la dispersión de recursos, de forma tal que la seguridad de alimentación del área cubra sus probabilidades críticas de alimentación. Solo si esto se da los individuos podrán sobrevivir y reproducirse.

Para explorar diferentes escenarios de dispersión de recursos dentro de un territorio o área de actividad minima, los autores consideraron dos valores: uno es la heterogeneidad ambiental (H), determinada como la desviación estándar de la distribución normal de recursos y el otro valor es la productividad o cosecha promedio (R media) de un territorio, que es el valor promedio de unidades de recurso en cada parche dentro de todo el territorio. Al aumentar H, los territorios deben aumentar en tamaño para garantizar la *seguridad de alimentación* de los ocupantes primarios del área, a una determinada probabilidad crítica. Esto tiene como consecuencia un aumento en la R media del área. Mientras más heterogéneo es el ambiente, esta seguridad se alcanzará a niveles mayores de riqueza promedio en el territorio y por tanto será más factible la inclusión de animales secundarios con requerimientos menores y en consecuencia se forman grupos que denominan espaciales, pues su asociación se debe a razones espaciales y no necesariamente a interacciones sociales.

Macdonald y Carr (1989), retomaron su trabajo inicial para incorporar al modelo los costos y beneficios derivados de la sociabilidad. El argumento base que consideran, es sí para los ocupantes primarios los costos de tolerar ocupantes secundarios exceden o no los costos de expulsarlo y cómo esto puede ser mitigado por los beneficios derivados de tolerarlos. Los autores, enfatizan al término de su trabajo que la evolución de la sociabilidad y el que esta conducta se mantenga, se explica tanto por las circunstancias ecológicas presentadas en su primer modelo (e.g. que la oportunidad de coexistencia se basa en la heterogeneidad ambiental) como por los factores sociales analizados en su segundo modelo (e.g. ventajas y desventajas de adecuación derivadas de vivir en grupos).

Posteriormente Bacon *et al.* (1991a) hicieron una revisión cuidadosa del modelo de Carr y Macdonald (1986) y encontraron problemas derivados del planteamiento metodológico, particularmente del suponer que la productividad de recursos de un territorio tiene una distribución discreta. Por esto, estos autores propusieron un nuevo modelo más flexible y manejable, más robusto matemáticamente, en el que consideran a la riqueza dentro de un parche, como una variable continua más que como disponible o no (Bacon *et al.*, 1991b). En este nuevo modelo los autores asumen que los territorios o áreas de actividad están determinados por la distribución de los recursos alimenticios. Estos autores desarrollan el modelo y lo exploran analíticamente bajo diferentes combinaciones de parámetros, entre otras el caso de un territorio en el cual los recursos tienen una distribución marcadamente estacional, con diferentes tipos de recursos disponibles en diferentes periodos del año. Su modelo predice que el tamaño del territorio y el tamaño del grupo no deberán estar correlacionados.

De la revisión de estos trabajos se desprende la predicción teórica de la independencia entre el tamaño de las áreas de actividad y el tamaño de los grupos que lo pueden habitar, en diferentes condiciones ambientales. También la revisión muestra como el tamaño de las áreas de actividad en ambientes heterogéneos esta determinado en buena medida por el patrón de distribución espacial y temporal de los recursos. El argumento base de la Hipótesis de la Dispersión de Recursos considera la dispersión de recursos como un factor fundamental para la distribución espacial y la estructura social de los carnívoros sociales. Y aún cuando se explora en particular el recurso alimento, la mayor parte de los argumentos pueden aplicarse también a otros recursos limitantes (Macdonald, 1983; Kruuk y Macdonald, 1985).

En el presente trabajo se ha considerado que el tejón o coatí *Nasua narica*, un carnívoro social, común y abundante en ambientes heterogéneos, deberá comportarse conforme a lo que predice la HDR, es decir que el número de individuos en sus grupos deberá estar ajustado a la abundancia de aquellos recursos limitantes tales como el alimento o el agua, y que, por otra parte, el tejón ajusta el tamaño de las áreas que ocuparán estos grupos a la dispersión de tales recursos. En particular se ha explorado esta última suposición. El estudio de esta relación y de las predicciones de la HDR, es importante en un contexto general, pues contribuye al entendimiento de los mecanismos mediante los cuales esta especie enfrenta la marcada estacionalidad climática presente en el sitio de estudio. Es también relevante para el entendimiento de mecanismos que afectan la abundancia y la distribución espacial de este carnívoros dentro de la reserva.

En capítulos anteriores se han presentado resultados que apoyan parcialmente las predicciones derivadas de la hipótesis central del trabajo, tales como diferencias en densidad y en el tamaño de las áreas de actividad entre zonas con disponibilidad de recursos contrastante. En particular, los resultados del capítulo anterior, apoyan la predicción de que el tamaño de las áreas de actividad está relacionado con la dispersión del recurso más limitante, en este caso el agua durante la larga estación seca.

Resultados más concluyentes requieren de la realización de experimentos manipulativos en el campo. Kruuk y Macdonald (1985) han propuesto algunas manipulaciones, modificando la abundancia o la dispersión de los parches de recursos limitantes. Una modificación en la dispersión de los recursos limitantes debería causar cambios predecibles en las áreas de actividad. Para poner a prueba esta hipótesis se aumento el número de fuentes de agua y se alteró la dispersión de éstas en la zona de estudio, con esto se buscó que éstas fuesen más accesibles a los grupos de tejones, dentro y fuera de sus áreas de actividad. Con la manipulación anterior se esperaba una reducción en la distancia promedio que los animales necesitaban recorrer para acceder al agua y por tanto, una reducción en el tamaño de sus áreas de actividad, en proporción a la disminución en la dispersión de agua de cada área de actividad.

MATERIAL Y MÉTODOS

Sitio de Estudio

El sitio de estudio fue Cumbres, en la porción central de la Reserva de la Biosfera de Chamela-Cuixmala (Figura 1 en la página 46). Esta área está caracterizada por una topografía irregular con pequeños cerros de hasta 400 m.s.n.m. y sobre todo por una gran variación estacional en la disponibilidad y dispersión de agua. En Cumbres el agua solo es abundante en los arroyos que llevan agua durante la estación lluviosa y es extremadamente limitada y muy dispersa durante la estación seca. En general, se pueden identificar tres tipos de vegetación en Cumbres: 1) la vegetación dominante es la selva baja caducifolia que cubre la mayor parte del sitio, 2) selva mediana en pequeños parches en algunos valles y en las áreas de mayor concentración de humedad y 3) selva mediana a lo largo de los cauces de los arroyos temporales, que en este trabajo se denominará selva de arroyo. En Cumbres existe un sistema de caminos de terracería de cerca de 20 kilómetros que llega hasta la cima de uno de los cerros de mayor altitud en el centro de este sitio de estudio (Figura 2). Este camino cruza casi todo Cumbres de oeste a este y de sur a norte, y pasa también por casi todas las áreas de actividad de los tejones estudiados.

Diseño del experimento

El experimento se limitó a la estación seca, pues en Cumbres el agua se convierte en el factor más limitante durante este periodo, restringida a unos pocos depósitos naturales, pequeños y muy dispersos. Estos cuerpos de agua fueron identificados y mapeados con el empleo de un posicionador geográfico y un mapa topográfico del área. Al mapa de Cumbres se sobrepuso una cuadrícula de celdas equivalentes a un kilómetro cuadrado, en la escala del mapa. Se consideró como área de referencia para el experimento una superficie de 4 x 6 kilómetros, que incluyó todas las celdas de 1 km^2 en las que se localizó un depósito de agua, un sitio de trampeo o se localizó un tejón mediante radiotelemetría con fecha anterior al inicio del experimento. En esta área de 24 km^2 se localizaron en total 17 cuerpos de agua: una represa de aproximadamente 1 ha, 1 poza de

18 m^2, 1 de 8 m^2, 8 de 4 m^2 y 6 de 2 m^2. Después cada celda de 1 km^2 se subdividió en celdas de 200 x 200 m para estimar la distribución de los cuerpos de agua y se obtuvo un promedio 0.03 cuerpos de agua por celdilla (ds = 0.171; CV = 5.69; n = 600; Figura 2a), es decir, un cuerpo de agua aproximadamente cada 33 celdas de 200 m^2 o un cuerpo de agua cada 1.33 km^2.

El experimento se realizó en 1996, durante los meses de mayo y junio, cuando la disponibilidad de agua llega a su nivel menor. El tratamiento consistió en colocar en forma regular depósitos artificiales de agua, de tal manera que durante este periodo crítico aumentara la disponibilidad de agua y disminuyera la dispersión de las fuentes de agua. Para lograr esto, se trató de colocar las fuentes de agua adicionales en aquellos sectores del área de estudio en los que no hubiese cuerpos de agua, sin embargo la principal limitante para su colocación fue la posibilidad de mantener los depósitos artificiales con agua. Por esta razón la mayor parte de estos depósitos fueron ubicados a los lados del camino que bisecta la reserva (y también las áreas de actividad de los grupos seguidos) de tal manera que la distancia entre tinas o entre tinas y los depósitos ya existentes fuera de 500 m (Figura 2b). Esta disposición permitió llenar una vez por semana, todas la tinas mediante una pipa que recorría los caminos. Los depósitos artificiales fueron tinas de 100 l, preparadas cortando en sentido vertical 12 tambos de metal de 200 litros, lavando después cada mitad hasta eliminar restos de pintura o aceite. Todas las tinas (n = 24) se pusieron a los lados del camino salvo tres, que se colocaron en el cauce de arroyos a más de 500 m del camino y se llenaban una vez por semana empleando bidones de 25 l. Todas las tinas fueron puestas en sitios sombreados para minimizar la perdida de agua por evaporación y se determinó su ubicación mediante un posicionador geográfico. Las colocación de las tinas representó un cambio importante en la disponibilidad y dispersión de agua, pues el promedio de cuerpos de agua por unidad de superficie, aumento 2.3 veces a 0.068 por celdilla de 200 m^2,(ds =

0.252; *CV* = 3.69; *n* = 600, Figura 2b), es decir un cuerpo de agua aproximadamente cada 15 celdas de 200 m^2 o un cuerpo de agua cada 0.615 km^2.

