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UNIVERSIDAD NACIONAL AUTONOMA DE MEXICO

FACULTAD DE CIENCIAS
DIVISION DE ESTUDIOS DE POSGRADO

IMPLICACIONES PARA LA CONSERVACION Y EL MANEJO DE PUMAS (*Puma concolor*) UTILIZANDO COMO MODELO UNA POBLACION SUJETA A CACERIA DEPORTIVA

T E S I S

QUE PARA OBTENER EL GRADO ACADEMICO DE

DOCTOR EN CIENCIAS (BIOLOGIA)

P R E S E N T A:

CARLOS ALBERTO LOPEZ GONZALEZ

MEXICO, D. F. 1999

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TESIS DIRIGIDA POR:

DR. BRIAN JAMES MILLER

MEXICO, D. F. 1999

TESIS CON
FALLA DE ORIGEN

A Alicia, porque todo lo que hecho es para estar contigo.

A mi mamá, a mi papá, y a mi hermano Ernesto

A la pequeña Monica Fernanda

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RESUMEN GENERAL

La tesis se encuentra dividida en cuatro capítulos. El primero es una revisión bibliográfica sobre el conocimiento ecológico que se tiene hasta este momento en el puma, se hace una síntesis sobre parámetros poblacionales, densidad, uso de habitat, habitos de alimentación y metodología para llevar a cabo censos poblacionales.

En el segundo capítulo describo la dinámica poblacional del puma en un área naturalmente fragmentada. De 1987 a 1995 se llevo a cabo la estimación del número de animales presentes. Cada animal se clasificó socialmente como residente, transeunte o cría. Se encontró que la proporción de sexos en la población es de 2 hembras por cada macho. Se calculó la supervivencia de adultos y crías. En el primer caso, la supervivencia anual, se calculo mediante el numero de días que se tuvieron animales con radio transmisor. En las crías la supervivencia se estimó por medio del número de animales en cada mes hasta la época de dispersion transformándolo a proporciones. La supervivencia promedio de los adultos fue del 70.1%, en el caso de las crías fue del 41.5%. La primera reproducción en una hembra se llevó a cabo alos 17 meses, el tamaño de camada fue de 2.5 crias/hembra. El tiempo entre camadas fue de 15 meses, del mismo modo la dispersión de las crías tomo un tiempo semejante. La proporción de sexos en crias que llegaron a la etapa de dispersión fue de 5 machos por hembra. La taza de reemplazo en la poblacion es baja y relativamente constante, esta dada por el número de crías hembra que permanece dentro del área de estudio y una proporción de transeuntes hasta del 23%.

En el tercer capítulo se utilizan los datos de los pumas que se han dispersado exitosamente para proponer la creación de reservas utilizando esa información. Se calculó el área de influencia de los dispersores por medio de tres estimadores de áreas de actividad: el método de polígono

convexo (MPC), la media harmónica (MH)) y el kernel adaptativo (AK), en los últimos dos se calcula probabilidad que un animal llegue a dicho punto en el espacio. Del mismo modo se calculó el tamaño del población del vecindario por medio de una relación de distancias. Se encontró que los pumas se dispersaron un promedio de 192.1 km al azar. Las distancias extremas fueron de 409 y 420 km. El área afectada por los dispersores por medio del MPC fue de 100,500 km^2, área relativamente semejante a la calculada por el tamaño del vecindario (112,500 km^2). Se discute el uso y tamaño de corredores, así como el área nucleo mínima de reserva (3,700 km^2) y como deben conectarse con el resto de otras áreas protegidas.

En el cuarto capítulo se propone el uso de un modelo para calcular los requerimientos energéticos del puma y como consecuencia describir la tasa de depredación en el área de estudio. Se utiliza un modelo que incorpora el metabolismo basal, asi como el costo energético para mantenerse parado y el tiempo que ocupa en esta actividad, el costo y duración de la alimentación y otras actividades localizadas, y se incorpora el gasto energético al caminar "*n*" número de km durante 24 h. Se compara el modelo utilizando valores observados en laboratorio y los que predice la teoría. A los resultados obtenidos en calorías, se les calcula su aprovechamiento y se estima la biomasa por día que deben consumir, para obtener dichos requerimientos energéticos. Así mismo se obtiene el número de días que deben transcurrir entre la captura de dos animales. Los resultados obtenidos muestran un gasto energético predictivo menor al observado en laboratorio en multiplos de 1.3. Se obtuvieron necesidades de consumo de carne de 3 kg para hembras y 5 kg para machos. Por lo que que estos animales deberian cazar una presa de tamaño grande cada 11 a 14, y 8 a 11 dias respectivamente. Esto refleja un consumo mínimo de 1200 venados por año dentro del área de estudio que es alrededor del 20% presente en potencia.

GENERAL ABSTRACT

This dissertation is divided in four chapters. The first one, is a recently published literature review about the current ecological knowledge of the puma, including population parameters, density, habitat use, food habits, and census methodology.

In the second chapter, the population dynamics on a naturally fragmented is described. From 1987-1995 the number of pumas present was determined. Each animal was classified as resident, transient and kitten. The sex proportion was 2 females per 1 male. Adult and kitten survival was estimated. Annual adult survival was estimated trough radiotelemetry. Kitten survival was estimated as the number of animals alive per month up to dispersal age, as proportion. Adult average survival was 70.1%, where kitten survival was 41.5%. First female reproductive event was at 17 months of age. Litter size was 2.5 kittens/female. Tiem between litters was 15 months, similarly dispersal age. Kitten sex proportion that reached dispersal age was 5 to 1. Turnover rate is low and relatively constant and, is the result of the number of females that remain within the study area and a transient proportion up to 23%.

The third chapter uses the data of pumas that have successfully dispersed as a tool to create protected areas. The dispersal influence area was estimated by three home range estimators: minimum convex polygon (MCP), harmonic mean (HM) and adaptive kernel (AK), where the last two methods estimate the probability of an animal reaching a given point in space. Neighborhood size was estimated through a distance relationship estimator. It was found that pumas dispersed on average 192.1 km on a random direction. Extreme distances were 409 and 420 km. The area influenced by dispersers with the MCP was 100,500 km², area similar in size to the negihborhood estimate (112,500 km²). A discussion about corridors use and size, and minimal core areas for

protection (3,700 km^2) and how connectivity should be maintained .

In the fourth chapter a model of energetic requirements by the puma is proposed. By using this model predation rates were estimated. The model uses basal metabolic rate, and the energetic cost of daily activities (i.e. standing or walking), the number of km traveled during 24 h is incorporated. Caloric utilization and daily biomass consumed was calculated, also the time between prey capture. The results obtained show a lower energetic expense than that observed in the laboratory. Daily consumption needs were 3 kg and 5 kg for females and males, respectively. As a consequence this animals should kill a large prey each 11-14 days and 8-11 days, for females and males, respectively. This predation rate reflects a minimal consumption of 1200 deer per year in the study area, approximately 20% of the estimated population size.

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INTRODUCCION GENERAL

A la fecha se reconocen 236 especies de carnívoros (Wosencraft 1989), donde la gran mayoría de éstas carecen de estudios, siendo algunas especies solamente conocidas por escasos datos históricos de colecta (i.e. *Felis iriomotensis*). Algunos carnívoros han sido el centro de estudios a largo plazo, como es el caso del lobo gris (*Canis lupus*) de Isla Royale, Estados Unidos (Allen 1993), o el león africano (*Panthera leo,* Packer and Pusey 1993). Los grandes carnívoros terrestres pueden agruparse como las especies cuyo peso promedio excede los 18 kg y están representados por las siguientes especies: lobo gris (*Canis lupus*), lobo de las pampas (*Chrysocyon brachyurus*), dholes (*Cuon alpinus*), perros salvajes del Africa (*Lycaon pictus*, Canidae), oso malayo (*Helarctos malayanus*), oso perezoso *(Melursus ursinus),* oso de anteojos *(Tremarctus ornatus),* oso negro *(Ursus americanus),* oso pardo y grizzly *(U. arctos),* oso polar *(U. maritimus),* oso negro asiatico *(U. thibetanus,* Ursidae); oso panda (*Auliropoda melanoleuca*, Auliropodidae); hiena manchada (*Crocutta crocutta*), hiena cafe (*Hyaena brunnea*), hiena rayada (*H. hyaena*, Hyenidae), jaguar (*Panthera onca*), león africano (*P. leo*), leopardo (*P. pardus*), tigre (*P. tigris*), pantera de las nieves (*P. uncia*), pantera nebulosa (*Neofelis nebulosa*), guepardo (*Acinonyx jubatus*), puma (*Puma concolor*, Felidae).

Este número tan reducido de especies las hace herramientas perfectas para la conservación, ya sea como especies clave (keystone), paraguas (umbrella), bandera (flagship) o indicadoras (indicator). Miller et al (1999) en resumen definen dichas categorías por su contexto funcional o la manera en que contribuyen a la planificación de una reserva. Donde una especie clave está definida por su valor ecológico, por ejemplo el caso de los grandes felinos. Una especie paraguas es la base para la toma de decisiones, en particular sobre tamaño, forma y la distribución espacial

de áreas protegidas, el caso de los grandes felinos o los osos grizzly . Una especie bandera es carismática y puede utilizarse en relaciones públicas o para obtener fondos, como es el caso de los lobos y tigres. Finalmente, una especie indicadora es útil en determinar y monitorear la calidad del habitat, en este caso se puede citar a los grizzlys o los tigres; como se puede observar una especie puede ser utilizada dentro de varias categorías.

En la actualidad no podemos hablar de áreas sin influencia humana, a pesar de que existan sitios tan remotos como el llamado Serengeti de América (Alaska y el Noroeste de Canada), las estepas de Mongolia o la cuenca del Amazonas. Estas áreas relativamente primitivas, en un futuro no lejano se verán directamente afectadas por las actividades humanas. El ser humano desafortunadamente es el instrumento más importante, tanto de destrucción como de conservación de dichos lugares. Esta categoría, única dentro del reino animal, lo que nos indica es que somos parte del sistema y como tal debemos tratar de mitigar o limitar de manera sistemática y científica nuestra influencia en los ecosistemas, es por ello que los grandes carnívoros son piezas determinantes para mantener o definir la integridad de un sistema, así como crear una conectividad de caracter funcional entre parches existentes de habitat.

Algunas especies de grandes carnívoros terrestres estan asociadas a ecosistemas con amplia cobertura vegetal y/o en condiciones políticas inestables, factores que han propiciado un retraso en su estudio, por lo que muchas veces tenemos que basar nuestros manejo en modelos desarrollados con especies más comunes o que son relativamente más fáciles de estudiar, sin perder de vista que dichas sugerencias tienen limitantes y que deben eventualmente ser avaladas con estudios regionales (Quigley y Crawshaw 1992).

Ninguna de las especies de grandes carnívoros se encuentra en inminente peligro de extinción, pero aún las especies que aparentemente se encuentran en buen estado pueden verse afectadas subitamente por factores que no eran percibidos como una amenaza, como es el caso de catástrofes ambientales o alguna zoonosis (Schaller 1996). En la mayor parte de las especies carecemos de información básica, y como consecuencia desconocemos la mayoría de las enfermedades potenciales que pueden existir o las consecuencias de fenómenos naturales como huracanes o erupciones volcánicas.

Los capítulos que a continuación presento tienen la finalidad de ampliar el conocimiento que se tiene sobre el puma, particularmente sobre los efectos que la fragmentación tienen en procesos como son la dinámica poblacional, con la finalidad de mantener la productivad de la especie para llevar a cabo una explotación racional y sostenida. Así mismo el contribuir a entender un poco más sobre el proceso de la dispersión y las posibiles implicaciones que tiene para el mantenimiento de metapoblaciones y su posible uso como herramienta en la conservación de la biodiversidad en una región ampliamente fragmentada por actividades humanas de los Estados Unidos. De la misma manera comprendiendo cuales son los requerimientos energéticos del puma, se puede llegar a contemplar el número mínimo de presas que se necesita para mantener una población saludable y en un momento dado poder aplicar dichos conocimientos al manejo y conservación del puma en otras regiones donde este habite, cuya situacion particular dificulten su estudio, como es el caso de algunos sitios de México, Centro y Sudamérica.

La tesis sigue un formato relativamente nuevo dentro de la Facultad de Ciencias por lo cual esta organizada como posibles publicaciones, siguiendo las normas editoriales de las distintas

revistas cientificas a las cuales se enviará el trabajo. Como requisito para la titulacion, la Facultad de Ciencias requiere por lo menos un capitulo de la tesis publicado. Fuera de esto, no existe una guia o formato a seguir para la presentacion del trabajo de tesis.

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CAPITULO I

UNA SÍNTESIS DE LITERATURA Y CONOCIMIENTO ACTUAL SOBRE LA ECOLOGÍA DEL PUMA (*PUMA CONCOLOR* LINNAEUS).

Acta Zool. Mex. (n.s.) 75: 171-190 (1998)

A SYNTHESIS OF CURRENT LITERATURE AND KNOWLEDGE ABOUT THE ECOLOGY OF THE PUMA (*PUMA CONCOLOR* LINNAEUS)

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RESUMEN

Se llevó a cabo una revisión bibliográfica en varias universidades y bases de datos de los Estados Unidos y México, del mismo modo se estableció contacto con investigadores de carnívoros para tratar de resumir en forma comprensiva el conocimiento actual sobre la ecología del puma (*Puma concolor*). El objetivo principal fue el actualizar nuestro conocimiento ecológico desde las últimas revisiones bibliográficas publicadas en 1987. Se hacen comentarios sobre los tamaños de muestra, asi como de las diferentes metodologias y como éstas dificultan la comparasión entre áreas y estudios, del mismo modo se sugieren direcciones que deben tomar las investigaciones en el futuro con base en los huecos encontrados de la revisión bibliográfica.
Palabras clave: *Puma concolor*, revisión bibliográfica, ecología, demografía, densidad, estado de conservación.