Para evaluar el resultado del experimento se planteó estimar las áreas de actividad bimensuales de los animales seguidos, en los periodos enero - febrero, marzo - abril y mayo - junio de 1996, así como la dispersión de los cuerpos de agua presentes en cada área bimensual. Se esperaba encontrar diferencias significativas entre los valores de los dos primeros bimestres y los del bimestre en el que los depósitos de agua artificiales estuvieron presentes. Particularmente esperaba que la dispersión de agua al interior de cada área de actividad fuera significativamente menor en el último bimestre y por tanto también las áreas de actividad. También, esperaba que el cambio en el tamaño de las áreas de actividad, fuera proporcional a la disminución en la dispersión de agua. Por tanto esperaba una regresión lineal negativa y significativa entre ambos valores.

Areas de actividad y dispersión de agua

Para obtener información de las áreas de actividad bimensuales de los grupos de tejones, se procuró tener el mayor número posible de grupos de tejones marcados. Se consideró a los grupos que ya estuvieran marcados antes del inicio del experimento y se trató de capturar más, para lo que se emplearon trampas Tomahawk cebadas con sardinas. Los animales capturados fueron sedados con Ketamina, para tomar los valores morfométricos estándares y marcarlos con aretes de plástico de color numerados y con collares de radiotelemetría para obtener las localizaciones que definieran las áreas de actividad de los animales. Se procuró al menos dos veces por semana, ubicar a cada hembra marcada desde tres estaciones de recepción fijas (cada una con un arreglo de dos antenas de 11 elementos y una caja interruptora de señal nula y señal pico; AVM, Inc.). Además, se hicieron mensualmente dos sesiones de monitoreo nocturnas (de las 1900 hr a las 0800 hr) y dos diurnas (de las 0800 hr a las 2100 hr) en las que se registró cada 30 minutos la presencia o ausencia de la señal, su azimuth o procedencia en grados y características de la misma relacionadas con la actividad del animal. Estos datos se procesaron con el programa TRITEL (Biggins *et al.*, 1992) para convertirlos a coordenadas UTM y ubicarlos en el mapa topográfico del (1:50,000). Los datos se analizaron empleando el programa TRACKER (ABS Radio Location Systems, Suecia). Se estimaron las áreas de actividad bimensuales y totales como el Polígono Convexo Mínimo (PCM) del 95 % de todos los puntos independientes (Swihart y Slade, 1985) obtenidos en cada periodo para cada animal.

La dispersión del agua dentro de cada área de actividad para cada periodo bimensual se estimó de dos maneras: 1) como el promedio de cuerpos de agua por cuadro de 200 x 200 m, en el total de cuadros incluidos en cada PCM y 2) como el promedio de las distancias de cada localización a la fuente de agua más cercana, con agua en la fecha de su obtención. Se obtuvieron estos valores para comparar cambios en los movimientos de los animales al colocar las tinas. Las diferencias entre las áreas de actividad bimensuales y en la dispersión de agua dentro de cada área de actividad antes y después de la colocación de las tinas se evaluaron con pruebas de *t*. Para evaluar la relación entre las áreas de actividad y la dispersión de los cuerpos de agua en los diferentes periodos bimensuales se hicieron análisis de correlación.

RESULTADOS

Al inicio de la temporada seca 95-96 se tenía a tres hembras marcadas con collares de radiotelemetría, por lo que se procedió a capturar más hembras. Se logró la captura de dos hembras entre diciembre y enero y dos más, a principios de mayo. Por tanto, el tamaño máximo de muestra fue de siete individuos. El pequeño tamaño de muestra, limitó la posibilidad de llevar a cabo el experimento, lo que además se vio afectado por problemas en la localización de los individuos durante enero y febrero, pues en estos meses la señal de radio de dos hembras, no se pudo registrar en más de cuatro ocasiones. Pese a esto se obtuvieron datos para los bimestres de marzo - abril (anterior a la colocación de las tinas) y mayo - junio (ya con las tinas colocadas) de 1996.

La colocación de las tinas si representó un cambio en la dispersión de las fuentes de agua dentro de cada área de actividad, aumentando en forma significativa el número promedio de fuentes de agua por cuadro de 200 m^2 dentro de cada área de actividad (t = -2.9082; ν = 10; P = 0.0113; Tabla 1). Sin embargo esto no redujo la distancia promedio de cada localización de los animales seguidos a los cuerpos de agua (t = 0.776; ν = 10; P =0.4658; Tabla 1), ni en el área de actividad bimensual promedio (t = 0.3606; ν =10; P = 0.7657; Tabla 1).

El tamaño de las áreas de actividad bimensuales no se correlacionó con el promedio de fuentes de agua por cuadro de 200 m^2 (r = 0.133, P = 0.174, n = 10) ni con el valor promedio de las distancia de cada localización a la fuente de agua más cercana (r = -0.129, P = 0.72, n = 10).

DISCUSION

Tanto la relación entre el tamaño de las áreas de actividad y la dispersión de agua encontrada en el capítulo anterior como, como los modelos teóricos acerca de la HDR sugieren que es factible esperar que cambios en la dispersión de un recurso tan limitante en la zona de la RBCC como el agua, tuvieran un efecto concomitante en el tamaño de las áreas de actividad de los grupos de coatí que habitan esta zona y sin embargo con este diseño experimental no se pudo detectar.

Un factor a considerar son los problemas logísticos para el desarrollo del experimento, no obstante, fue posible obtener datos para cinco hembras en el bimestre previo a la colocación de las tinas y en el bimestre en el que las tinas funcionaron, este tamaño de muestra pudo afectar la detección de un efecto del cambio en la dispersión de las fuentes de agua sobre las áreas de actividad bimensuales de los tejones.

Además, una combinación de varios factores pudieron causar que no se detectase un efecto del tratamiento. La primera podría ser una apreciación sobrestimada del nivel y la velocidad a la que la respuesta se presentaría. Esto significaría que el impacto de un experimento como éste tendría que evaluarse en un periodo de tiempo mayor, particularmente si se esperase un ajuste del tamaño de las áreas de actividad total, pues de acuerdo con la HDR, el ajuste de las áreas de actividad a la dispersión de recursos deberá ser de tal manera que garantice suficientes recursos para la reproducción o sobrevivencia, de al menos una unidad reproductiva, durante el periodo de mayor escasez (Macdonald, 1984; von Schantz, 1984).

Por tanto, puede ser que el tamaño de las áreas de actividad de los coatíes en un sitio como la RBCC, esté ajustado en particular a la dispersión de las fuentes de agua en los años más secos, (e.g. la temporada de lluvias de 1994, en la que llovió solo 467 mm). La temporada seca durante la que se realizó el experimento siguió a una temporada de lluvias típica, en la que llovió 782 mm , un poco más que el promedio anual de 748 mm reportado para la zona entre 1977 y 1984, con un intervalo entre 585 y 961 mm (Bullock,1986).

Para mitigar este efecto no se buscó evaluar la respuesta al experimento como un ajuste en las áreas de actividad totales, sino más bien como un cambio en la distancia promedio a la que un animal tendría que desplazarse en busca de agua y por tanto la respuesta se podría detectar como un ajuste del área de actividad bimensual. Sin embargo, aún evaluando estas respuestas, no se encontró una correlación significativa entre estos valores. Es posible que desde la perspectiva de las necesidades de los animales, la colocación de las tinas no haya representado una disminución significativa en la dispersión de fuentes de agua.

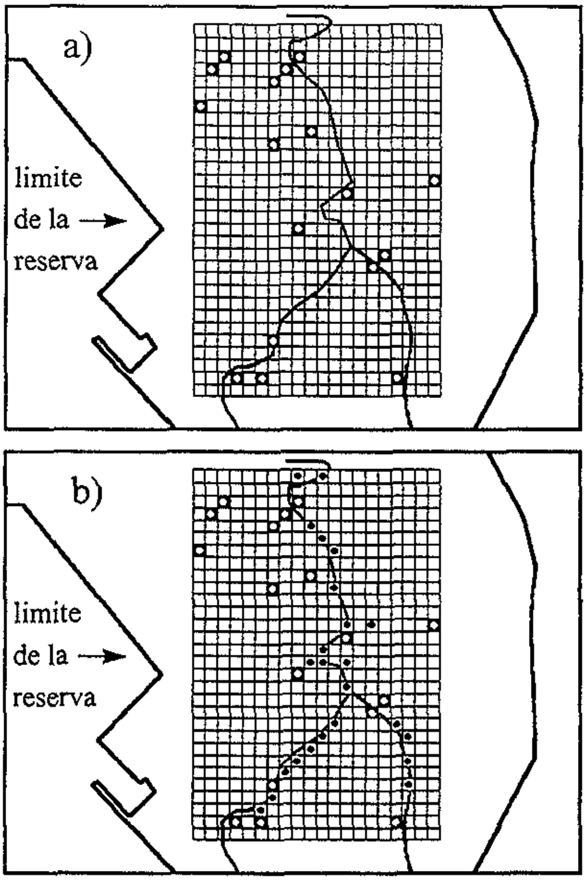
Una explicación alternativa a esto sería que, no es solo la dispersión del agua la que afecta el tamaño de las áreas de actividad de los tejones, si no también la disponibilidad de artrópodos. Conforme la época seca avanza la abundancia de artrópodos disminuye y aumenta su dispersión. Si el agua suplementada esta disponible para los tejones, pero no para los artrópodos, entonces los tejones aún tienen que desplazarse mucho para obtener suficiente alimento. Finalmente es posible también que el resultado del presente experimento este indicando justamente, que el movimiento de los tejones y el tamaño de sus áreas de actividad no responde a la dispersión de los recursos, o lo hace solo en forma secundaria. En este caso, otro factor u otra combinación de factores ambientales pueden determinar los movimientos y el tamaño de las áreas de actividad de los tejones, como por ejemplo la competencia intra o entre especies por los recursos limitantes, o la depredación.

Aportar evidencias concluyentes para esto, dados los resultados del experimento realizado, implica otro diseño experimental tomando en consideración las dificultades anteriormente mencionadas y explorando otras alternativas que afectan el movimiento de los animales.

Tabla 1. Tamaños estimados para las áreas de actividad bimensuales (AB) y valores de dispersión de agua en cada área de actividad: promedio de fuentes de agua por cuadro de $200m^2$ (AC) y el promedio de las distancias de cada localización de un animal, a la fuente de agua más cercana al momento de registrarlo (DAg).

	marzo-abril			**mayo-junio**		
Grupo	**AB (ha)**	**AC**	**DAg (m)**	**AB (ha)**	**AC**	**DAg (m)**
1	103.2	0	1011.0	205.8	0	912.0
2	433.0	0.011	614.4	257.0	0.065	757.6
3	274.9	0.024	485.2	130.0	0.099	451.2
4	274.9	0.010	625.5	459.8	0.085	413.5
5	-	-	-	340.6	0.048	374.9
6	-	-	-	47.8	0.096	402.1
7	144.1	0.020	408.8	71.8	0.037	384.1

Figura 2. Distribución de cuerpos de agua dentro del área de estudio, en Cumbres, dividida en 600 cuadros de 200 m². a) Ubicación de los cuerpos de agua naturales (cuadros oscuros con centro claro); b) Ubicación de cuerpos de agua y además la ubicación de las tinas (cuadros claros con un punto oscuro en el centro). La línea en el centro de la cuadrícula representa el camino de terraceria que cruza la reserva.



CAPITULO V

CONCLUSIONES

CONCLUSIONES

Con este trabajo obtuve resultados sobre la historia natural del tejón (*Nasua narica*) en la RBCC, porción media de su área de distribución geográfica, que apoyan patrones de la especie, previamente observados al norte y al sur de su distribución.

La densidad del tejón en la RBCC confirmó el patrón de variación latitudinal reportado para la especie, con un valor intermedio entre los reportados en sitios al sur y al norte de la reserva. La disponibilidad de recursos y su variación estacional tiene un efecto importante en la variación en la densidad de tejones, aun a una escala geográfica reducida, como lo sugiere el hecho de que la densidad de tejones, aún dentro de la RBCC fue casi el doble en el sitio con mayor disponibilidad de recursos (agua y alimento) y menor variabilidad estacional en este parámetro.

En cuanto al tamaño promedio de los grupos de coatí, los valores encontrados no difierierón de lo reportado para otros sitios y tampoco difirieron entre zonas dentro de la reserva, por lo que no es claro el efecto de la estacionalidad sobre el número de individuos por grupo.

En cuanto a los hábitos alimentarios del tejón, se encontró que en la RBCC su dieta se compone sobre todo de artrópodos y fruta, como en otros sitios. Sin embargo los coatíes en la RBCC, presentaron un mayor consumo de vertebrados y la mayor diversidad alimentaria reportada. Además esta diversidad cambió estacionalmente; fue menor en la estación lluviosa en la que no consumieron vertebrados y aumentó durante la estación seca, para alcanzar el valor más alto al final de este periodo. Lo que está relacionado con cambios estacionales en la disponibilidad de los artrópodos y la fruta.

El tamaño estimado de sus áreas de actividad también apoyó el patrón de variación latitudinal, que se ha explicado por diferencias en la productividad de cada sitio. El tamaño promedio de área de actividad en la zona de estudio, fue mayor que en selvas tropicales al sur de su distribución y menor que al norte, en zonas semiáridas. Además, dentro de la reserva, fue posible apreciar este patrón, pues las áreas de actividad de los grupos de tejón en la RBCC fueron casi cinco veces menores, en el sitio más productivo y con menos variación estacional en los recursos disponibles, que en el sitio con menos recursos y mayor variación estacional.

Los resultados respecto a la distribución de la actividad de los tejones a lo largo de las horas del día, a las distancias recorridas por día, al uso de sus áreas de actividad y la selección de hábitats, en conjunto, muestran que los tejones enfrentan la estacionalidad ambiental con una serie de ajustes en su comportamiento. Esto posiblemente les permite tener acceso a aquellos hábitats con mayor disponibilidad de recursos y compensar la reducción progresiva que se da, durante la estación seca, en este factor ambiental. Esta estrategia de comportamiento difirió entre sexos. Durante la estación seca, la distancia recorrida por día, la frecuencia de actividad por hora del día y el tamaño de las áreas de actividad, no difirió entre las bandas de hembras y los machos solitarios. Sin embargo durante la estación lluviosa, las bandas de hembras se desplazaron menos por día, presentaron una menor frecuencia de actividad por hora y usaron áreas de actividad menores que durante la estación seca, a diferencia de los machos solitarios que no presentaron variación estacional en estos parámetros. Asimismo, los machos solitarios de tejón, presentaron más actividad nocturna que las hembras durante todo el año.

En cuanto al uso y selección de hábitats, tanto los machos solitarios de tejón, como las hembras en grupos, seleccionaron la selva de arroyo sobre otros hábitats. Esta selva presenta, durante la estación seca, mayor humedad edafica y más abundancia de artrópodos de la hojarasca que la selva seca adyacente. Además, este tipo de selva tiene las fuentes de agua disponibles en el periodo crítico del año. Sin embargo, también la selección de este tipo de hábitat difirió entre sexos, pues las bandas de hembras seleccionaron la selva de arroyo, en la escala que se denominó gruesa o amplia, pues sus áreas de actividad incluyen una mayor proporción de este hábitat, que la esperable por azar en relación a los hábitats disponibles en el sitio de estudio. Por el contrario, en las áreas de actividad de los machos, la proporción de diferentes hábitats no fue distinta de la esperable por azar, pero sí usaron la selva de arroyo incluida en sus áreas de actividad, con mayor frecuencia de la esperable por azar, es decir presentaron una selección de hábitat en una escala que se denominó fina o detallada.

En conjunto los resultados apoyan el patrón esperado de variación latitudinal en la densidad, el tamaño de los grupos y el tamaño de las áreas de actividad de los tejones atribuido a diferencias latitudinales en la productividad y es interesante como la variación local dentro de la reserva parece reproducir este patrón. Así mismo es importante destacar que la variación en el tamaño de las áreas de actividad de los tejones, dentro de la reserva, se relacionó en forma inversa con la dispersión de las fuentes de agua durante la estación seca, relación que apoya las predicciones de la Hipótesis de Dispersión de Recursos. Aunque los datos obtenidos en el experimento de manipulación de la dispersión de agua, sugieren que esta relación no es tan estrecha ni tan directa como podría parecer solo por las correlaciones encontradas.

La información generada en esta investigación ayuda a entender los efectos de la estacionalidad ambiental sobre el tejón y puede ayudar a predecir algunas de las tácticas que pueden usar otros carnívoros presentes en la reserva para enfrentar las limitantes estacionales de este sitio. Este tipo de respuestas pueden contribuir al éxito de las poblaciones de esta especie en los neotrópicos. Este trabajo también contribuye a entender la relación de la heterogeneidad ambiental con los parámetros básicos de la sociabilidad (e.g. densidad, tamaño de los grupos y el tamaño de las áreas de actividad) en carnívoros. Información que puede ser importante para el diseño de estrategias de manejo, administración y conservación de la biodiversidad de la RBCC. La población de tejones estudiada en la RBCC podría ser considerada como un modelo para predecir que tipo de respuestas conductuales a la estacionalidad ambiental pueden presentar otras poblaciones de tejón en selvas secas en México y Centro América.

LITERATURA CITADA

Aebisher, N. J., P. A. Robertson y R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology, 74: 1313-1325.