ABSTRACT

A literature survey was carried out in several universities and databases from the United States and Mexico, and discussions were held with many carnivore biologists to summarize the current and most relevant knowledge on the ecology of the puma (*Puma concolor*). The main objective was to update our ecological knowledge from the last literature reviews published in 1987. Comments are made on sample sizes, different methodologies, and how these make comparisons hard to achieve between areas or studies, and suggest where research should be directed in the future based upon gaps found in this literature survey.
Key Words: *Puma concolor*, ecology, literature review, demography, density, conservation status.

INTRODUCTION

Large mammalian carnivores may be facing their last chance to survive on the planet, and several factors are influencing the durability of these species, among them are their scarcity, habitat and food specialization, and large areas required to live (Eisenberg 1989, Schonewald-Cox *et al.* 1991). A review of large carnivore (>20 kg) research shows that many of those species lack information on any basic conservation biology needs to preserve them (Fuller 1994). On the other

hand there is sufficient information on some species to use them as model organisms with which humans can experiment, in order to preserve the more vulnerable species of carnivores. The puma has been the subject of one of the most extensive databases of the carnivore world (Fuller 1994), with well designed experiments in temperate North America (U.S. and Canada), but yet there are many questions to be answered in this "common" animal that can help some of the less abundant cats of the world.

The main objective of this article is to give an overview of the actual state of knowledge on pumas. The chapter is organized in descriptive and basic biology, the ecology of the species including habitat association, feeding ecology, home range, density and behavior. Finally the global conservation status of the species is reviewed.

METHODS

Literature surveys have been carried out through reviewing current summaries of literature (i.e Anderson 1983, Currier 1983, Dixon 1981, Lindzey 1987) and surveying Wildlife Review (CD-ROM 1993) and recent literature found at the Instituto de Ecologia, UNAM, Chamela Biological Station, IBUNAM, Idaho State University, Scripps Oceanographic Institution- University of California San Diego, University of California Davis, and personal communication with many puma researchers from 1992 to 1996.

RESULTS

Nomenclature

The puma's latin name *Felis concolor* was first assigned by Linnaeus in 1771, and it was placed later as genus *Puma* (Jardine 1834). The current name as recognized by Wozencraft (1993) is *Puma concolor*. This name comes from a vernacular indian name of South America and a latin root word. Puma was given by the Quichua tribe, and also acknowledged by the Incas (Young and Goldman 1946). The word concolor, meaning one plain color, describes the pelage of the cat (Nowell and Jackson 1996). Common names for the puma include cougar, mountain lion, catamount, panther, painter (USA); leon, onza (Mexico); puma (Peru), and onca vermelha (Brazil)(Emmons 1990, Young and Goldman 1946).

Taxonomic classification historically produced up to 30 different subspecies of pumas (Currier 1983), but Stephen O'Brien's group proposed a new revision of the subspecific contents of the genus, leaving only 18 races as valid (Nowell and Jackson 1996).

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Fossil Records

Puma fossils date from the Irvingtonian and middle Rancholabrean period (≈300,000 years B. P.) within the Pleistocene (Kurten and Anderson 1980, Webb 1985), although non published fossil evidence from South America exists ( ). It has been suggested that pumas and cheetahs (*Acinonyx)* have a common origin with an extinct species of cheetah exhibiting a number of puma-like characters (Adams cited in Kurten and Anderson 1980).

South American invasion by the puma probably happened when tropical rain forest was the dominant environment through the Americas (Hershkowitz 1972).

Distribution

The puma was one of the most widespread species of the Americas (Currier 1983, Hall 1981). The species ranged on a longitudinal basis from British Columbia, Canada to southern Chile and Argentina and, on a latitudinal one from across the widest part of the United States (Young and Goldman 1946). Hunting pressure and habitat loss/transformations caused the extirpation of the puma from eastern North America, although isolated populations may exist in New Brunswick (Cumberland and Dempsey 1994). The current distribution of pumas in Mexico, Central America and parts of South America is mostly unknown (Nowell and Jackson 1996).

Reproductive Biology

The puma is a polygamous species that can be reproductive at any time of the year. The estrous cycle of the female is 23 days with a gestation period of 82 to 96 days (Eaton and Velander 1977, Rabb 1959). The litter size ranges from one to six with an average litter size of three.

The incisor teeth appear at age 8 to 20 days (Toweill 1986) and permanent dentition start replacing the primary teeth at about 5½ mo. Canines appear at 8 mo., and for a short time both permanent and primary canines are present (Currier 1983).

A puma kitten stays with its mother until age 9 to 24 months. Young animals (<12 mo. old) usually disperse because they became orphans, but dispersal at later stages has not been related to either carrying capacity, food availability or social organization (Hornocker 1970, Ross and Jalkotzy 1992, Seidensticker *et al.* 1973, Sweanor 1990). Age at first reproduction ranges from 17 to 36 months of age with males reaching sexual maturity closer to 36 mo. (Currier 1983, Lindzey *et al.* 1994, Maehr *et al.* 1989).

Habitat association

Currier (1983) states that puma distribution in the western hemisphere is probably limited by human interference, lack of prey, and/or lack of stalking cover. The species has been reported from sea level to 5,800 masl and from deserts to tropical rain forests (Currier 1983, Redford and Eisenberg 1992). It is probably the most successfully adapted feline of the New World. Habitat that can be considered typical in Western North America is oak, pinyon pine, and mountain mahogany forests (Lindzey 1987). In the Florida peninsula pumas are associated with hardwood forests (Maehr *et al.* 1991). Microhabitat preferences in those habitats are cliffs, and rock ledges, dense vegetation thickets, areas that provide some cover (Dixon 1981). In Mexico, they have been associated with all habitat types except lower Sonoran desert (McIvor *et al.* 1995). Bisbal (1989) found an association of pumas with tropical dry forest and tropical humid forests in Venezuela.

A characteristic of pumas is the avoidance of agricultural and clear-cut areas (Van Dyke *et al.* 1986, Lopez-Gonzalez 1994, Maehr *et al.* 1991). Fragmented patches of rain forest are used by pumas but detrimental effects have been recorded on nearby farms with varying degrees of predation affecting the survival of the population (Mazzolli 1993).

Feeding Ecology

The puma is considered an opportunistic predator, and since they can catch so many different kinds of animals, they should not be limited by lack of any given prey species (Currier 1983). That is probably the reason why the known food habits of pumas cannot be generalized throughout its distributional range.

In western North America pumas feed mainly on deer (Iriarte *et al.* 1990 and references therein). In Florida they feed on wild boar (*Sus scrofa*), white-tailed deer (*Odocoileus virginianus*) and raccoon (*Procyon lotor*) (Maehr *et al.* 1990). In southwestern Arizona, pumas depend on mule deer (*Odocoileus hemionus*), peccary (*Tayassu tajacu*), and bighorn sheep (*Ovis canadensis*) (Cashman *et al.* 1992).

A recent study has shown that individual pumas may produce a "en extinction" effect on small populations of prey specifically bighorn sheep, where this process seems to be individual and learned puma behavior (Ross *et al.* 1997). In contrast, a bighorn sheep population in the deserts of New Mexico remained relatively stable and was found inconsequential to puma predation and density (Logan *et al.* 1996).

The food habits of the puma in central and South America are not well known, and Iriarte *et al.* (1990) summarized the studies. Prey items used by pumas in the southern hemisphere, especially in tropical regions, are mainly medium to large

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animals (1 to 15 kg.) with some small size (<1 kg) animals. Olmos (1993) pointed out the importance of armadillo (*Dasypus novemcinctus)* in the diet of pumas in the tropical dry forest of Brazil. Another one from the alpine meadows of Peru (Romo 1995) showed the importance of mountain paca (*Agouti taczanowskii*). Enders (1935) stated that the diet of the puma for Barro Colorado Island, Panama, included collared peccaries (*Tayassu tajacu*), brocket deer (*Mazama* sp.), white tailed-deer, pacas (*Agouti paca),* agoutis (*Dasiprocta* sp.), spiny tailed-rats (*Proechimys* sp.), iguanas and snakes. The puma in the northern Yucatan Peninsula, Mexico; consumed peccaries, pacas, agouti, coatis (*Nasua narica*) and sometimes howler (*Alouatta palliata*) and spider (*Ateles geoffroyi*) monkeys (Gaumer 1917).

A synthesis of published mean vertebrate prey weight (MVPW) used by puma in tropical America is shown in Figure 1. From North to South America, there is not a clear pattern on how MVWP use changes. Sample size for the different Latin American studies listed here is very small (range 3-9 scats) compared to North American studies (see Anderson 1983).

Prey diversity is higher and more variable in tropical areas than in temperate North America. North American studies usually present ungulates as the main prey, but seasonal use of alternative prey have been recorded for the cold desert at the foothills of the Sierra Nevada (Nevada, United States); the use of foals (*Equus caballus*) is important during summer months when mule deer are absent from the area (Turner *et al.* 1992).

In the tropics large rodents and armadillo seems to be the average prey size used by pumas (Iriarte *et al.* 1990, Emmons 1990), with the exception of Brazil where the main prey is cattle (Crawshaw and Quigley unpubl. data), but this study used kills and the rest of the studies relied on scat analysis.

The plains Vizcacha (*Lagostomus maximus*) was selected by pumas in Argentina because it was a clumped and predictable resource (Branch *et al.* 1996). In this study, niche breadth was the lowest of the published ones both for North and South America.

Deer was the main prey item of the puma's diet in the "undisturbed" Biosphere Reserve of Calakmul (Aranda and Sanchez-Cordero 1996), but again the number of scats utilized was very small (N = 15) and deer preference is probably an artifact of the methodology used because the authors were not able to differentiate hair remains of brocket (*Mazama americana*) and white-tailed (*Odocoileus virginianus*) deer. We calculated the standarized niche breadth (Bs = B-1/N-1, Colwell and Futuyma 1971) for this area (0.35) with comparable results to Florida (0.37), Brazil (0.36) and Chile (0.34).

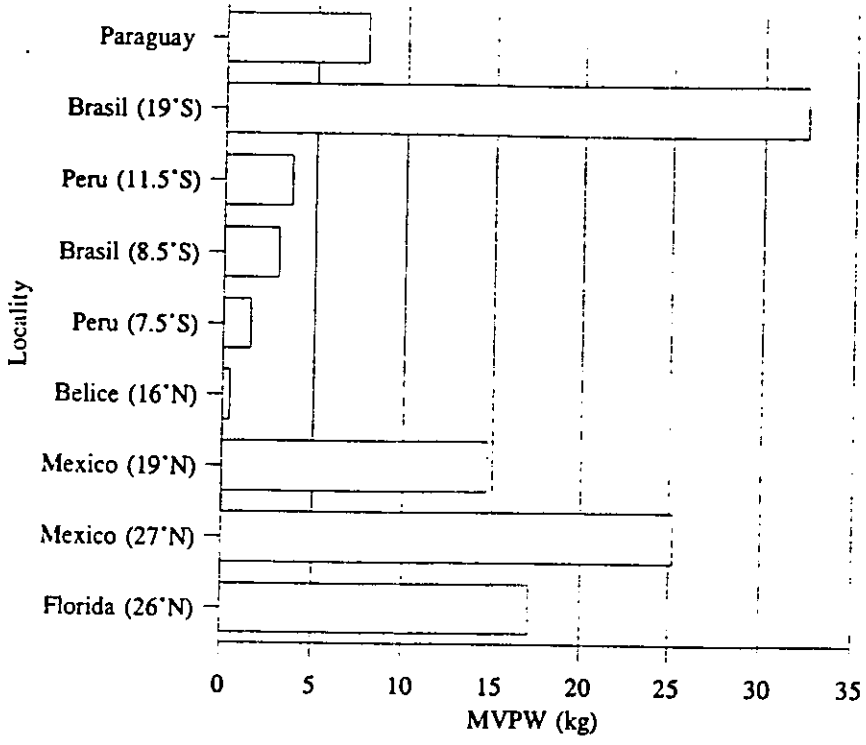

Figure 1
Comparison of mean vertebrate prey weight (MVPW) used by pumas through tropical America (Data from Iriarte *et al.* 1990, Lopez-Gonzalez *et al.* 1996, Olmos 1993, Romo 1995)

In the tropical rainforest of Costa Rica (Chinchilla 1994), pumas were feeding mainly on mammals, including tropical porcupine (*Sphiggurus [Coendu] mexicanus*) and spiny tailed-rats (Echymidae), primates (*Alouatta palliata, Ateles geoffroyi* and *Cebus capucinus*), brocket deer and iguanas. Sample size again was small (n = 11), and data were not available to perform any further analysis.

According to Crawshaw (1995) pumas at Iguazu National Park, Brazil, are using prey of an average of 10.8 kg where deer (*Mazama* spp) and peccaries (*Tayassu* spp) constitute the majority of the diet.

Pumas in the Paraguayan Chaco (Taber *et al.* 1997) are feeding on at least 16 prey items, where three species: *Mazama gouazoubira*, and peccaries accounted for 43% of the biomass consumed, but only 21% of the relative frequency of prey items. Pumas seem to use a diverse array of prey in this area. This is the only

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tropical study with a large sample size (N = 95), and standardized niche breadth was 0.68 (the most diverse found so far). MVPW for this study was 1.48 kg, not different from most tropical studies.