Aguirre, A. A. y E. E. Starkey. 1994. Wildlife disease in U.S. National parks: historical and coevolutionary perspectives. Conservation Biology 8: 654-661.

Alldredge, J. R. y J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management, 50: 157-165.

Andrewartha, H.G. y L.C. birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.

August, P.V. 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. Ecology 64 (6): 1495-1507.

Aranda, M. 1991. Wild mammal skin trade in Chiapas, Mexico, pp. 175 - 177. in Neotropical Wildlife Use and Conservation. (J. G. Robinson y K. H. Redford, eds.). University of Chicago Press, Chicago, E. U. A. 520 pp.

----. 1993. Hábitos alimentarios del jaguar (Panthera onca) en la Reserva de la Biosfera de Calakmul, Campeche. in Medellín, R. y G. Ceballos (eds.). Avances en el estudio de los mamíferos de México. Publicaciones Especiales, Vol. I, AMMAC. México, D.F., México. Pp. 464.

Bacon, P.J., F.G. Ball, y P.G. Blackwell. 1991a. Analysis of a model of group territoriality based on Resource Dispersion Hypothesis. Journal of Theoretical Biology 148: 433-444.

----. 1991b. A model for territory and group formation in a heterogeneous habitat. Journal of Theoretical Biology, 148: 445-468.

Beck, D.D. y C. H. Lowe. 1991. Ecology of the beaded lizard Heloderma horridum in coastal México. Journal of Herpetology 25: 395-406.

Begon, M., J.L. Harper and C.R. Townsend, 1986. Ecology. Individuals, Populations and Communities. Sinauer Associates Inc. Publishers, Sunderland, MA.

Bekoff, M., T. J. Daniels, and J. L. Gittleman. 1984. Life history patterns and the comparative social ecology of carnivores. Annual Review of Ecology and Systematics 15:191-232.

Biggins, D. E., L. R. Hanebury and J. L. Godbey. 1992. Instructions for radio-tracking and using program TRITEL. U. S. Fish and Wildlife Service, National Ecology Research Center, Fort Collins, Colorado, USA, 44 pp.

Bullock, S.H. 1986. Climate of Chámela, Jalisco, and trends in the south coastal region of México. Archives for Meteorology, Geophysics, and Bioclimatology. 36: 297-316.

Bullock, S. H. y J. A. Solis-Magallanes. 1990. Phenology of canopy trees of a tropical deciduous forest in México. Biotropica, 22 : 22-35.

Burger, J. y M. Gochfeld. 1992. Effect of group size on vigilance while drinking in the coatí, Nasua narica in Costa Rica. Animal Behavior 44: 1053-1057.

Byers, C. R. y R. K. Steinhorst. 1984. Clarification of a technique for analysis of utilization - availability data. Journal of Wildlife Management, 48: 1050-1053.

Camponotus AB. 1994. Tracker version 1.1. Wildlife tracking and analysis software. User manual. Sweden.

Carr, G. y D. W. Macdonald. 1986. The sociality of solitary foragers: a model based on resource dispersion. Animal Behaviour 34: 1540-1549.

Caso, A. 1994. Home range and habitat use of three neotropical carnivores in northeast México. Unpublished MS thesis. Texas A & M University, Kingsville. pp.1-86

Caughley, G. y A. Gunn. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, Massachusetts. 459 pp.

Conroy, J. D. 1964. Sarcoptic acariasis in a coatimundi. Modern Veterinary Practice, 45: 80-81.

Ceballos, G. 1989. Population and community structure of small mammals from tropical deciduous and arroyo forests in Western México. Ph. D. dissertation, The University of Arizona, 158 pp.

----. 1995. Vertebrate diversity, ecology, and conservation in neotropical dry forests. Pp 195-220. in Seasonally dry tropical forests (S. H. Bullock, H. A. Mooney and E. Medina, eds.). Cambridge University Press, 450 pp.

Ceballos, G. y A. Garcia. 1995. Conserving neotropical biodiversity: the role of dry forests in western México. Conservation Biology, 9: 1349-1356.

Ceballos, G. y A. Miranda. 1986. Los Mamíferos de Chámela, Jalisco. Instituto de Biología, Universidad Nacional Autónoma de México. México, D. F. 436 pp.

Clark, C. y M. Mangel. 1986. The evolutionary advantages of group foraging. Theoretical Population Biology, 30: 45-75.

Clutton-Brock, T.H. y P.H. Harvey. 1978. Mammals, resources and reproductive strategies. Nature 27: 191-195.

Coates-Estrada, R. y A. Estrada. 1986. Manual de identificación de campo de los mamíferos de la Estación de Biología "Los Tuxtlas". Instituto de Biología, Universidad Nacional Autónoma de México, México, D. F., 151 pp.

Chapman, C. A., R. Wrangham, y L J. Chapman (1994) Indices of habitat-wide fruit abundance in tropical forests. Biotropica, 26:160-171

Delibes, M., L. Hernandez, y F. Hiraldo. 1989. Comparative food habits of three carnivores in Western Sierra Madre, México. Zeitschrift Säugetierkunde, 54:107-110.

Diamond, J. 1986. Overview: laboratory experiments, field experiments and natural experiments. Community Ecology (eds J. Diamond & T. J. Case), pp. 3-22. Harper and Row Publishers Inc., NY, USA.

Doncaster, C. P. y D. W. Macdonald. 1992. Optimum group size for defending heterogeneous distributions of resources: a model applied to red foxes, *Vulpes vulpes*, in oxford city. Journal of Theoretical Biology 159: 189-198.

----. y R. Woodroffe. 1993. Den site can determine shape and size of badger territories: implications for group-living. Oikos 66: 88-93.

Estrada, A., G. Halffter, R. Coates -Estrada y D. A. Merritt. 1993. Dung beetles attracted to mammalian herbivore (Alloutta palliata) and omnivore (Nasua narica) dung in the tropical rain forest of Los Tuxtlas, México. Journal of Tropical Ecology, 9: 45-54.

Fedigan, L. M. 1990. Vertebrate predation in Cebus capucinus: meat eating in a neotropical monkey. Folia Primatologica, 54: 196-205.

Fleming, T. H. 1977. Response of two species of tropical heteromyid rodents to reduced food and water availability. Journal of Mammalogy, 58: 102-106.

Frankie, G.W., H.G. Baker y P.A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62: 881-919.

Foster, R. B. 1982. The seasonal rhythm of fruitfall in Barro Colorado Island. The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes. (eds E. G. Leigh, A. S. Rand & D. S. Windsor), pp. 151-172. 2nd. Printing. Smithsonian Institution. Washington, D.C.

Geffen, E., R. Hefner, D. W. Macdonald y M. Ucko. 1992. Habitat selection and home range in the Blanford's fox, Vulpes cana: compatibility with the resource dispersion hypothesis. Oecologia 91: 75-81.

Gilbert B, 1973. Chulo. New York: Alfred A. Knopf.

Gittleman, J. L.1989. Carnivore group living: comparative trends. Carnivore Behaviour, Ecology, and Evolution. (ed., J. L. Gittleman), pp. 183-207. Chapman and Hall, London.

Glanz, W.E. 1982. The terrestrial mammal fauna of Barro Colorado Island: censuses and long - term changes. in The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes (E.G. Leigh, A.S. Rand and D. S. Windsor, eds.) 2nd. Printing. Smithsonian Institution. Washington, D.C.

Glanz, W.E. 1990. Neotropical mammal densities: how inusual is the community on Barro Colorado Island, Panama?. Pp. 287-313 in Four Neotropical rainforests. (A.H. Gentry, de.). Yale University Press. New Haven, CT, USA.

Gompper, M. 1994. The importance of ecology, behavior, and genetics in the maintenance of coati (Nasua narica) social structure. Ph D dissertation. Knoxville: University of Tennessee. 238 Pp.

----. 1995. Nasua narica. Mammalian Species No. 487 pp. 1-10.

----. 1996. Sociality and asociality in white-nosed coatis (Nasua narica): foraging costs and benefits. Behavioral Ecology, 7: 254-263.

----. 1997. Population ecology of the white-nosed coati (Nasua narica) on Barro Colorado Island, Panama. Journal of Zoology (London), 241: 441-455.

Gompper, M. y J. L. Gittleman. 1991. Home range scaling: intraspecific and comparative trends. Oecologia, 87: 343-348.

Gompper, M., J.L. Gittleman y R. K. Wayne. 1998. Dispersal, philopatry, and genetic relatedness in a social carnivore: comparing males and females. Molecular Ecology 7:157-165

Grier, J.W. 1984. Biology of Animal Behavior. Times Mirror / Mosby College Publishing.

Hass, C. C. 1997. Ecology of the white -nosed coatis in the Huachuca Mountains, Arizona. Unpublished report, Arizona Game & Fish Department, Phoenix, Arizona. Pp. 52.

Hersteinsson, P. y D. W. 1982. Some comparisons between red and artic foxes, Vulpes vulpes and Alopex lagopus, as revealed by radio tracking. Proceedinga of the Symposia of the Zoological Society of London, 49: 259-288.

Holmes, J. C 1996. Parasites as threats to biodiversity in shrinking ecosystems. Biodiversity and Conservation 5: 975-983.

Janzen, D. H. 1970. Altruism by coatis in the face of predation by Boa constrictor. Journal of Mammalogy, 51: 387-389.