A correlation analysis between 14 studies of food habits showed that MVPW is related to the number of scats per study ($r^2 = 0.69$, $df = 13$, $p < 0.05$). When more representative samples from tropical areas exist, a more definite conclusion will be drawn on how pumas are using their trophic resources and will help explain if jaguars have an influence on the diet of pumas.

Kill rates

Several authors have attempted to estimate kill rate of prey species by puma (See Anderson 1983). Anderson (1983) points out problems in assessing the numbers of large prey killed in North America, these numbers varied from 12 to 91 individuals/puma on a year basis. Daily food intake range from 1.6 to 5.5 kg of meat (Hornocker 1970, Robinette *et al.* 1959, Shaw 1977, Ackerman *et al.* 1986). Ackerman *et al.* (1986) predict that a kill should occur between 8- 17 days for a resident adult, and each 3.3 days for a female with 3 large kittens.

Harrison (1989) intensively followed a couple of females and determined a predation rate of 1 ungulate every 3.3 to 10 days. A factor not really stressed in most predation rate studies is the impact of scavenging. Harrison (1989) demonstrated that areas subject to coyotes (*Canis latrans)* control reduced predation rates almost by half, this effect is probably more evident where complete carnivore assemblage are still present such as Glacier National Park (Montana, United States) or Yellowstone National Park (Wyoming, United States), or Manu National Park (Peru).

Population characteristics

As with many other species of carnivores, especially the felid family, population parameters are characterized by low numbers ranging over large areas (Schonewald-Cox *et al.* 1991). A typical puma population consists of male and female adult resident animals, juveniles, and transients. Within this classification the adult cohort can be divided into resident animals with area attachment and offspring production, and resident animals attached to an area without reproductive events. Adult resident sex ratios recorded for the cold desert of Utah (1:2, Lindzey *et al.* 1994), the mountains of Wyoming (1:3, Logan *et al.* 1986) or the mountains of Idaho (1:2 Seidensticker *et al.* 1973, Lopez-Gonzalez in review), are fairly similar.

Although breeding season may occur throughout the year, there seems to be reproductive peaks. Most Florida parturition events are reported between March and July (Maehr *et al.* 1991). For Utah and Nevada most events are recorded from June to October (Lindzey *et al.* 1994, Robinette *et al.* 1961). In Alberta (Canada) most births were associated with summer months (Ross and Jalkotzy 1992).

Human related mortality occurs also in non-hunted populations (Beier and Garrett 1993, Maehr *et al.* 1991) where highway collision was the most commonly documented cause for both studies. In Florida this cause of mortality averaged 17.2% of the total population. The natural causes of mortality range from congenital defects, rabies (Roelke 1990), injuries during prey capture (Ross *et al.* 1995), and parasitism (Maehr *et al.* 1991a, Sweanor 1990). Intraspecific aggression was the most important cause of mortality in a non-hunted population of New Mexico (Logan *et al.* 1996).

Population turnover in the puma has been characterized as low, and recently a 13-year cycle, dependent upon mule deer and climatic characteristics has been proposed (Smallwood 1994).

Social Organization

Puma social organization is similar to most solitary felid species of the world (see Sandell 1989 and references therein). One male home range overlaps up to four females, variations from one to four have been described throughout its range. Female home range can be exclusive (Neil *et al.* 1987) or overlapping (Anderson *et al.* 1992).

Pumas under extensive harvest are not able to recover normal population levels if adult resident extraction is larger than natural mortality, and it will take longer to recover if >25% of the population is removed on two or three consecutive years (Lindzey *et al.* 1992, Logan *et al.* 1996).

Home range

Home range size in pumas is quite variable, ranging from 32 to 1148 km² (Nowell and Jackson 1996, Maehr *et al.* 1992), the largest home ranges are for deserts (Hemker *et al.* 1984, McBride 1976, Sweanor 1990) and fragmented environments of Florida (Maehr *et al.* 1991a, 1992). The smallest home ranges are for the boreal forests in Canada (Spreadbury *et al.* 1996), Mediterranean California (Padley 1990) and the tropical rain forests of Belize (Rabinowitz and Nottingham 1986). Factors affecting the size of the area are related to sex and prey abundance (Dixon 1981, Currier 1983, Sandell 1989). This is especially important when assessing current rates of habitat transformation and loss. Maehr *et al.* (1991a) atributes the large

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home range of a resident male (1182 km²) to habitat loss and fragmentation in southern Florida. Padley's study (1990) took place in a fragmented area of California, and results from this study differ with those of Maehr *et al.* (1992) by a 10 fold. Lopez-Gonzalez (1994) presents results for a hunted population in a fragmented environment from Idaho (Mean = 62 km²) where patchiness and prey abundance seems to be responsible for the small size of the home ranges but behavior in this area is different from the other two studies on fragmented ecosystems. Rabinowitz and Nottingham (1986), using puma pugmarks, calculated a home range of 10 km².

Densities

The number of pumas per area unit (usually # adult ind./ 100 km²) varies with latitude and productivity of the system. Lower densities have been recorded for the cold deserts of Utah in North America (0.3-0.5/100 km², Hemker *et al.* 1984). The highest densities are recorded for a protected area of Patagonia with 7 animals/ 100 km² (Johnson *et al.* in press), and for the Sierra Nevada with 7.8 ind/ 100 km² (Steger 1988). A long term study in New Mexico, United States showed that under full protection the adult density was 2 ind/100 km² (Logan *et al.* 1996). An ongoing study in a tropical dry forest of the Pacific coast of Mexico has found a density of 3-4 animals /100 km² (Nuñez and Miller 1997). Crawshaw and Quigley (unpubl. data) calculated 4.4 animals per 100 km² on the Brazilian Pantanal. Eisenberg *et al.* (1981) calculated a density of 2 animals per 100 km² for the Venezuelan Llanos.

Lower densities have been atributed to low numbers of prey (Hemker *et al.* 1984), and high densities when carrying capacity is reached (4/100 km², Shaw 1989). No evident pattern is present either on latitude or longitude, or from protected areas or fragmented ones; the differences obtained between or within studies may be due to effective population sampling and the techniques used for this purpose (Nowell and Jackson 1996).

Parasites

Pumas are almost free of ectoparasites, problably due to solitary nature, low densities, and mobile habits (Currier 1983). Young and Goldman (1946) found fleas (*Arctopsylla setosa*), ticks (*Dermacentor variabilis, Ixodes ricinus*, and *I. cookei* and from South America, *Amblyomma cajennense, Boophilus microplus*, and *Dermacentor cyaniventris*), and lice (*Trichodectes felis*). Internal parasites are tapeworms (*Taenia omissa*), flukes (*Heterophyes heterophyes*) and nematodes (*Trichinella spiralis*) (Currier 1983). In Central Anmerica (Belize and Costa Rica),

coprological parasites of pumas are trematods (*Paragonimus* sp.), nematods (*Stringylida, Toxocara cati,* and *Capillaria* sp.), protozoa (*Hammondia pardalis, Giardia cati),* and amebas (*Entamoeba* sp. and *Retortamonas* sp.; Patton *et al.* 1986, Saenz-Jimenez 1996). Diseases known to affect pumas are anthrax, arthritis, feline panleukopenia, mange, piroplasmosis, and rabies (Currier 1983).

Behavior

Pumas can be active at any time of the day (Redford and Eisenberg 1992), but with a strong crepuscular activity present through its distributional range (Beier *et al.* 1995, Van Dyke *et al.* 1986, Lopez-Gonzalez 1994, Lopez-Gonzalez *et al.* 1996), the color of the pelage has been associated to diurnal activity and the trend of nocturnal activity is considered a result of human related interactions. Travel bouts are more frequent during the night (Beier *et al.* 1995, Lopez-Gonzalez 1994, Nuñez and Miller 1997). Traveling distances during 24 h range from 1 to 55 km, differences between sites are attributed to low cover and high heat incidence (i.e. deserts, Sweanor 1990), natural and agricultural patchiness (Beier *et al.* 1995, López-González 1994), hunting behavior (Beier *et al.* 1995, Maehr *et al.* 1989a), and levels of human habituation (Ruth 1990). Distances traveled per sex are larger for males than for females (Beier *et al.* 1995, López-González 1994, unpubl. data, Seidensticker *et al.* 1973).

Female Florida panther activity after parturition showed a reduction in home range size use, and activity pattern was highest between 1600 and 2400 h; absence from the den increased as kittens aged (Maehr *et al.* 1989). Den characteristics play an important role in protecting young defenseless kittens from thermal maxima (Shaw 1989), and they effectively moderate ambient temperatures (Bleich *et al.* 1996). Dens are usually associated with thickets and canyon bottoms to potentially avoid predator detection (Beier *et al.* 1995, Bleich *et al.* 1996).

Marking behavior has been related to home range maintenance, between and within sexes. Scrapes and scats are used to designate boundaries or overlap areas (Seidensticker *et al.* 1973, Sweanor 1990).

The puma hunting behavior is similar to that of many cat species, and several steps are recognized. Prey is detected through hearing and sight, then the puma approaches its prey by crouched walking at very reduced speed. Finally a short chase ends, if successful, with a bite on the nape for small prey and neck breaking for larger prey (Branch 1995, Robinette *et al.* 1959, Wilson 1984). Pumas have been observed killing black-tailed deer (*Odocoileus hemionus columbianus,* Wade 1929), goats (*Capra hircus*, Young and Goldman 1946), and collared peccaries (*Tayassu tajacu*, Van Pelt 1977). The puma hunting behavior on vizcachas (*Lagostomus maximus*) was observed in Argentina (Branch 1995) with an adult

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puma hiding behind a creosote bush (*Larrea divaricata*) then waiting until the vizcacha was closer and separated from the group before springing from a distance of 10 m. The puma held it with its forepaws until killing it with a nape bite. Hunting attemps observed in this study ended with a 10% success ratio.

Pumas have been recorded vocalizing while pursuing and killing black-tailed deer in California (Smallwood 1993). Pursuit lasting between 20-30 min with intermitent vocalizations at intervals of ≤ 5 min. Smallwood related vocalizations as a rare behavior associated with providing extra time to successfully accomplish prey capture by freezing some animals and/or confusing them cued by one or a combination of specific circumstances the predator encounters at the initiation of a pursuit.

Kills are usually dragged and stashed under trees, dense thickets or ledges (Beier *et al.* 1995). Large prey items are usually buried under leaves and dirt to keep them from scavengers (Hornocker 1970, Shaw 1979). Smaller prey are known to have been dragged into a repeatedly used cache site (Branch 1995). Larder hoarding behavior was observed in Montana, USA where a puma killed a bighorn sheep (*Ovis canadensis*), and two mule deer (*Odocoileus hemionus*, a doe and a buck); the puma bed was located 4 and 3.5 m away from the carcasses (Holt 1994).

Recorded instances of injuries sustained by pumas during predation of elk (*Cervus elaphus*)and mule deer are reported by several researchers (Brown *et al.* 1988, Hornocker 1970, Lindzey 1987). Ross *et al.* (1995) described deaths of four radio-collared pumas that were related to prey capture, and concluded that it can be a significant source of mortality for a population (27%). Injuries are more prevalent in young inexperienced or old and not socially established pumas.

Interspecific predator relations

The puma, throughout its range is sympatric with a variety of larger and smaller carnivores. In North America (Canada and the United States) the species is sympatric with two or three larger predators, namely wolves (*Canis lupus)*, grizzly (*Ursus arctos horribilis*) and black *(Ursus americanus*) bears. Interactions between these and other predator species have just recently begun to be acknowledged and therefore little quantified information exists.

Puma and grizzly bear interaction in Montana (Ruth and Hornocker 1996) have yield information regarding the dominance of grizzly bears over the puma. This is partially explained by the larger size and non hibernating habits of male bears, that resulted in den finding and killing of puma kittens reducing population recruitment. In the same area, wolves and grizzly bears are known to chase pumas away from their kills and tree them, although the study is not finished and the results are

preliminary, this could potentially become a factor influencing the physical condition and survival of females with kittens, due to a reduced food intake limited both by bears and wolves.

In Mesoamerica and tropical South America the puma is sympatric with the jaguar (*Panthera onca*). And several authors have stated the dominance of the latter over the puma. In such instances jaguars are considerably larger in size than pumas, with some size overlap between female jaguars and both sexes of the puma (Crawshaw and Quigley 1991, Emmons 1987, Schaller and Crawshaw 1980). Crawshaw and Quigley (1991) recorded jaguars encountering and killing pumas. Nevertheless where the jaguar reaches its distributional limits, pumas can be larger than jaguars (Allen 1906, B. Miller and C.A. Lopez-Gonzalez pers. obser.) as a result, competition could be more apparent in these areas. Mean dietary niche breadth for both species is fairly similar but mean vertebrate prey weight is twice as large for the jaguar (Oliveira 1994).

An allometric study on Neotropical cats (Kiltie 1984), using body mass, body length, relative maximum bite force and relative maximum gape, suggests that competitive character displacement is a possible explanation for the constant ratios in maximum gape differentiating and therefore allowing coexistence between jaguars, pumas, ocelots (*Leopardus pardalis*), and the functionally identical margay (*Leopardus weidii*)and jaguarundi (*Herpailurus yaguaroundi*). The puma is usually dominant over smaller carnivores, preying upon them and in some instances they can become important food items of its diet, for example the raccoon (*Procyon lotor,* Maehr *et al.* 1990), bobcat (*Lynx rufus,* Lopez-González 1994, Koehler and Hornocker 1991), and the ocelot (C.A. Lopez-Gonzalez unpublished data).