----. 1988. Tropical dry forests: the most endangered major tropical ecosystem. Biodiversity (ed E. O. Wilson), pp. 130-137. National Academy Press, Washington.

Janzen, D. H. y T. W. Schoener. 1968. Differences in insect abundance and diversity between more humid and drier sites during a tropical dry season. Ecology, 49: 96-110.

------ y D. E. Wilson. 1983. Mammals. Pp. 426-442. in: Costa Rican natural history (D. H. Janzen, ed.). University of Chicago Press, Chicago, 816 pp.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, 6: 65-71.

Kalema, G. 1997. An outbreak of a skin disease in free-ranging Mountain Gorilla, Gorilla gorilla beringei in Bwindi Impenetrable national Park, southwestern Uganda. Pp. 190. Seventh

International Theriological Congress. Abstract of oral and poster papers. Acapulco, México. September 6-11.

Kaufmann, J.H. 1962. Ecology and social behavior of the coati, Nasua narica on Barro Colorado Island, Panama. University of California Publications, Zoology, 60: 95-222.

Kaufmann, J. H., D. V. Lanning and S. E. Poole. 1976. Current status and distribution of the coati in the United States. Journal of Mammalogy 57: 621-637.

Krebs, Ch. J. 1989. Ecological Methodology. Harper Collins, New York.

Krebs, J. R. y N. B. Davies. 1987. An Introduction to Behavioural Ecology. Second Edition. Blackwell Scientific Publications, Oxford.

Krinsley, J.S. 1989. An ethogram of the white-nosed coati (Nasua narica narica). M. Sc. Thesis, University of Wisconsin, Madison, 106 pp.

Kruuk, H. y D. Macdonald. 1985. Group territories of carnivores: empires and enclaves. Pp. 521-536. in Behavioral Ecology: Ecological Consequences of Adaptative Behaviour (R. M. Sibley and R. H. Smith, eds.). Blackwell Scientific Publications, Oxford, 620 pp.

------ y T. Parish. 1982. Factors affecting population density, group size and territory size of the European badger Meles meles. Journal of Zoology, London 196: 31-39.

Lanning, D.V. 1976. Density and movements of the coati in Arizona. Journal of Mammalogy 57: 609-611.

Leigh, E.G., A.S. Rand y D.M. Winsor. (Eds.). 1985. The Ecology of a Tropical Forest: Seasonal Rhytms and Long Term Changes. 2nd. Printing. Smithsonian Institution. Washington, D.C.

Leopold, S.A. 1959. Wildlife of México. University of California Press. Berkeley, California, USA. 568 pp.

Levings, S. C. y D. M. Windsor. 1982. Seasonal and annual variation in litter arthropods populations. The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes. (eds E. G. Leigh, A. S. Rand & D. S. Windsor), pp. 355-388. 2nd. Printing. Smithsonian Institution. Washington, D.C.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princetown University Press, Princetown, USA. 120 pp.

Lister, B. C. y A. García . 1992. Seasonality, predation, and the behaviour of a tropical mainland anole. Journal of Animal Ecology 61: 717-733

Lominicki, A. 1988. Population Ecology of Individuals. Princetown University Press, Princetown, NJ.

MacArthur, R. H. 1972. Geographical Ecology. Patterns in the Distribution of Species. Princetown University Press, Princetown, NJ.

Macdonald, D. W. 1981. Resource dispersion amd the social organisation of the red fox, Vulpes vulpes. Pp. 918-949. Proceeding of the Worldwide Furbearer Conference, Vol. 2 (J. A. Chapman y D. Pursley). University of Maryland Press.

----. 1983. The ecology of carnivore social behaviour. Nature, 301: 379-384.

----. 1984. Reply to von Schantz. Nature 307: 390.

Macdonald, D. W. y G. Carr. 1989. Food security and the rewards of tolerance. Comparative Socioecology: The behavioural ecology of humans and other mammals. (eds V. Standen & R. A. Foley), pp. 75-99. Blackwell Scientific Publications, Oxford.

Mace, G. M., P. H. Harvey y T. H. Clutton-Brock. 1984. Vertebrate home-range size and energetic requirements. Pp.32-53. in The ecology of animal movement (I. R. Swingland and P. G. Greenwood, eds.). Clarendon Press, Oxford, UK. 311 pp.

MacKinnon, J., K. MacKinnon y , G. Child y J. Thursell (compilators). 1986. Managing Protected Areas in the Tropics. IUCN / UNEP, Glan, Switzerland.

Martinez-Yrizar, A. y J. Sarukhan. 1990. Litterfall patterns in a tropical deciduous forest in México over a five-year period. Journal of Tropical Ecology, 6: 433-444.

May, R. 1988. Conservation and disease. Conservation Biology 2: 28-30.

McCallum, H. y A. Dobson. 1995. Detecting disease and parasite threats to endangered species and ecosystems. Trends in Ecology and Evolution 10: 190 - 194.

Meier, J. E. 1976. Sarcoptic mange in Yucatanian coatimundis (Nasua narica yucatanica). Journal of Zoo Animal Medicine, 7: 31

Milton, K. 1990. Annual mortality patterns of a mammal community in central Panama. Journal of Tropical Ecology 6: 493-499.

Mohr, C. O. 1947. Table of equivalent populations of North American mammals. American Midland Naturalist, 37: 223-249.

Muller, G. H., R. W. Kirk y D. W. Scott. 1990. Small Animal Dermathology. W.B. Saunders Company, Philadelphia, PA, USA.

Murphy, P. G. y A. E. Lugo. 1986. Ecology of tropical dry forest. Annual Review of Ecology and Systematics 17: 67-88.

Neu, C. W., C. R. Byers y J. M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management, 38: 541-545.

Newcomer, M. W. y D. D. DeFarcy. 1985. White-faced capuchin (Cebus capucinus) predation on a nestling coati (Nasua narica). Journal of Mammalogy, 66: 185-186.

Nuñez, R. 1999. Habitos alimentarios del jaguar (Panthera onca, Linnaeus 1758) y del puma (Puma concolor, Linnaeus 1771) en la Reserva de la Biosfera Chamela-Cuixmala, Jalisco, México. Tesis de Licenciatura, Universidad Michoacana de San Nicolas Hidalgo, Morelia, Michoacan, México.

Orians, G. H. y J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. The American Naturalist, 137: S29-S49.

Pearson, D. L. y J. A. Derr. 1986. Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. Biotropica, 18: 244-256.

Pulliam, H. R. y T. Caraco. 1984. Living in groups: is there an optimal group size?. In: Behavioural Ecology: An Evolutionary Approach (eds J. R. Krebs y N. B. Davies), pp. 122-147. Second Edition. Sinauer Associated, Inc. Sunderland.

Primack, R. B. 1993. Essentials of Conservation Biology. Sinauer, Sunderland, MA, USA.

Ratnayeke, S., A. Bixler y J. L. Gittleman. 1994. Home range movements of solitary, reproductive female coatis, Nasua narica , in south eastern Arizona. Journal of Zoology (London), 233: 322-326.

Risser, A.C. Jr. 1963. A study of the coatimundi (Nasua narica) in southern Arizona. M.S. Unpublished thesis, University of Arizona, Tucson, 77 pp.

Rood, J. P. 1986. Ecology and social evolution of mongooses. In: Ecological aspects of social evolution. Birds and mammals (D. I. Rubenstein y R. W. Wrangham, eds). Princeton, New Jersey: Princeton University Press; 131-152.

Russell, J. K. 1979. Reciprocity in the social behavior of coatis (Nasua narica). Ph D. dissertation. University of North Carolina, Chapel Hill, USA, 64 pp.

Russell, J. K. 1982. Timing of reproduction by coatis (Nasua narica) in relation to fluctuations in food resources. Pp. 413-431. in: The Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes (E. G. Leigh, A. S. Rand and D. S. Windsor, eds.). 2nd. Printing. Smithsonian Institution, Washington, D. C. 468 pp.

Sáenz, J. 1994. Ecología del pizote (Nasua narica) y su papel como dispersador de semillas en el bosque seco tropical, Costa Rica. Tesis de Maestria en Manejo de Vida Silvestre. Universidad Nacional, Costa Rica. 186 pp.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pp. 164 - 182. in Carnivore behavior, ecology, evolution (J. L. Gittleman, ed.). Chapman and Hall, London, UK. 282 pp.

von Schantz T. 1984. Carnivore social behavior - does it need patches?. Nature 307: 389-390.

Schoener, T.W., 1971. Theory of feeding strategies. Annual review of Ecology and Systematics 2: 369-404.

Schubert, C. A., R. A. Rosatte, Ch. D. MacInnes y T.D. Nudds. 1998. Rabies control: an adaptative management approach. Journal of Wildlife Management 62: 622-629.

Scott, M. E. 1988. The impact of infection and disease on animal populations: implications for conservation biology. Conservation Biology, 2: 40-56.

Simberloff, D. 1986. The proximate causes of extinction. Pp. 259-276 in Patterns and processes in the history of life. Springer-Verlag, Berlin.

Smythe, N. 1970. The adaptative value of the social organization of the coati (Nasua narica). Journal of Mammalogy, 51: 818-820.

Sweatmann, G. K. 1973. Ectoparasites in J.W. David y R. C. Anderson (eds.) Parasitic Diseases of Wild Mammals. Iowa State Press, Anues, IO, USA.