Jorgenson and Redford (1993) in a comparative study of food habits between pumas, jaguars, and subsistence hunters, found considerable overlap among major mammalian taxa used by the three species. Humans do not partition resources with the other predator species in order to coexist, therefore where pumas and jaguars are sympatric with human hunters, the big cat populations may decline as a result of interference competition occurying in the Neotropics and perhaps other rural areas of Latin America.

Puma as a keystone species

The role of large carnivore in the ecosystem is still unclear, as two main tendencies exist. One supports the classical keystone species concept, where the species play an essential role within the system and whose activities are critical to the maintenance of entire communities and/or as a major depressor of prey species (Paine 1966, 1969). As a consequence of such depressing action they have a directional effect on the plant community, namely regeneration and/or

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reforestation (Terborgh 1990). On the other hand we have the trend where the presence or absence of top predators within the system would not alter the outcome of such system (Wright *et al.* 1994).

Wright *et al.* (1994) studying the possible effects of lack of predators at Barro Colorado Island tested for differences of prey densities with and without large felids and failed to support the hypothesis that felids control prey abundance, but they still recognize the lack of sufficient information.

However on temperate ecosystems there is some evidence supporting the keystone hypothesis. Specifically in the great basin desert, Berger and Wehausen (1991) described the effects of human disruption in the "natural" community. They used historical, and anthropological data to reconstruct the expansion of mule deer (*Odocoileus hemionus*) and the consequent follow up by the puma. Incorporation of these two species to the system was determined by the transformation of extensive areas of grass into a forb and shrub dominated environment more suitable for deer, pumas, and reciprocally other species. This experience could explain and partially reflect the great distribution of pumas in areas where they otherwise would not be suited to exist. A clear example is Joshua Tree National Park (California, United States) where isolation and lack of proper food and cover for deer prevents the existence of the former and also seems to limit pumas.

Survey and Census Methods

As we have seen through this manuscript, differences in methodology (and sample size) are possibly accountable for the variability observed in food habits, densities, or home range size. Capture recapture methodology yields the best results to estimate population numbers, but is expensive and time consuming (Logan *et al.* 1996). Track surveys have been tested to detect population trends, and have proven not to perform accurately (Beier and Cunningham 1996). Identification of individual pumas using a multivariate analysis of paw measurements yielded positive results, yet the population studied was unknown, therefore the results are of limited use until tested with a control set of animals (Fitzhugh and Smallwood 1995). No method is free of limitation but a standard uniformity protocol should be assessed by puma researchers to make comparisons, between and within sites, through time and space.

PROTECTION STATUS

The puma has different classifications under several international agencies. The International Union for Conservation of Nature (IUCN) considers the species as common and less vulnerable, with the lowest conservation priority on a global

scale (Nowell and Jackson 1996). Nevertheless the regional or local situation has particular situations.

The species is listed under Appendix II of the Convention of International Trade on Endangered Species (CITES), *Puma concolor coryi, P. c.costaricensis* and *P. c. cougar* are listed under Appendix I.

The Florida panther (*Puma concolor coryi*) is the only subspecies with an extant population in the eastern United States (Currier 1983, Maehr 1991). The eastern cougar (*Puma concolor cougar*) is also protected by the United States Endangered Species Act (1973). The status of this subspecies is currently under debate, and the increasing number of reports in the Maritime Provinces, New Brunswick, Ontario, and Vermont (Cumberland and Dempsey 1994, Stocek 1995, Neil Peck Ontario Ministry of Natural Rsources, Pers. Com.) could be related to a remnant population in eastern Canada and/or the spread and subsequent migration of western cougars via Canada's less populated territories, but not enough samples of animals or reliable spoor are present to determine which may be the leading hypothesis.

Hunting of pumas is prohibited troughout South America with the exception of Peru. In Central America the species is protected except in El Salvador, and this country currently states the species to be almost extinct. Regulated hunting exists in Canada, Mexico, United States, and Peru. No legal protection is present at Ecuador, El Salvador and Guyana (Nowell and Jackson 1996 and references therein). Hunting regulation for Canada and the western United States is given by particular needs of State or Territory. Mexico hunting regulation is given on a permit basis per State, but no scientific studies or surveys accompany it.

CONCLUSIONS

The puma, although one of the better studied feline species of the world, still presents many research, management and conservation challenges, especially for central American and South American countries, where hardly anything is known about the species. Research emphasis should be aimed to develop survey and census techniques that are cost effective and easily replicated through time and space.

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Appendix 1.- Notas complementarias al Capítulo I.

A sugerencia de un revisor se anexan un par de parrafos explicando algunos resultados que se citan en el capitulo I.

Las diferencias entre los estimadores para calcular los ámbitos hogareños podrían explicar las diferencias en el tamaño y uso referidos en la página 9 del capitulo I, sin embargo todos los estudios utilizan el polígono mínimo convexo para efectuar comparasiones con otros estudios. Esto apoya lo antes ya mencionado.

Smallwood (1997) realiza un análisis de las densidades poblacionales del puma y su relación con la denominada "área de estudio" encontrando que las densidades más altas están sesgadas a lugares donde se sabe de antemano existen "muchos" pumas. Dicho autor concluye que no es posible extrapolar estas densidades a áreas más extensas a menos que el tamaño del área estudiada sea mayor a 1700 km^2.

Existen citas que no contribuyen de manera significativa al conocimiento ecologico del puma. Citas que reportan registros de puma en areas donde se sabe existen o existieron, por ejemplo.

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CAPITULO II

DINAMICA POBLACIONAL DEL PUMA EN LOS LIMITES FRAGMENTADOS DE UTAH - IDAHO.

PUMA POPULATION DYNAMICS IN THE FRAGMENTED IDAHO-UTAH BORDER.

ABSTRACT

A hunted puma population was studied from 1987 to 1995 on a 2500 km² study area of South central Idaho and Northwestern Utah, United States to monitor its size and age and sex composition. Capture-recapture and radiotelemetry techniques were used to determine survival, mortality, natality and dispersal dynamics. A total of 91 pumas were monitored through the period study. Average adult density was 0.96 pumas/100 km². The resident cohort of the population was comprised of young adults (<5 years old). Adult resident females could breed as young as 17 mo. and produced litters that averaged 2.5 kittens at 17 months intervals. Kittens had a 52.9% chance of surviving. Adult survival was 70.2 ± 23.5%. Most mortality was human related. Dispersal occurred after independence but female philopatry was present until an apparent reach of carrying capacity.

RESUMEN

De 1987 a 1995 se estudió una población de pumas en una área de aproximadamante 2500 km², localizada en la porción central Sur del Estado de Idaho y el Noroeste del Estado de Utah, en los Estados Unidos de América (41°40' y 42°30' Latitud N, y 113° y 114°42' Longitud W). Para monitorear el tamaño y composición de la población se utilizaron técnicas de marcaje-recaptura y radio telemetría . Como parte del estudio se calcularon la densidad, supervivencia, mortalidad, natalidad y dispersión de la población. Un total de 91 pumas fueron monitoreados a lo largo del

periodo de estudio. La densidad promedio de los adultos fue de 0.96 pumas por 100 km². La edad de la cohorte residente se considera joven (<5 anos). La edad de la primera reproducción de las hembras fue de 17 meses, con un tamaño de camada promedio de 2.5 crías y un intervalo entre camadas de 17 meses en promedio. La probabilidad de supervivencia de las crías es del 52.9% y la de los adultos de 70.2 ± 23.5%. La mayoría de las muertes registradas en la población estuvo relacionada a actividades humanas. La mayoría de los pumas se dispersaron al alcanzar su independencia, sin embargo las hembras fueron filopátricas hasta que la población aparentemente alcanzó su capacidad de carga.

INTRODUCTION

In order to understand the factors that are regulating animal populations, studies should foccus on several basic parameters. Such elements include how the population numbers change through time and why, natality and mortality factors and, how humans fit in the "natural" system (Caughley 1994).

Population characteristcs of pumas have been examined throughout the western United States, Florida, Alberta and British Columbia; Canada, and Chile (e.g. Anderson 1983, Iriarte et al. 1990, Lindzey et al. 1994, Maehr et al. 1991a, Ross and Jalkotzy 1992, Spreadbury et al. 1996). Most studies have either determined densities, home ranges, population fluctuations or other factors affecting population size (Ross and Jalkotzy 1992). Hunting has been identified as a factor limiting and/or reducing populations (Lindzey et al. 1992, Shaw 1980, Ross and Jalkotzy 1992). Social interactions and prey densities are factors that help control population numbers (Hemker

et al. 1984, Lindzey et al. 1994, Seidensticker et al. 1973, Sweanor 1990). Recently, mortality during prey capture have been suggested as an important aspect influencing population size (Ross et al. 1995). In some isolated populations habitat fragmentation (as a consequence of human activity) can possibly explain the demography of such areas (Beier 1993, Maehr et al. 1991a).

What can be expected? From reviews on spacing patterns (Sandell 1989), life-history traits (Gittleman 1989), and body size (Eisenberg 1989). We predicted: 1) The puma population in the study area should have similar demographic characteristics to others. 2) If human hunting and fragmentation have any effect in the population it will probably be reflected in higher replacement rates, lower survival, and mortality patterns. 3) As a result of hunting, natural mortality should be considerably reduced, since replacement is taking place at a more constant and predictable rate than natural causes.

In this study we wanted to describe and monitor the size, composition, natality, and mortality to understand the population characteristics of hunted pumas in the Idaho-Utah border in order to help make management decisions in areas of similar habitat and vegetation characteristics.

STUDY AREA

The study area was located in the Northwestern United States and forms part of South-central Idaho and North-western Utah (Figure 1). The study area is ≈2,500 km² within the polygon located at 41°40' and 42°30' N, and, 113° and 114°42' W.

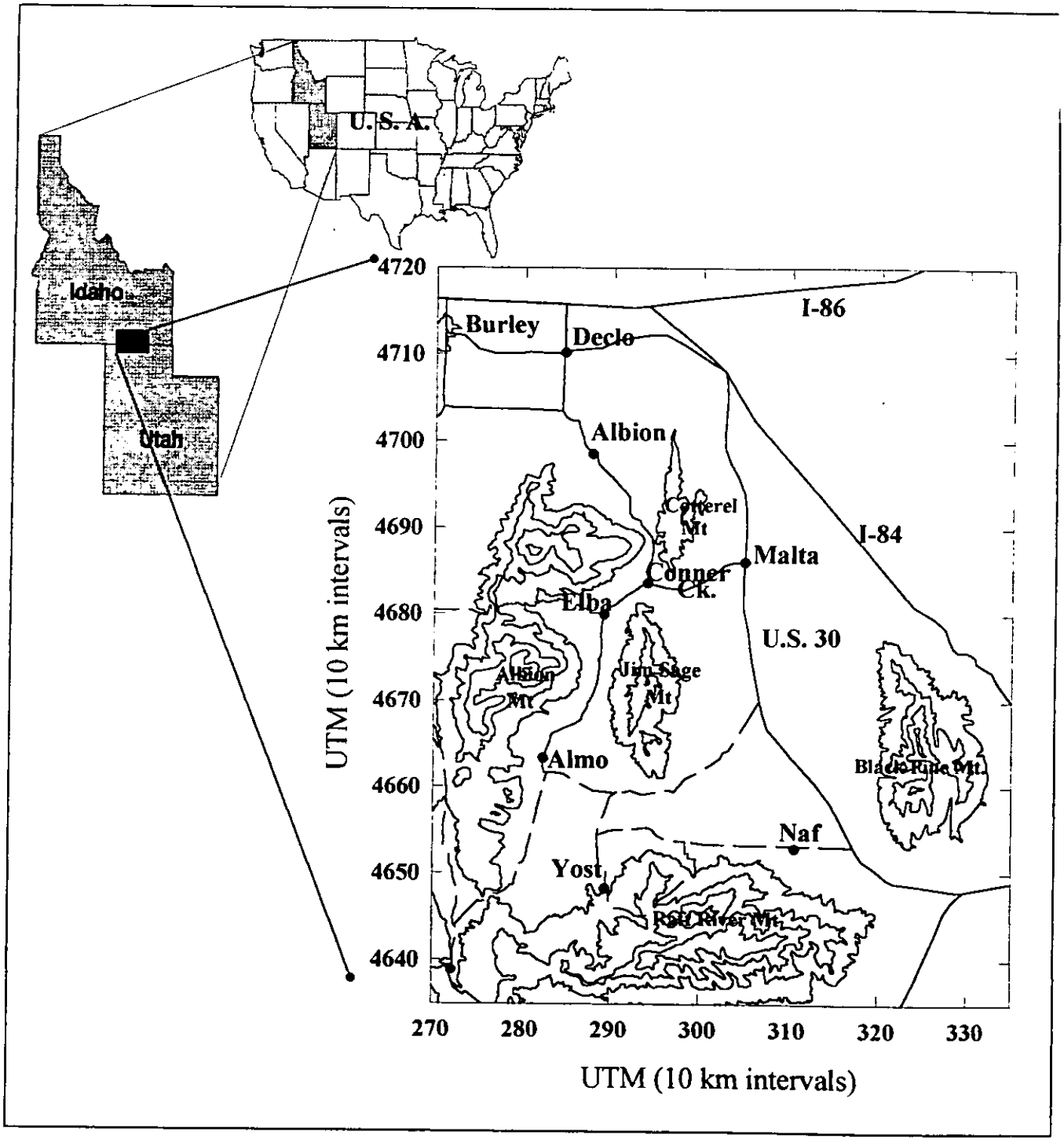


Figure 2.- Map of the United States of America showing the States of Idaho and Utah with a schematic view of the study area. Contour lines are 300 m apart, starting at 1800 masl.

Elevations range from 1585 to 3151 masl (U. S. Geological Survey 1990). The valleys range from 1585 to 1829 masl, and the mountains from 1830 to 3151 masl. Precipitation (approximately 300 mm) was usually present in the form of snow, from late October early November into late February, occasional showers and thunderstorms were present in spring and summer.

The habitat is classified as great basin desert (Shelford 1978) with a landscape dominated by a sagebrush (*Artemisia*)- shadscale (*Atriplex*) association but also including small forested portions of juniper (*Juniperus*), pine (*Pinus*), douglas-fir (*Pseudotsuga*), and mahogany (*Cercocarpus*). Idaho's forests have not been studied in full detail (Caicco et al. 1995), and the study area was not well classified except for the City of Rocks National Preserve, therefore, partial classification of the vegetation communities were given through personal observations.

Throughout the area, valleys and open areas on the mountains were dominated by *Artemisia tridentata*. Forested associations are sparsely located through different altitudes and across the study area. The most dominant communities are Pine-Juniper (*Pinus edulis-Juniperus osteosperma*), Aspen-Pine (*Populus tremuloides-Pinus edulis*), Mountain mahogany-Douglas fir (*Cercocarpus ledifolius-Pseudotsuga menziesii*), Juniper (*Juniperus osteosperma*) and Mountain mahogany (*Cercocarpus ledifolius*). Alpine meadows are also present at higher elevations and mesas. A large proportion of the valleys was transformed by human activities. Crops present in the area are alfalfa, barley, and potatoes (Ken Jafek, Simplot Farms, pers. com.). Localized logging and mining operations are present, but the main activity is livestock management in the mountains. The land tenure system is private property, National Forests, and Bureau of Land

Management lands; the National Park Service is present with the small City of Rocks, National Preserve.

Mule deer (*Odocoileus hemionus*) were the most common ungulate, and small numbers of elk (*Cervus elaphus*) are present and scattered through the study area. Pronghorn (*Antilocapra americana*) are distributed in small numbers (< 200) on the valley floors. Other potential prey species present are porcupine (*Erethizon dorsatum*), ground squirrels (*Spermophilus townsendii*), golden mantle ground squirrels (*Spermophilus lateralis*), black tailed jack-rabbits (*Lepus californicus*), snowshoe hare (*Lepus americanus*), and desert cottontail (*Sylvilagus audubonii*). No published mammal inventory exists for the study area, so the species listed have been gathered through interviews with locals and personal observations.

METHODS

Pumas were captured from 1987 to 1995 by searching for tracks on roads and trails mainly during times of snow cover. Once a track was found, the animal was pursued by trained hounds until treed and tranquilized with an intramuscular injection of ketamine hydrochloride and xylazine hydrochloride fired from a Cap-chur® rifle dart. The drug dosage follows López-González (1994). Immobilized pumas were lowered from the tree with a rope to avoid injury. Age was estimated by dental characteristics (Shaw 1979). Morphometric measurements taken from captured pumas were total length, tail length, hind foot, ear length, and body weight. Measurements from the front and hind paws were also recorded. Each puma was tattooed in both ears with an identification number and, when age allowed it (> 6 mo. old), fitted with a radiocollar

containing a motion sensitive transmitter (Wildlife Materials, Inc.®).

The social condition of pumas was determined by age, reproduction, and residency status. Resident adults were independent pumas ≥ 17 mo of age with established home ranges, and were the breeding members of the population (Laing and Lindzey 1993, Seidensticker et al. 1973). Numbers of known resident animals per year were assessed during winter when new individuals could be determined by track sets.

We calculated the population size with a mark resight survey using the modified Lincoln-Petersen population estimate for the years when data were more complete (90-95). The Emigration/Immigration estimator of the computer program NOREMARK was used to compensate for the violation of geographic closure (Hein and Andelt 1995, White 1996). Then the observed population was compared to the calculated one.

Kittens were discovered and parturition dates fixed by monitoring female behavior and home area in particular home area use was reduced, Maehr et al. 1989a). Older litters were discovered by walking on females or by coming across tracks in the snow. Most kittens were aged within days of birth and in some instances with a month difference.

Time of independence was determined by following pumas until we saw no associations mother. Mortality data was pooled from different sources, and kitten survival was estimated by pooling data for the total length of the study in order to have larger sample size.

We calculated daily adult survival rate by the formula (White and Garrott 1990): $s_i = (x_i - y_i)/x_i$. Where x_i is the total number of transmitter days in the interval and y_i is the total number of deaths, respectively, in interval i. The probability of survival for interval i is then the product of

the daily survival rates: $S_i = s^L$. Where L is the length in days of interval i.

Hunting permits on the Idaho side are determined by a female quota, where *n* number of males can be harvested until the female quota is reached. Female quota from 1987 to 1991 was three females, and from 1992 to 1994 it was one female. Due to local (deer and puma) hunters pressure, a three female quota was reestablished in 1995. In the Utah side 10 permits are issued per hunting season, regardless of sex and age.

Budget restrictions prevented us from performing mule deer (main prey, López González 1994) or alternative prey surveys. Nonetheless we obtained the number of deer hunted from the Idaho Fish and Game, the number of permits issued, and the numbers of days hunted on a given year. These parameters were combined into an effort-success hunt index developed with the proportion of deer/permit success divided by the proportion of deer/days. This way comparable unitless numbers could be used in deer population trend to be correlated with the number of pumas present on the study area. In addition, regular driving of roads, walking on trails, and interviews with local wildlife managers yielded some qualitative observations on how the species population varied from year to year.

All data was tested for normality (Kolmorogov-Smirnov) and equal variance (Leven median). All data is reported as mean and standard deviation. Simple linear correlation analysis tested for differences in size between sexes. All tests had a probability value of 0.05. All statistic tests were performed with Sigmastat for Windows 1.0 (Jandel Corporation®) and following Zar (1974).

RESULTS

Population size and structure

Ninety-one pumas in the study area were monitored for a mean 1.7 years (SD=1.09, range 1-5), representing a total of 56,465 animal-telemetry-days.

The mean number of pumas present per year was 25.88 (SD=13.05, range 7-43). Using this figure as a density estimator we have 1.03 pumas per 100 km^2. Another estimator of density was calculated with the total number of resident pumas in the year of study with the most animals. Twenty-four resident pumas were present during 1994 for a density of 0.96 puma per 100 km^2. Both calculations are close to 1/100 km^2.

The largest number of pumas present within the population at the peak observed during 1993 was 43 animals. We do not believe however, that incorporating transient and kitten cohort in calculations presents a reliable estimate of density.

Average sex ratio was of 1.0 male to 1.95 female, and variation between years was 1.0 M:0.8 F (1990) to a higher 1.0 M:3.0 F (1987, 1988,and 1991). There was no significant deviation from a 1M:1F ($z= 0.83$, $p > 0.05$).

We wanted to compare the number of pumas per year, so we calculated a heterogeneity chi-square to test for independence with the acceptance of a null hypothesis of data being part of the same population and with no independence between years ($X^2=12.76$, df = 56, $p>0.99$).

We wanted to know if there was any dependence between the number of resident males and transients so we correlated them under the assumption that the number of transients will be reduced by an increase in the number of resident males. Linear regression yielded a light positive

correlation (r^2= 0.34, df = 8, p>0.05) with an increase in the number of transients as the number of males increased. Similarly, juveniles should be related to number of resident females with the number of kittens increasing positively with the number of females. This linear regression was positive (r^2=0.439, df = 8, p>0.05). Both of the regressions did not explain most of the variance present on the samples, 58.9 and 66.3 respectively for males and females.

An apparent trend is observed when considering the raw data from 1990 to 1995. There was an increment in resident animals until 1994 and then a reduction in 1995. The number of resident pumas by sex for the study area is 4.55 (SD= 2.67) males and 8.88 females (SD=5.13) per year. Mean number of transient pumas was 3.88 (SD=1.66) and kittens were 8.66 (SD=5.57). The number of resident females was correlated with the number of males present per year in the study area (r^2=0.831, df = 8, p<0.005).

During the first three years, the study was restricted to the Idaho portion resulting in low capture success and consequently low numbers. In 1990 capture efforts started on the Utah side, yielding better results and increasing sample size. Number of resident animals was relatively constant during the first three years of the study, showing the same results and relatively lower densities. When including the rest of the study area a change in numbers is evident (Figure 2). A trend seemed to be present with increasing numbers from 1990 to 1993 almost tripling the number of animals. During the peak year of resident animals (1994) poor recruitment on the transient and kitten cohorts of the population is observed.

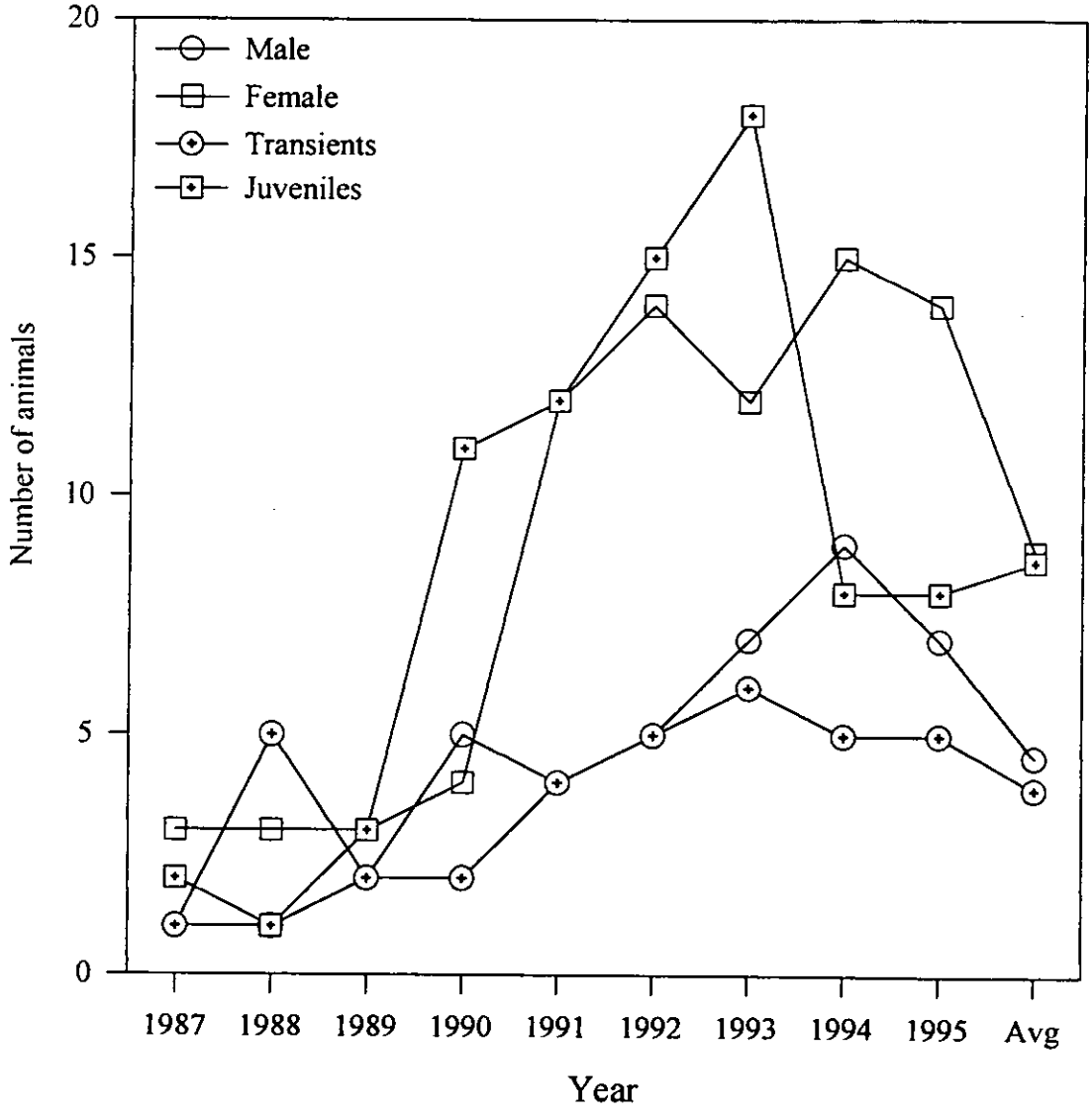


Figure 3.- Number of pumas per year on different social categories from 1987-1995. (for 1987 to 1989 data only includes the Idaho portion of the study area).

Data per year yielded very little information on the age structure of the population therefore we pooled data from the different years and constructed a pyramid (Figure 3). The oldest age recorded for the study was a female with >8 years. More than half of the population had an age <2 years. Most productive females in the population were included in the interval between 2 and 5 years old. It is interesting that most of the males were less or equal to four years old.

The number of pumas from 1990-1995 was negatively correlated to the hunter-success index (r^2= -0.8364, $p<0.05$). In other words, the number of deer tend to increase while the number of cougars decreases. This result should be considered of indicative value because the hunter-success index used may or may not be reflecting the trend on the deer population, although when observing the number of deer taken per year from 1980 to 1995, it appears to have a cyclic pattern (≈ 16 years).