Swihart R. K. y N. A. Slade. 1985. Testing for independence of observations in animal movements. Ecology, 66: 1176-1184.

Thomas, D. L. y E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management, 54: 322-330.

Vaughan, C. y M. McCoy, 1984. Estimación de las poblaciones de algunos mamíferos en el Parque Nacional Manuel Antonio, CostaRica. Brenesia 22: 207-217.

Valenzuela, D. en prensa. Tejón, Coatí. Nasua narica (Linnaeus, 1766). En: G. Ceballos y H. Arita, eds. Atlas Mastozoologico de México. Instituto de Ecología / CONABIO.

Wallmo, O.C. y S. Gallizioli. 1954. Status of the coati in Arizona. Journal of Mammalogy, 38 (1): 123.

White, G. C. y R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic press, Inc., NY, USA. 383 pp.

Wiens, J.A. 1986. Spatial scale and temporal variation in studies of shrubsteppe birds. In: Diamond, and T.J. Case (Eds.) Community Ecology. Harper and Row Publishers Inc.

Wilson, D. E.. 1971. Food habits of Mycronycteris hirsuta (Chiroptera: Phyllostomidae). Mammalia, 35: 107-110.

Wolda, H. 1988. Seasonality and the community. Pp. 69-95. in The organization of communities (J.H. Gee and P.S. Giller, eds.). Blackwell Scientific Publications, Oxford, UK.

Wozencraft, W. Ch. 1993. Carnivores. Mammal species of the world. A taxonomic and geographic reference. (eds D. E. Wilson & D. M. Reeder), pp. 279-344. Second Edition. Smithsonian Institution Press. Washington, DC, USA.

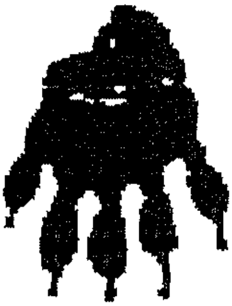
Wright, S.J., M.E. Gompper y B. DeLeon. 1994. Are large predators keystone species in Neotropical forests?: The evidence from Barro Colorado Island. Oikos 71: 279-294.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice Hall, New Jersey, USA. Pp. 717.

APENDICE I

MANGE EPIZOOTIC IN WHITE–NOSED COATIS IN WESTERN MEXICO

(Escrito en el formato de Journal of Wildlife Diseases)



MANGE EPIZOOTIC IN WHITE – NOSED COATIS IN WESTERN MEXICO

David Valenzuela[1], Gerardo Ceballos[2], and Andres García[2]

[1]Instituto de Ecología, UNAM, A. P. 70-270, Ciudad Universitaria, México, D.F. C.P. 04510.

[2]Fundación Ecológica de Cuixmala, A. C., A. P. 161, Melaque, Jalisco, México, C.P.48980.

ABSTRACT: From November of 1994 to June of 1996, we studied an epizootic of mange, probably caused by the mite Notoedres cati, occurred in white-nosed coatis (Nasua narica) in the tropical dry forests of the Chamela-Cuixmala Biosphere Reserve in western Mexico. We implemented a monitoring scheme to determine the extent and severity of the epizootic within coatis. Trapping periods and transects were conducted for two years. To control the spread of the disease, all captured infected coatis were either euthanized or treated with the application of acaricides (i.e. Butox® and Ivomec-F®) depending on the severity of their infection. Four other species of wild mammals and feral cats had skin conditions resembling mange. We predicted, and latter confirmed, a more severe problem with the disease in the less isolated areas of the reserve, with a higher coati density. Our results are consistent with the concept that diseases should be an important factor to consider in long-term plans for management and conservation of biodiversity in protected areas, and that epizootic outbreaks are more prone to occur in areas with more fragmentation and less isolation from anthropogenic influence.

Key words: conservation of biological diversity, mange, Nasua narica, reserve management, survey, tropical dry forest, wildlife diseases.

INTRODUCTION

A controversial area of research is the impact of diseases in populations of wildlife and hence in the long-term conservation of biological diversity (MacKinnon et al., 1986; May, 1988; McCallum and Dobson, 1995). Infection agents could play important roles in the structure and function of natural populations and communities (McCallum and Dobson, 1995; Caughley and Gunn, 1996). By differentially affecting individuals and species, diseases could change the genetic composition, density, and distribution of wild populations, and shape the community structure and composition (Scott, 1988). Although infection agents are components of natural communities, they may cause severe problems when they are accidentally introduced into new regions or where environmental conditions have been changed by human activities (Simberloff, 1986; Holmes, 1996). This is particularly relevant in nature reserves and fragmented habitats, where diseases are becoming major management and conservation problems (Aguirre and Starkey, 1994; Holmes, 1996). The probability of epizootics in reserves is apparently related to their fragmentation, because feral and domestic animals such as dogs, cats, and cattle may disperse and transmit diseases into natural habitats and populations (Caughley and Gunn, 1996).

In this paper we present information on an epizootic of mange in white – nosed coatis (Nasua narica; Procyonidae) at the Chamela-Cuixmala Biosphere Reserve (CCBR), in western Mexico, and the strategy that we implemented to limit the spread of the disease. While conducting research on the ecology of the coati in the CCBR in 1994, we detected an increasing number of individuals in poor condition, with extensive fur loss and flaky skin. We designed a management strategy to evaluate and control this epizootic that involved the identification of the disease and the assessment of specificity and severity of infection in the population of coatis. We also evaluated the relationship between the prevalence of the disease, host density and site isolation. We expected higher prevalence in Cuixmala, which was the area of the reserve with a higher coati density and more anthropogenic perturbation.

MATERIAL AND METHODS

The Chamela-Cuixmala Biosphere Reserve (CCBR) was created in December of 1993. It comprises 13,142 hectares and it is located in the coast of the state of Jalisco in western Mexico, between 19° 22' 03" and 19° 35' 11" N and 104° 56' 13" and 105° 03' 25" W. The physical and biotic characteristics of the region are described in detail elsewhere (Bullock 1986, Ceballos and Garcia 1995). The tropical climate is classified as hot and humid, characterized by a strong seasonality in rainfall and an annual mean temperature of 24.9°C. Rainfall is concentrated from July to October, followed by a pronounced dry season from November to June. Average annual precipitation varies from 748 to 1,000 mm. The CCBR is included in one of the most extensive remnants of dry forest in Mexico and Central America. There are approximately 429 species of vertebrates and over 1,200 species of vascular plants in the reserve; many of these species are endemic to Mexico and/or considered at risk of extinction (Ceballos and Garcia, 1995). Plant species composition has a high degree of heterogeneity associated with soil depth, soil type, and exposure. Physiognomically, dry forests are characterized by trees 5 to 15 m height, with a relatively even canopy and a few emergent trees.

The reserve is divided into two zones (Fig. 1 in page 46). The Cuixmala zone comprises near 900 hectares along the flood plain of the Cuixmala River, where there are nine vegetation communities including dry forests, and abundant permanent water bodies. This zone is in contact with perturbed areas, used for agriculture and cattle ranching; a relatively small town (1,000 people) is located 2 km to the south. In contrast, the Cumbres zone, which comprises around

12,200 ha, presents a complex topography in which tropical dry forests are the dominant vegetation; there are no permanent water sources, and no human activities. The coati is the most abundant carnivore in the CCBR (Ceballos and Miranda, 1986), and is the only social carnivore present in neotropical forests (Gompper, 1995), living in cohesive groups of up to 20 individuals, and adult males living as solitary individuals. Besides, home ranges of neighboring band and males overlaps extensively (i.e. 30-40%; Valenzuela, unpuglished data). In the reserve, coatis have a higher density in Cuixmala than in Cumbres (Valenzuela, in press).

To determine the cause of the disease we captured four infected coatis. All were thin and weak in appearance and had diffuse alopecia (partial to complete), thickened skin, covered with gray - yellowish crusts, and excoriations. Skin lesions in these animals were mainly found in the ears, supraorbital arcs and top of the head, posterior legs, basal part of the tail, and posterior portions of the flanks. Infected coatis were very pruritic and two of them also had diarrhea. Diagnosis of the disease was obtained by examination of scraps from crusted skin areas and fecal parasite analysis. The analyses of the skin scrapings, fecal samples and the identification of mites was carried out by a regional laboratory of the Department of Animal Health from the National Ministry of Agriculture (Report No. 4853, Case No. 214, April 10, 1995). To evaluate the prevalence of the infection and to monitor the spread of the disease across the reserve, we carried out surveys and an intensive trapping of live animals. Prevalence was calculated as the percentage of diseased coatis. Finally, to score disease severity, each captured animal was inspected by dividing the body in 10 sections, and by scoring five points to each section with partial loss of hair and 10 points to each section having complete loss of hair and skin crusts (Fig. 2). Individual disease severity scores (0 -100 %) were averaged for trapping period.

Surveys were made by walking through roads and trails within the reserve and registering all observed coatis, considering as infected all individuals showing clearly a portion of the body surface without hair. Our predictions were that there would be a prevalence and a high disease severity score in Cuixmala which has a two times higher coati density, than in Cumbres (Valenzuela, in press), and where there was a greater exposure of wildlife to domestic animals. We used G-tests (Zar, 1984) to compare prevalence and severity scores between Cuixmala and Cumbres. A total of 20 surveys were conducted, covering 54 km, from November 1994 to January 1996. Based on the data from the surveys, an intensive and systematic trapping program was initiated in both Cuixmala and Cumbres, using Tomahawk Live Traps baited with sardines. Parallel with the trapping program for coatis, personnel from the health department of the Cuixmala Ecological Foundation conducted a trapping program of feral cats in areas adjacent to the reserve. Trapping periods were distributed in four periods of approximately three months: November 1994 to January 1995; late March to early June 1995; October to December 1995; and late March to early June 1996. In Cuixmala, trapping was initiated in 17 different sites where diseased animals had been observed. In Cumbres, trapping was not conducted in the first period; however, in the following periods trapping was carried out at 24 different sites. Traps were set at each site until no diseased animals were captured for three consecutive days.

All captured coatis that were healthy or had less than 30% of the body surface affected by mange, were treated with a subcutaneous injection of Ivermectine and Clorsulon (0.03 ml/kg; IVOMEC – F®; Merck) and an immersion in a solution of Deltametrine (1ml/lt; BUTOX®; Rousell). The application of acaricides is recommended for animals infected with mange (Muller et al., 1990). Altogether, 25 healthy coatis were given preventative treatment as they were captured together with infected individuals. In contrast, all coatis with more than 30% of the body surface infected were euthanized. For this we applied to the animals an intramuscular injection of Ketamine (IMALGEN ®1000; Rhone Merieux) at a dosage of 16 mg/kg, followed after induction time, by an intracardiac injection of Sodic pentobarbital (ANESTESAL®; Smithkline Beechman®) using a dosage of 0.8 ml/kg.

RESULTS

The diagnosis showed that infected coatis had mites and ova of *Notoedres cati*, a mite responsible for notoedric mange. The two coatis with diarrhea had coccidiasis and high levels of *Escherichia coli*. Based on this diagnosis we subsequently considered a coati as infected if it presented fur loss and skin lesions similar to those shown by the coatis analyzed in the lab.

Mange was very specific to coatis. Other researchers working in the same region at the same time, found that out of 39 species of mammals and more than 1400 captured individuals, only one raccoon (*Procyon lotor*), two ocelots (*Leopardus pardalis*), one gray squirrel (*Sciurus colliaei*) and six feral cats, presented skin conditions similar to those of coatis on which mange was confirmed.

The overall prevalence of the disease in coatis was 46.8 % (66 diseased animals / 141 captured animals), and the average severity score was 35.4 ± 5.8 % ($\bar{X}$ ± 95% confidence interval; *n* = 66). As expected, mange was more prevalent and more severe in the reserve's section less isolated and with a higher coati density. Comparing the last three trapping periods, prevalence and severity were statistically higher in Cuixmala than Cumbres (Table 1; *G*-test $_{(0.05)}$ *d. f.* = 2, *G* = -93.2; *P*< 0.000; *G* = -59.9; *P*< 0.000, respectively). Both all euthanized and 20 treated coatis came from Cuixmala; in contrast, only seven coatis required treatment in Cumbres.

Treated coatis that were recaptured showed signs of recuperation, indicated by a lower proportion of body surfaces without both hair and skin crusts. Of the 66 diseased coatis, 27 were treated and 39 were euthanized and cremated (Table 1).

The overall prevalence of the disease was 52% in Cuixmala and 26% in Cumbres (Table 1). In Cuixmala it remained high during the study period, but in Cumbres it was relatively low at the end of the observations. Within both zones, there were areas where infected coatis were concentrated. In Cuixmala, the highest capture rate occurred at one site, with 38.6% of total captures, 35.6% of the diseased animals, and 35.9% of all euthanized animals. In Cumbres almost half of the total captures (44%) occurred at two sites, and 6 out of 7 infected coatis were captured at those sites. The remaining captures were evenly distributed among nine additional sites, there were no captures in the other 13 trapping sites. Based on observations and trapping data, a pattern of the spreading of mange in the reserve was established and a distribution map of the disease in Cuixmala was obtained (Fig. 3a-d). Initially, mange was present on few points (Fig. 3a); however, its dispersion increased rapidly, particularly on the areas closer to the town, where the six infected feral cats were captured. During the second trapping period, the disease was more widely spread (i.e. infected coatis were observed and captured in more sites), and many more infected animals were captured (Fig. 3b). This period of high severity coincided when most of the infected coatis were captured in Cumbres. Culling the animals in worst conditions at Cuixmala helped to reduce the disease's dispersion and to maintain it at a relatively low level (i.e. few sites where sick animals were observed); prevalence in those sites remained relatively constant (Table 1; Fig. 3c and 3d). In Cumbres, only one infected animal was captured during the last trapping period.

DISCUSSION

This is the first report of a mange epizootic in a wild population of coatis. Previous reports of mange in this species have been caused by Sarcoptes scabei, and have been reported in individuals in captivity (Conroy, 1964; Meier, 1976). Mange can severely weaken the affected animals. The mite burrows beneath the skin to reach the lower dermic layer where the mite feeds and lays its eggs (Sweatman, 1973; Muller et al., 1990). This causes an intense reaction in the skin which thickens, forms folds, and becomes covered with gray or yellow crusts, resulting in hair loss. The infected animal suffers intense itching, and the lacerations caused by scratching become secondarily infected. Crusts around the eyelids create difficulties in vision and loss of foraging ability. At an advanced stage, the infection can produce weight loss and general weakness that sometimes result in death due to facilitation of secondary complications. Mange epizootic can threaten wildlife in general, but its effects can be severe in endangered species, such as Mountain gorillas (Gorilla gorilla beringei; Kalema, 1997).

Notoedric mange is a highly contagious disease that is mainly present in felines, but also affects many other species including members of the orders Rodentia, Carnivora, Lagomorpha, Didelphimorphia, and Chiroptera. Notoedric mange occurs in epizootic events and in some cases has been argued to significantly reduce wild populations, as with the Californian Grey squirrel (Sciurus griseus griseus) in northern California, USA, during the 1920's (Sweatman, 1973; Muller et al., 1990). However, any claim that a disease is having a significant impact in a wildlife population must be based in experimental studies testing this hypothesis, comparing results with reference areas (Schubert et al. 1998).

In the present case, the gregarious nature of coatis probably favored contagion of individuals and spread of the disease. Notoedres mites are obligate parasites that live only for a few days off the host and are transmitted among hosts primarily by direct contact. Contact with bedding sites or recently visited sites by an infected individual, might also result in spread of the disease (Muller et al., 1990). In general, the prevalence of parasites and diseases depends on the susceptibility of on individual to each disease agent, which is determined by genotype, physical condition, and the individuals response to natural or human - induced environmental changes (Caughley and Gunn, 1996). At a population level, the dispersion of disease is related to density, number of infected individuals, number of parasites per host, and the rate of contact between hosts (Holmes, 1996). The increased dispersion of disease in wildlife populations may be compounded by a combination of factors, including habitat perturbation, presence of domestic animals acting as carriers, and unnaturally high densities of wild populations in fragmented protected areas (Primack, 1993; Aguirre and Starkey, 1994).

We suspect that the mange epizootic started in Cuixmala, because there were few infected coatis in Cumbres. This may be related to the higher density of coatis and greater contact with domestic animals in Cuixmala. The higher density of coatis in Cuixmala may be attributed to more water and food availability in this site than in Cumbres. Also, before the reserve was established, it was a common practice in Cuixmala to supplement food for the coati groups in order to observe them (Valenzuela, in press). There were reports of congregations of 70-80 coatis at the sites in which supplemental food was provided. Such abnormal densities may have played an important role in facilitating the start of the mange epizootic. Interestingly the disease was initially detected at sites were food supplementation was carried out for a longer period and where the larger groups were observed.

In order to minimize the negative impacts of the disease in the reserve, a strategy was designed to optimize the use of limited resources in the control of the disease. Although the reserve covers more than 13,000 ha, infected coatis were initially detected in few localized areas. Therefore, we decided to concentrate our trapping efforts in those sites where infected coatis were detected, and to halt the spread of mange while minimizing the negative impact of the control strategy on the coati population. We tried to do this by culling intensely infected individuals, and by treating all individuals showing no symptoms or a low disease severity. We expected that by decreasing the number of infested hosts we could limit the spread of the disease to other species and areas of the reserve. Our strategy was successful because the epizotic was restricted to few sites inside Cuixmala.

We found that the control of the outbreak was justified for several reasons. On the one hand, although the disease primarily affected coatis, there was a potential risk of infecting other species, particularly endangered ones, such as jaguars (Phantera onca). Coatis are a major prey of jaguars in the reserve (Nuñez, 1999) so the disease could pose a serious threat to these key predators that have very low densities in the area. Endangered species with small populations are unlikely to sustain diseases caused by virulent pathogens or macroparasites; they tend to acquire virulent diseases only after exposure to infected hosts of another more abundant and widespread species (McCallum and Dobson, 1995). Coatis are the most abundant medium-sized carnivores in the reserve, are gregarious and have large overlapping home ranges, therefore they could be particularly good means for spreading a disease such as mange.