Natality and kitten survival

We observed 24 litters between 1987 to 1995. Litters were born in every month of the year except February, April, May and December (Figure 4a). A peak in births was observed between July and October (75%) including June and November (87.5%) most births occured during the summer and fall. Average litter size was 2.5 kittens (SD=0.591, range 2 - 4). Most litters (55%) had two kittens and 40% had three. Sex ratio of kittens in 20 litters from which all kittens were sexed slightly favored males (1.12 M: 1.0 F) but was not different from a 1.0: 1.0 (z=0.23, $p>0.05$).

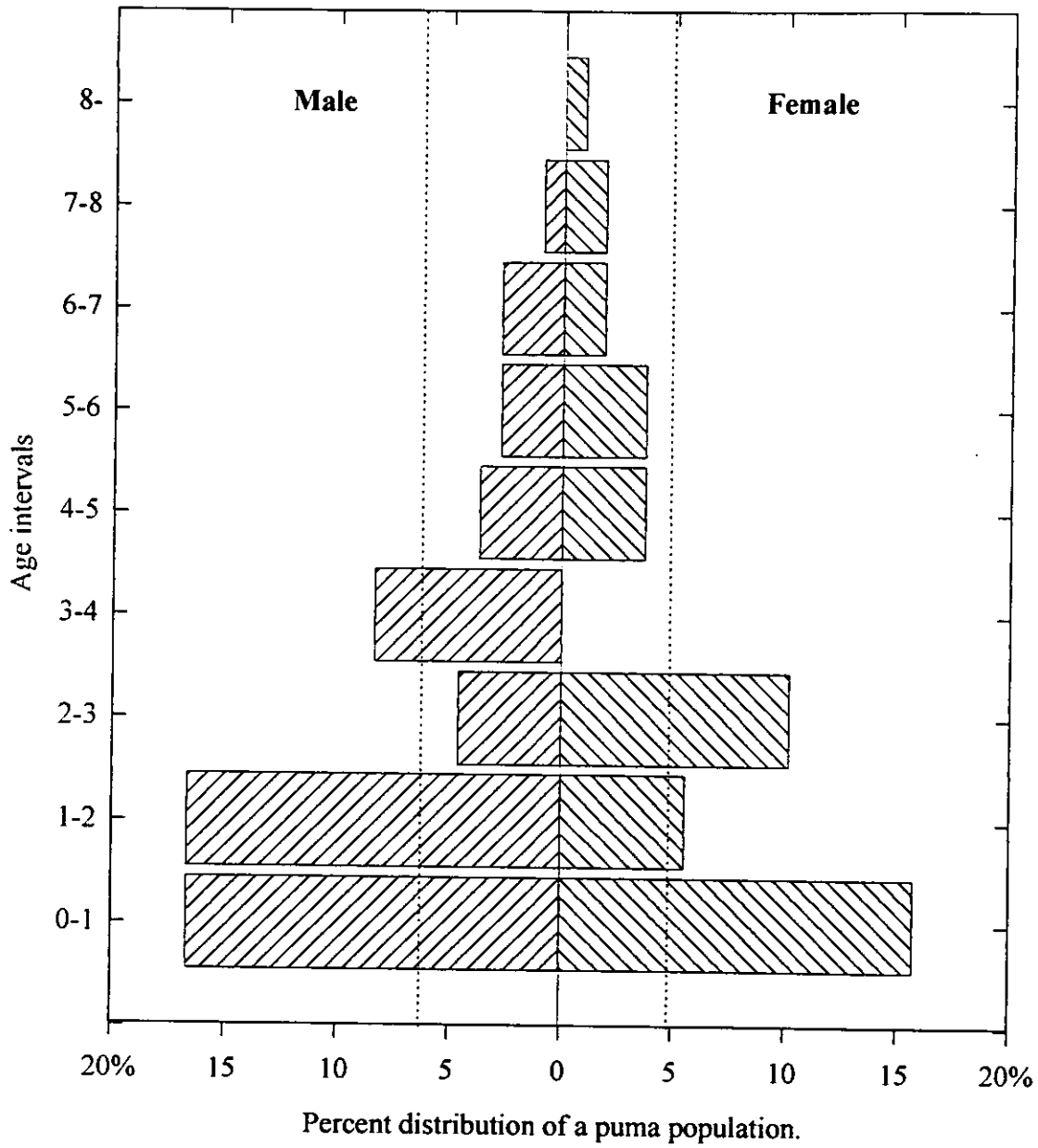


Figure 4.- Age structure of pumas (*Puma concolor*) in South central Idaho and NW Utah.

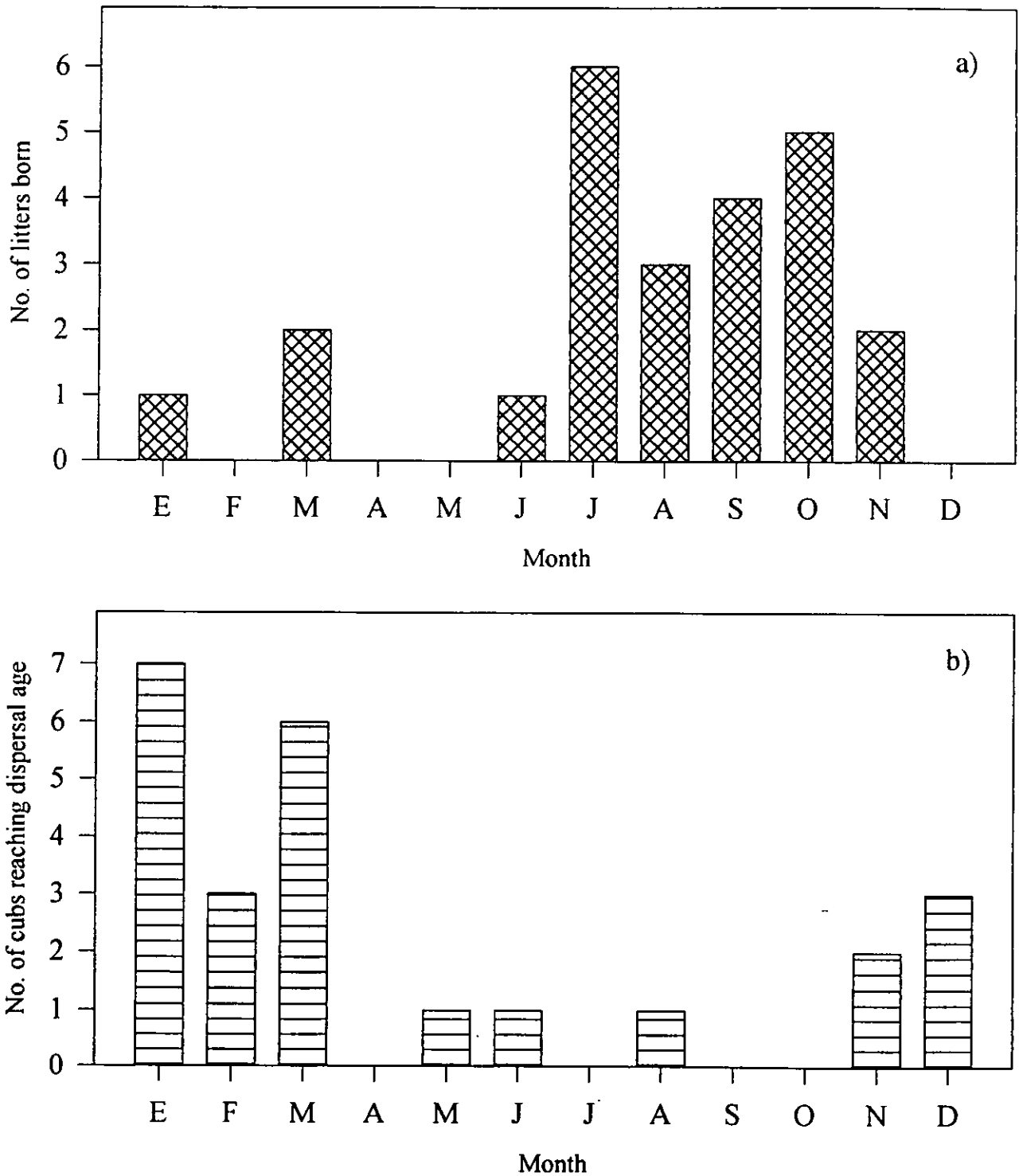


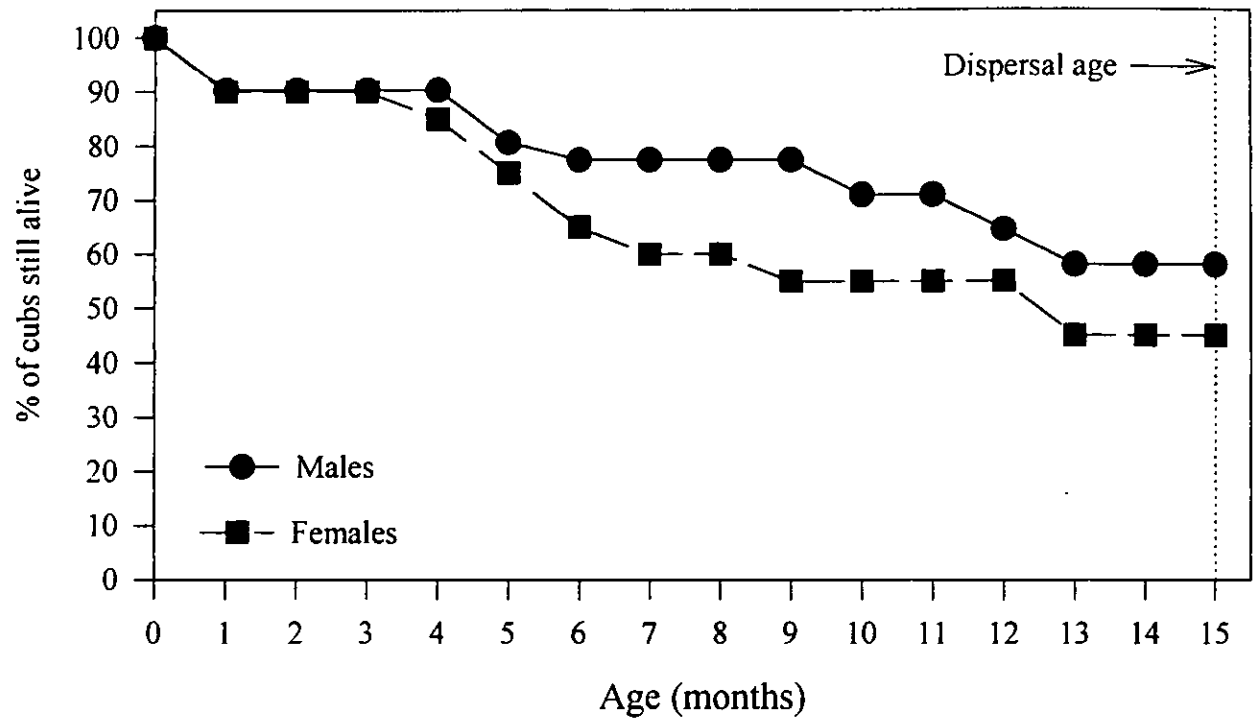
Figure 5.- Month of birth (a) and independence (b) for pumas in the Sawtooth National Forest, Idaho-Utah, 1987-1995.

Only the birth intervals for three females in the study area were determined. Two had consecutive litters in a single year because they lost their first litter, one to starvation and the other one to infanticide. The third one was monitored through three consecutive litters, with intervals between litters at 18 and 16 months (mean = 17.3 mo). First reproduction was recorded as early as 17 mo. for two females. An interesting feature is that both of these "first time" mothers lost their litters, probably related to selection of inadequate den sites.

Kitten survival was calculated through the numbers of cubs alive at a given age and pooled together for a larger sample size. Data was pooled by month and sex in known kittens and unknown sex when kittens were found by other people. We assumed that all kittens survive the first month of their lives and determine their permanence within the population until reaching dispersal age. Overall kitten male survival (58.06%) was higher than female (45.0%). Male survival was similar to female survival for the first four to five months of age, after which, male survivorship was considerably larger than female (Figure 5a). When comparing overall survival from known-sex kittens with that of all cubs included (Figure 5b) , survival is higher for known kittens (52.94%). All cubs included is 41.53%. Female mortality is relatively constant at 55% from 10 to 13 months of age, decreasing to 45% after the 14 mo.

Dispersal

Monitoring of kittens was done in order to determine the time of dispersal. A total of 24 kittens were followed from birth and/or when <6 mo of age until dispersal.



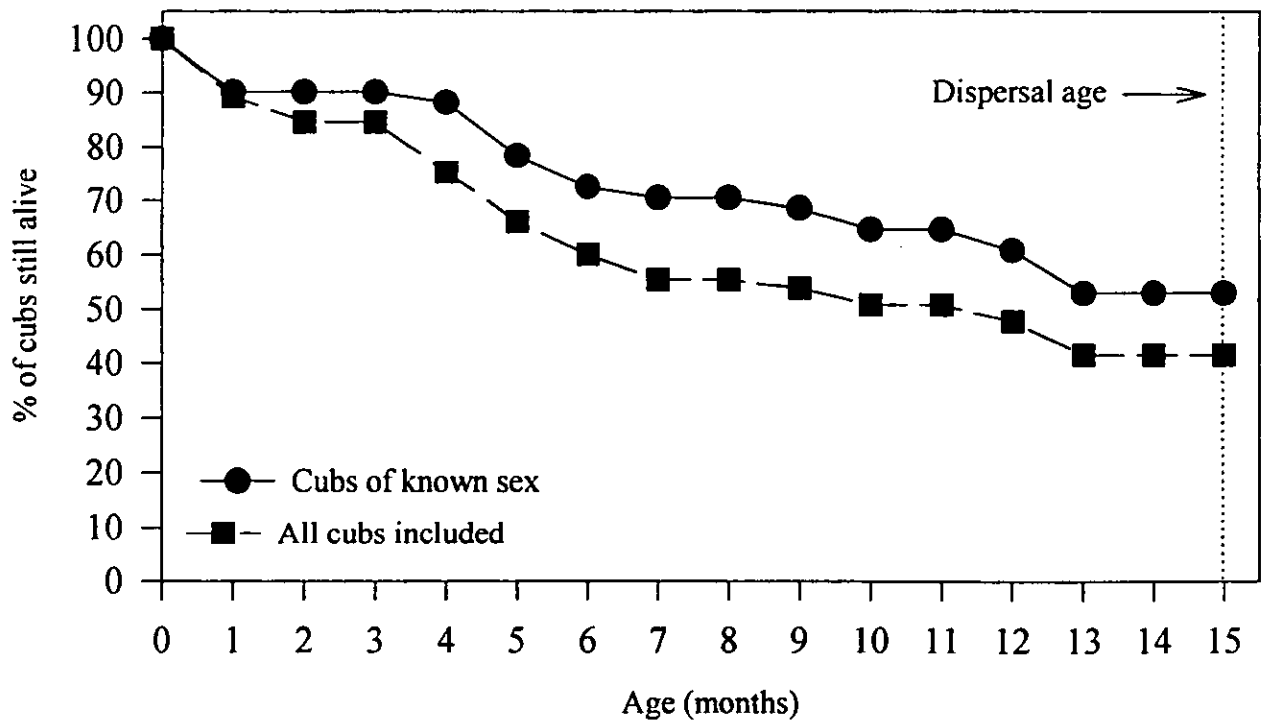


Figure 6.- Kitten survival in the Sawtooth National Forest, Idaho-Utah, 1987-1995.
a) Comparative survival of known male and female kittens.
b) Comparative survival of pooled known and unknown sex kittens.

Pumas disperse at any time of the year (Figure 4b) but a peak is present between January and March (66.66%), and November and December (20.83%). If pooled together on a biological concept, 87.49% of dispersing takes place in late fall and winter. Five females that reached dispersal age remained on their natal grounds, but only one replace the home range of the parent.

Adult survival and mortality

Average annual survival rates for pumas (females and males combined) was 70.2 ± 23.5% with a range from 35.4 to 100%. Average male survival was 61.7 ± 36.5% and female average survival was 77.3 ± 25.4%, there was no significant difference between sex survival ($t = -1.02$, $df = 14$, $p>0.05$). There is a low turnover in home range and therefore tenure systems last for several years (between 2 - 3 years). Average mortality could be considered low (1- survival) in the population regardless of the hunting regime. Mortality was produced by several causes. Human activity was most important. It could be direct (hunting) and indirect (killing a female which causes her kittens to starve). Intraspecific mortality accounted for kitten deaths (n= 3). Only one mortality in relation to prey capture was recorded. Capture mortality was present on the study (n= 2).

Population morphometrics

Morphometrics were obtained for 73 pumas (31 females and 42 males). Pumas were measured each capture and/or recapture. There was no significant difference between sexes in total length ($t = 289$, $df = 31$, $p=0.12$). Males (57.7 kg) were significantly heavier than females

(41.1 kg)($t=2.17$, $df= 30$, $p<0.05$). Predictive relationships were developed through correlation analysis. Raw data was transformed into log normal. Weight in females can be predicted by the relationship log Fw is equal to (0.344 * log total length) - 27.6 (Figure 6) and male weight is predicted by log Mw equal to (0.619 * log total length) - 69.0 (Figure 6).

DISCUSSION

The number of pumas estimated for this area falls between that of a slightly hunted population in Central Idaho (Hornocker 1970) and a non-hunted population in apparently less productive habitat (Lindzey et al. 1994).

Population densities for the study area were within published estimates for Nevada's Great Basin (Ashman et al. 1983) with 1.02 puma per 100 km², with only one wilderness area of Nevada having a density of 1.56/100 km². The Rockies of Central Idaho had a density of 2.9/100 km² (Hornocker 1970) and Central Colorado had a density of 1.1/100 km² (Anderson et al. 1992). The canyonlands of south central Utah described by Hemker et al. (1984) do not differ too much from the geomorphological and vegetation structure of the study area, nevertheless density there was 0.3-0.5 ind/100 km², but averaged 0.37/100 km² at the end of a long term study (Lindzey et al. 1994). For the Sierra Nevada of California a density of 3 pumas/100 km², and no seasonal migration occured (Neal et al. 1987). The highest densities were recorded for a protected area of Patagonia with 7 animals/ 100 km² (Johnson et al. in press), and for the Sierra Nevada with 7.8 ind/ 100 km² (Steger 1988), although for these last two studies we believe all social classes were included.

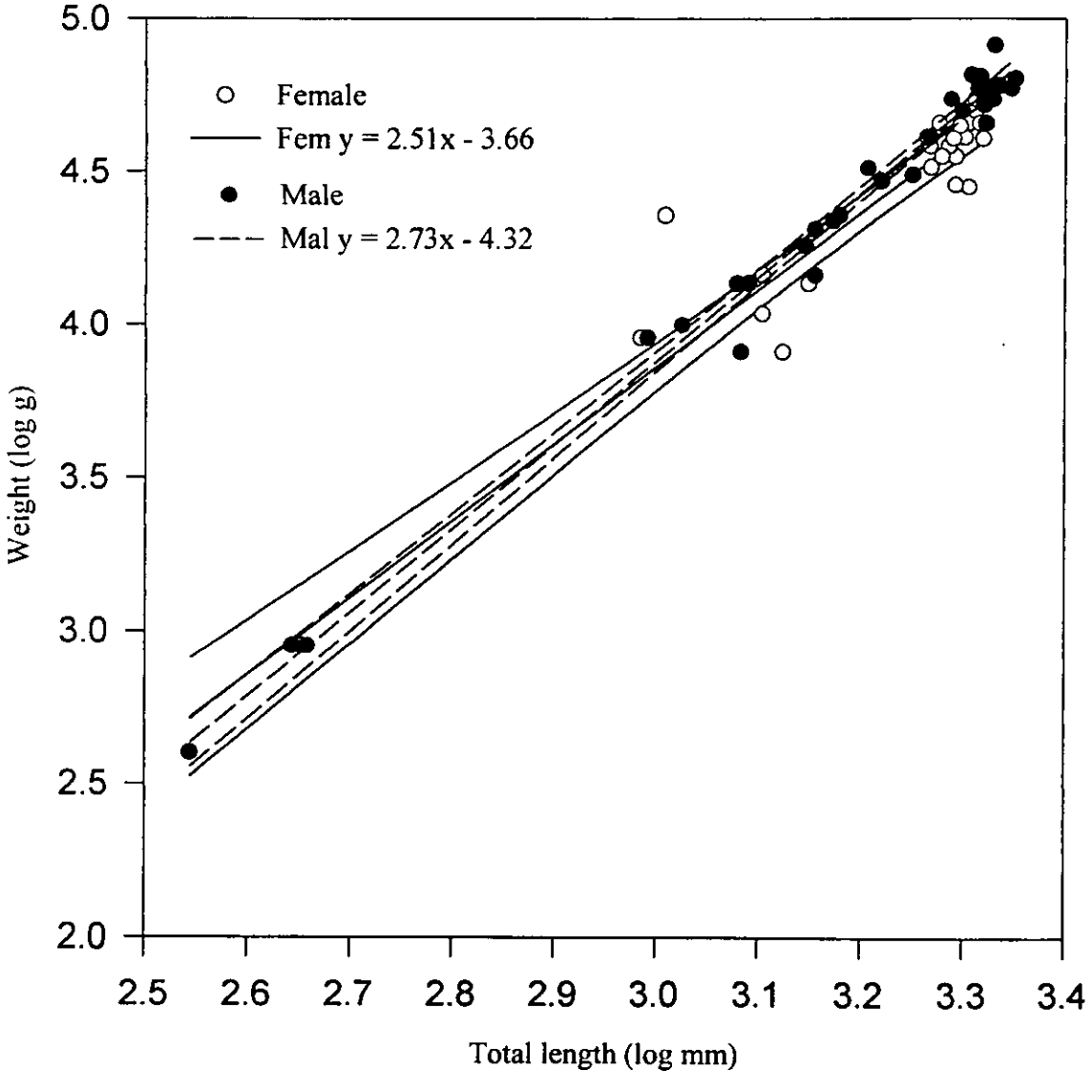


Figure 7.- Linear regression of the log total length of the body against log body weight for pumas in the Sawtooth National Forest, Idaho-Utah.

An ongoing study in a tropical dry forest of the pacific coast of Mexico has a density of 3-4 animals /100 km² (R. Nuñez and B. Miller pers. com.). Crawshaw and Quigley (unpubl. data) calculated 4.4 animals per 100 km² on the Brazilian Pantanal. Eisenberg et al. (1979) calculated a density of 2 animals per 100 km² for the Venezuelan Llanos. For the Chihuahuan desert of New Mexico, an adult density of 2.01 pumas /100 km² was found, this study area is supposed to be less productive than other North American ones, yet it harbors one of the highest adult densities, apparently related to their protected status (Logan et al. 1996).

Lower densities have been atributed to low numbers of prey (Hemker et al. 1984), lower habitat quality (Sweanor 1990) and stalking cover (Seidentsticker et al. 1973), or high densities when a proposed carrying capacity is reached (4 adults/100 km², Shaw 1989). Lower densities are also related to habitat fragmentation such as Florida panthers (1.1/100 km², Maehr et al. 1991a).

A factor affecting density calculations for the study area is the amount of land not used by pumas because of poor habitat quality both in cover and prey abundance (pers. obser.), but this unused space is affecting the animals of such areas and therefore should be included in the density estimates. , *probably representing an asymptote in the carrying capacity for the area.*

No evident pattern is present either with latitude or longitude, or from protected areas or fragmented ones. The differences obtained between or within studies may be due to effective population sampling and the techniques used for this purpose (Nowell and Jackson 1996). Concurrent with this comment, results presented by Gros et al. (1996), when comparing different methods to calculate the population of cheetahs (*Acinonyx jubatus*), found the method that best fit the observed population was an indirect one, through interviews. Both density estimates

extrapolating known numbers and radio telemetry were lower than the observed size. Density estimates for tigers (*Panthera tigris*) have been related to both prey biomass and vegetation charactertistics (Karanth 1991).

Woodroffe and Ginsberg (1998) indicate that the major cause of death for large carnivores living in protected areas comes when they are at the boundary or cross it into the unprotected exterior. Large carnivores are affected by forces outside the boundaries. Small parks present a higher risk for this. Low density would also increase home range size and movement to put more carnivores at risk. Smallwood (1997) reveals possible confounding effects in puma research trends; he also says that most of the variation is explained by the spatial extent of study area. Coupled with this would be the intensity and length of time of a given study.

The numbers of animals calculated with the NOREMARK program parallel the estimates from track and radio telemetry sampling. It has been suggested that open mark-recapture methods often inflate the numbers present in the population (McClure et al. 1996, Miller et al. 1997), but this does not seem to be the case here. Minimal total population known alive was 26 individuals, which is relatively close to the 23 resident adults of 1994, a difference of 11.53%.

Adult sex ratios for this study are similar to other northern temperate puma studies, where hunting at different levels occur (Logan et al. 1986, Seidensticker et al. 1973). Two non hunted populations reported a sex ratio of 1: 1 (Anderson et al. 1992, Logan et al. 1996). An interesting area is located in southeastern Arizona where, regardless of being heavily hunted, a parity sex ratio was observed (Cunningham et al. 1995). Anderson (1983) reports that most cougar populations have a parity sex ratio, when sample size is above 30.

Other asocial felids have a sex ratio favoring females over males. Tigers 2.5-4:1 (Schaller 1967, Sunquist 1981) and leopards 2:1 (Schaller 1972). For another african leopard study sex ratios were slightly favored to females 1.1: 1 (Bailey 1993).

The population of this study reflects a large proportion of prime young felids, attributable to the hunting effect. A non hunted population in California showed an average age of 39 mo. or more in both sexes (Hopkins 1989). On the other hand a non-hunted population of Colorado had an average age of 20 and 21 mo. for males and females respectively (Anderson et al. 1992). For a desert non-hunted population of New Mexico most of the animals were adults (Logan et al. 1996). In a heavily hunted population from Arizona, most adult males were between 25 to 48 mo. old, and, most females were more than 25 mo. old (Cunningham et al. 1995).

Offspring sex ratios for this population were similar to other populations of pumas. For central Utah a 1.31: 1 sex ratio was detected (Lindzey et al. 1994). For the Florida panther a sex ratio of 6:1 was determined (Maehr et al. 1991a). For the desert of New Mexico a 1: 1.27 ratio was observed (Sweanor 1990).

Average litter size (mean = 2.5) was slightly lower than the data published by Anderson (1983) for 407 postnatal litters (mean = 2.67). For two Canadian studies, in British Columbia a litter size of 3.1 was observed (Spreadbury et al. 1996), a 20% difference of our data. For Alberta mean litter size was 2.2 kittens (Ross and Jalkotzy 1992). Logan et al. (1996) calculated a mean litter size of 3.02 for the Chihuahuan desert.