Mange epizootic events are more prone to occur during the dry season in tropical regions (Sweatmann, 1973). In the CCBR, water and food resources become limited during the dry season and affects coatis and many other species of animals and plants (Ceballos, 1995). Such effects were quite pronounced during the 1994-1995 dry season, which was particularly severe due to an atypical low precipitation, in comparison with an 8 year average data (Bullock, 1986).

Precipitation was 30 % lower and, during the 2 months of higher precipitation, it rained 3 times less. Many species of animals, including coatis, concentrated around the few available waterholes at a dry season like that. In these circumstances an infested animal could become an effective source of mites for other wildlife species.

We believe that the mange epizootic increased the effect of other natural mortality factors for coatis. Although we expected a higher mortality of coatis in Cumbres during the dry season due to the lack of permanent sources of water, we found a 40% decline in coati density in both Cumbres and Cuixmala (Valenzuela, in press). It is likely that the decline in coati density in Cuixmala, where water and food are abundant, was probably related to weakness caused by mange.

MANAGEMENT IMPLICATIONS

Our results have regional and general management implications. At a regional level they are relevant for the long-term conservation of the biological diversity of the Chamela-Cuixmala Biosphere Reserve. Based on our study we have begun the implementation of a permanent control and monitoring program, that consists of a continuous observation of coatis or other mammals showing abnormal behavior or disease signs (e.g. apparent weakness, loss of hair, crusted skin) and the eradication of feral cats and dogs.

At a general level our results are consistent with the idea that diseases should be an important factor to consider in long-term plans for management and conservation of biodiversity in protected areas. We suggest, however, that to clearly determine cause and effects, experimental studies on the impact of diseases in populations of wild animals should be carried out (McCallum and Dobson, 1995). Learning from cases like the present one can provide useful information to successfully deal with this kind of problems and to form a basis for designing and performing those experimental studies.

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LITERATURE CITED

AGUIRRE, A. A. AND E. E. STARKEY. 1994. Wildlife disease in U.S. National parks: Historical and coevolutionary perspectives. Conservation Biology 8:654-661.

BULLOCK, S. 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. Archives for Meteorology, Geophysics, and Bioclimatology, Series B 36: 297-316.

CAUGHLEY, G. AND A. GUNN. 1996. Conservation biology in theory and practice. Blackwell Science, Cambridge, Massachusetts, 459 pp.

CEBALLOS, G. 1995. Vertebrate diversity, ecology, and conservation in Tropical Deciduous Forests. In Seasonally Dry Tropical Forests, S. Bullock, E. Medina, and H. Mooney, (eds.) Cambridge University Press, Cambridge, U.K., pp. 195-220

-------, AND A. GARCÍA. 1995. Conserving neotropical biodiversity: the role of dry forests in western Mexico. Conservation Biology, 9: 1349-1356.

------, AND A. MIRANDA. 1986. Los Mamiferos de Chamela, Jalisco. Instituto de Biología, Universidad Nacional Autónoma de México, Mexico, D.F., 436 pp.

CONROY, J. D. 1964. Sarcoptic acariasis in a coatimundi. Modern Veterinary Practice, 45: 80-81.

GOMPPER, M. 1995. Nasua narica. Mammalian Species, 487:1-10.

HOLMES, J. C. 1996. Parasites as threats to biodiversity in shrinking ecosystems. Biodiversity and Conservation, 5: 975-983.

KALEMA, G. 1997. An outbreak of a skin disease in free-ranging Mountain Gorilla, Gorilla gorilla beringei in Bwindi Impenetrable national Park, southwestern Uganda. In Abstracts of the Seventh International Theriological Congress, Asociación Mexicana de Mastozoologia, México, D.F. pp. 190.

MACKINNON, J., K. MACKINNON, G. CHILD AND J. THURSELL (Editors). 1986. Managing Protected Areas in the Tropics. IUCN / UNEP, Gland, Switzerland, 314 pp.

MCCALLUM, H. AND A. DOBSON. 1995. Detecting disease and parasite threats to endangered species and ecosystems. Trends in Ecology and Evolution 10: 190 - 194.

MAY, R. 1988. Conservation and disease. Conservation Biology 2: 28-30.

MEIER, J. E. 1976. Sarcoptic mange in Yucatanian coatimundis (Nasua narica yucatanica). Journal of Zoo Animal Medicine, 7: 31

MULLER, G. H., R. W. KIRK AND D. W. SCOTT. 1990. Small Animal Dermathology. W.B. Saunders Company, Philadelphia, PA, 1068 pp.

NUÑEZ, R. 1999. Hábitos alimentarios del jaguar (Panthera onca, Linnaeus 1758) y del puma (Puma concolor, Linnaeus 1771) en la Reserva de la Biosfera Chamela-Cuixmala, Jalisco, Mexico. Tesis de Licenciatura, Universidad Autonoma de Michoacán, Morelia, Michoacán, México. 74 pp.

PRIMACK, R. B. 1993. Essentials of Conservation Biology. Sinauer, Sunderland, MA, 564 pp.

SCHUBERT, C. A., R. A. ROSATTE, CH. D. MACINNES AND T.D. NUDDS. 1998. Rabies control: an adaptative management approach. Journal of Wildlife Management 62: 622-629.

SCOTT, M. E. 1988. The impact of infection and disease on animal populations: implications for conservation biology. Conservation Biology, 2: 40-56.

SIMBERLOFF, D. 1986. The proximate causes of extinction. In D. M. Raup and D. Jablonski (eds). Patterns and processes in the history of life. Springer-Verlag, Berlin, pp. 259-276.

SWEATMANN, G. K. 1973. Ectoparasites. In J.W. Davis and R.C. Anderson (eds.) Parasitic Diseases of Wild Mammals. Iowa State Press, Anues, IA, USA. 428 pp.

VALENZUELA, D. in press. Natural history of the White-nosed coati, Nasua narica, in the tropical dry forests of western Mexico. Revista Mexicana de Mastozoologia.

ZAR, J. H. 1984. Biostatistical Analysis. Second Edition. Prentice-Hall, Inc. NJ, USA. 718 pp.

Table 1. Prevalence and severity score of mange in coatis (Nasua narica) at both sites (Cuixmala / Cumbres). TD = trap days; TC = total captures; TS = total sick animals; TE = total euthanized animals; TT= total treated animals; CS= capture success (TC / TD by 100); DP= disease prevalence (TS/TC by 100); SS = disease severity score (i.e. average percent area of body surface infected).

Trimester	TD	TC	TS	TE	TT	CS	DP	SS
First	176 / --	48 / --	11 / --	10 / --	1 / --	27.2 / --	22.9 / --	54 / --
Second	255 / 569	42 / 14	32 / 6	21 / 0	11 / 6	16.5 / 2.5	76.1 / 43	40 / 20
Third	210 / 293	14 / 4	8 / 0	0 / 0	8 / 0	6.7 / 1.4	57.1 / 0	16 / 0
Fourth	251 / 1380	10 / 9	8 / 1	6 / 0	2 / 1	4.0 / 0.6	80.0 / 10	50 / 10
TOTAL	892 / 2242	114 / 27	59 / 7	37 / 0	22 / 7	13.6 / 1.5	51.7 / 25.9	

Figure 2. Different degree of mange infection in coatis. Shaded areas indicate fur loss and dermic scabs. All individuals with more than 30% of the body surface affected by the disease were euthanized.

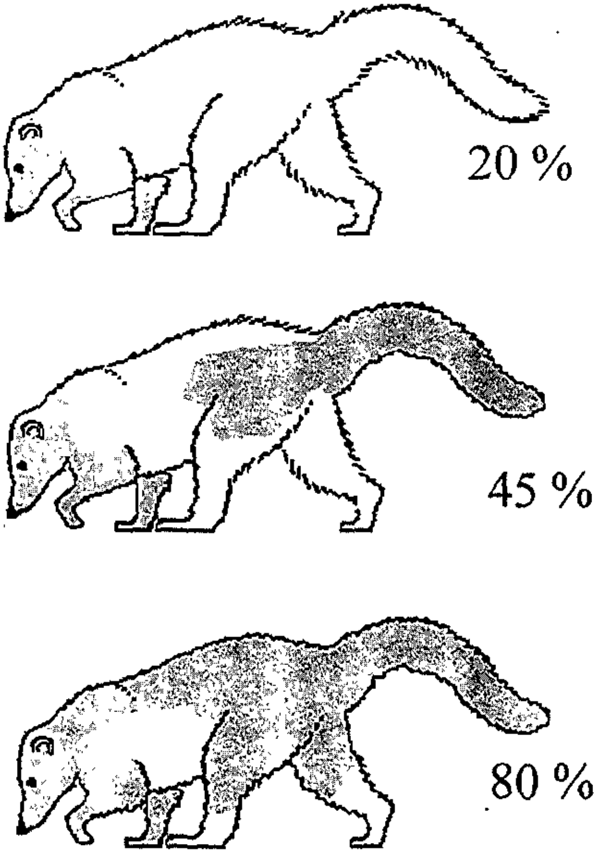

Figure 3. Spatial distribution of disease in Cuixmala site by trimester: a) November, 1994 to January, 1995, b) March to early June 1995, c) October to December 1995; and d) late March to early June 1996. Dark dots are trapping sites and shaded circles are trapping sites where sick animals where captured. Each histogram shows total number of coati individuals captured (TC), and the total number of sick (TS), euthanized (TE) and treated (TT) individuals on each trapping period.