Overall kitten survival is similar to that calculated for Southern California (Beier and Barrett 1993), but lower than Nevada (Ashman et al. 1983), Utah (Lindzey et al. 1988) and Alberta

(Ross and Jalkotsky 1992). Nevertheless only those studies have calculated kitten survival. A similar survival rate has been documented for the African lion in the Serengeti plains (Bygott et al. 1995) where no hunting pressure is present, but long traveling distances and prey migration reduces energetic intake and consequently favors mortality. Mortality causes were not documented in all cases, but indirect effects from hunting were present when a female was illegally taken, she lost a litter of three. Apparently some young reproductive females do not conceal initial den sites from predators or weather, and this case was observed twice when litters were lost. This could reflect a learned behavior, because not all first mothers lost the litters. The successful nature of concealed den sites from weather (Bleich et al. 1996) and predators both intra and interspecific (Beier et al. 1995) has been tested.

Infanticide was recorded in two instances on the study area. The impact of Carnivore infanticide on populations is not well understood (Packer 1983). It is currently considered a mechanism to increase the fitness of a newly arrived male into the population. Yet new information, has demonstrated that female grizzly bears will mate with more than one male (Craighead et al 1995) as a possible explanation to avoid infanticide, and this process is allowed by delayed implantation (Mead 1989) . This has not been documented in pumas, but Beier et al. (1995) observed a male courting two females at the same time. Even those studies with really intensive field seasons can miss an association event such the one needed to create a dual parenthood, but we do not know if the physiological possibility exists from captive studies.

Female reproductive events were not documented for a large sample size in the population. The listed period between successful litters (17 mo.) lays within published estimates (see review

in Anderson et al. 1992). Estrous was induced within a month of losing a litter, regardless of what caused the loss. First reproduction time was similar to the one described by Maehr et al. (1989b) for Florida panthers and slightly younger than other nearby populations (i.e. Hornocker 1970, Lindzey et al.1994).

Litters were born throughout the year with a peak in summer-fall. The time of the year when most litters were born can be related to high availability of both young deer and other species, and this time is less stressful than winter season. The plasticity of pumas is reflected by the ability to produce kittens at any time of the year. This pattern has been related to the diversification of the species in tropical areas where seasons are less significant (H. Shaw unpublished) but this hypothesis is yet to be tested. Seasonality of temperature may not be as great, but seasonality of other events (i.e. rainfall) can be pronounced in some parts of the tropics. Another possibility is that, year-long breeding is an inherited trait because of competition with larger carnivores present until Late Pleistocene (i.e. *Panthera atrox, Panthera onca and Smilodon* spp., Kurten and Anderson 1980, Jesús M. Castillo Cerón, UAEH, pers. com), a similar situation can be observed with cheetahs, competing with african lions (*Panthera leo*) and spotted hyenas (*Croccutta croccutta*, Caro 1994, Laurenson 1995).

Since there doesn't seem to be any apparent difference between sexes of kittens produced an interesting question would be: When do pumas produce more males or more females, and can this be related to the number of resident females in the area that will in turn reflect the number of males migrating into newer areas or staying within their natal area. No large database exists in order to answer this question but knowing when more female progeny are produced would have

strong management implications.

Dispersal takes place throughout the year in this population of pumas, but most frequently occurred during winter, a stressful time of year. Of 9 pumas in southern California, dispersal time was present throughout the year (Beier 1995). In Colorado (Anderson et al. 1992) dispersal occurred mostly during spring and summer. In Alberta, Canada (Ross and Jalkotsky 1992) independence was documented in every month but june.

Philopatry was observed in this study for five dispersing females. This pattern has been reported in different habitats and populations. Murphy (1983) observed one philopatric female in Yellowstone. Two studies in southern Florida observed one philopatric female each (Maehr et al. 1991a, Smith and Bass 1994). Laing and Lindzey (1993) reported the patterns of replacement in pumas from Utah, they recorded 5 philopatric females. This process has not been proximally related to adult animal density (Logan et al. 1986, Seidensticker et al. 1973), but it plays an important role for the recovery of lost resident females with independent progeny (Laing and Lindzey 1993) that will cluster in an area formerly occupied by a single animal, and raise total density.

Adult survival can be considered within the published estimates for the species but on the lower side. Estimators are different within studies and therefore should be considered indicative. Florida panthers have an 82% probability of survival (Maehr et al. 1991b), which is similar to a non-hunted population of Utah (74%, Lindzey et al. 1988) but lower than the 88% for a non-hunted population of Colorado (Anderson et al. 1992). Cunningham et al. (1995) has calculated the lowest survival probabilities for pumas (55%), and their study area was subject to a high

hunting pressures. A fragmented population from southern California had an annual survival estimate of 75% (Beier and Barrett 1993). Differences between studies can be attributable to the relative importance of mortality causes. In our study area hunting accounts for most of the mortality. In Florida (Maehr et al. 1991b) and British Columbia (Spreadbury et al. 1996) the main mortality cause was related vehicle collision. In southern Utah (Lindzey et al 1988) as in New Mexico (Sweanor 1990), intraspecific mortality was a very important cause, which can account for differences with other areas. A cause of mortality recently discussed is prey capture, Ross et al. (1995) have pointed out that this can be as high as 27% of total deaths. We did not documented any capture prey related mortality but there could be instances where this mortality is present at a higher proportion. Prey scarcity and/or hunting cover that is not ideal are possible scenarios that may force pumas into situations that can increase the potential of such mortalities. Hunting mortality should be approximately 25% of the harvestable cohort population numbers to maintain stability (Lindzey et al. 1992), although recent findings from New Mexico say that for control purposes, 28% killing in the population should be enough, these authors also state that sustainable adult male harvest should not exceed 8% (Logan et al. 1996).

Pumas in the study area have similar length published in other studies (see Anderson 1983). Mass was similar but males were slightly lighter than nearby males (i.e. Hornocker 1970, Ackerman et al. 1986). Masses can be related to energy intake and behavioral patterns, and pumas in our study area travel longer distances than other published data (Beier et al. 1995, Maehr et al. 1990) therefore energy should be allocated in travel more than in increasing weight.

MANAGEMENT IMPLICATIONS

The life time productivity of a female puma in the study area is three litters with 2 or 3 kittens, successfully producing a total of 6 to 9 in her life span. From this total, only half will reach dispersal age. Adulthood survival for a philopatric female is higher than male dispersal. Approximately 30% of 6 or 9 kittens will survive to become a resident productive adult, and less than 5% of the male progeny will become part of the original population. Female recruitment is limited by the carrying capacity, with a top of 60% incorporation into the original population.

Hornocker and Bailey (1986) proposed that felid populations are regulated mainly by social organization, but recent studies (i. e. Logan et al. 1996) have also included factors negligible at the time of such publication. Mortality caused by intraspecific encounters and interspecific non agonistic behaviors such as prey encounters may surpass agonistic mortality. Patterns of the importance of one or the other cannot be known this time because most studies differed on their objectives and did not publish such results. Quigley and Crawshaw (1992) point out the need to develop site-specific and local conservation and management plans for large carnivores.

Several of the differences or similarities between studies are probably related to cyclic environmental patterns that are variable on time and space. Such cycles have been acknowledged for long time intervals for relatively simple ecosystems (i.e. Yukon, Boutin et al. 1995). These cycles are not known for areas where the puma has been studied, and for a long term monitoring. The state of California has proposed a 13 year cycle (Smallwood 1994). This may be a scenario that all northern and some tropical populations of pumas are facing, but no long-term study exists

to provide such data.

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CAPITULO III

LA DISPERSIÓN EN EL PUMA (*PUMA CONCOLOR*) Y SUS IMPLICACIONES EN EL DISEÑO, TAMAÑO Y FORMA DE RESERVAS EN LA REGIÓN DEL DESIERTO "GREAT BASIN", ESTADOS UNIDOS.

PUMA (*Puma concolor*) DISPERSAL AND ITS IMPLICATIONS ON RESERVE SHAPE, SIZE AND DESIGN IN THE GREAT BASIN AREA, USA.

ABSTRACT

Little information exists on dispersal of pumas (*Puma concolor*) and there has been little discussion as to how this information can help determine reserve areas. Age, sex ratios, direction, and length of movements were studied for the Great Basin desert of Idaho and Utah, USA. Average age at dispersal was 15.3 ± 2.7 mo., sex ratios favored males (16 M: 8 F). Pumas exhibited random dispersal movements. Mean distance was 192.1 ± 130.8 km. Dispersers ended within three subspecies' range supporting the hypothesis of less valid races. Dispersal data was used to calculate an affected area of 100,000 km² (95% Minimum Convex Polygon) and determine a minimum reserve core area of 3880 km² (50% MCP). No large (>1000 km²) protected areas exist within the study area in Southcentral Idaho or Northwestern Utah. Three corridors were identified through the study. One was as much as 20 m wide in some places, and more than 10 km long.

RESUMEN

Existe poca información sobre la dispersión en los pumas (*Puma concolor*) y no se ha descrito como puede utilizarse esta información para determinar el tamaño de las áreas de reserva. En el desierto denominado "Great Basin" de los Estados de Idaho y Utah, Estados Unidos se estudiaron la edad, proporción de sexos, así como la dirección y longitud de los movimientos de los pumas dispersores . La edad promedio al tiempo de dispersión fue de 15.3 ± 2.7 meses, la proporción de sexos favoreció a los machos (16 M: 8 H). Los pumas exhibieron movimientos de

dispersión al azar. La distancia media fue de 192.1 ± 130.8 km. Los dispersores acabaron en el área de influencia de tres diferentes subespecies apoyando la hipótesis de que deben existir menos razas. Los datos de dispersión se utilizaron para calcular un área de influencia de 100,000 km² (95%MCP) y se determinó un tamaño mínimo de reserva de 3880 km² (50%MCP). Dentro del área de estudio no existen áreas protegidas de gran tamaño (>1000 km²), ni en los alrededores de la región Sur central de Idaho y Noroeste de Utah. Se identificaron tres corredores a lo largo del área de estudio, uno de ellos se caracterizó por tener un ancho de 20 m y un largo mayor a los 10 km.

INTRODUCTION

Most young animals leave the home range in which they were reared and wander to new breeding locations; this phenomenon is known as dispersal (Robinson and Bolen 1989, Shields 1987, Wolff 1994). This action has been related to several events such as inbreeding avoidance, maintaining genetic variability within species, competition for mates or other resources, repopulation of habitats where local extintion has occurred, and colonization of new areas where suitable habitat becomes available (Bekoff 1989, Robinson and Bolen 1989, Wolff 1994). Dispersal is considered one of the most important, but among the least understood factors of puma population biology (Anderson et al. 1992). This is also true for most carnivore species, and literature reviews usually lack information on this topic (i.e. Johnson and Gaines 1990).

In a polygynous system, it has been proposed that male biased dispersion is a consequence of several factors. First wandering fathers and/or male-male competition, and short tenure of

dominance (or in residence), can produce female philopatry and can result in male inbreeding avoidance (Wolff 1994). Male movement further away from home than females suggests selection against settling too close to the natal area or to a sibling (Wolff 1994).

As pointed out by Beier (1995) dispersal reports on cougars have been limited to documentation of age and net distance traveled (see references in Beier 1995). Beier (1995) described behavior of pumas in habitat limited by human activities, specifically cities, where pumas used traveling corridors and the authors speculated on necessary characteristics of such corridors in a Mediterranean environment with human impacts.

Pumas and other large carnivores have been used in conservation flags, as umbrella species to conserve different ecosystems (Harris 1984). Large carnivores can be used to determine corridor areas, and these areas have the potential to make a major contribution to regional conservation strategies by ameliorating the detrimental effects that habitat fragmentation and isolation have on wildlife populations (Bennett 1990).

Objectives of this study were (1) to understand dispersal parameters such as age, sex ratios, mortality, and directional movements of a population of pumas from South Central Idaho and Northwestern Utah; and (2) to determine the area needed by dispersal individuals, and with such information construct a hypothetical protected area suitable for the Great Basin and/or Western North America.

METHODS

We studied the puma population from 1985 to 1995, for this part of the study data included

was gathered from 1991 to 1996. Age of pumas was determined by denning behavior (Maehr et al. 1989) and physical characteristics (Shaw 1979). If we suspected a birth, homing on animals allowed confirmation of parturition. Second, age was assessed through physical characteristics (Shaw 1979), use of this procedure has proved to be accurate within a couple of months.

Records from hunter-killed, radio-collared (Wildlife Materials®) pumas were used to estimate survival and dispersal distances. Dispersal distances were calculated as the straight line distance between arithmetic center of natal home ranges to central point of permanent home ranges or harvest. Because some harvested animals may have still been in the process of dispersing, the calculations for reserve size are conservative.

We tested the distribution of dispersal distances against the expected distribution that would result from the competition hypothesis (Waser 1985). The competition hypothesis states that animals will occupy the first vacant territory encountered in dispersal because continued travel could risk loss of reproduction or increased mortality by travel in unfamiliar regions (Waser 1985). We followed Knick's (1990) methodology. We calculated an average home range diameter of 17.84 km, with a home range turnover of 29.8% (López González 1994, López González et al. in prep).

We calculated neighborhood population size, a measure of effective population size (Wright 1943), using the approach of Smith (1993) with the modified formula of Cavalli-Sforza & Bodmer (1971). Neighborhood population size (Ne) was defined by Wright (1943) as the number of animals living within an area defined by a circle with a radius of 2 standard deviations of the distribution of dispersal distances. This formula takes into account the unequal distribution

of dispersal in two dimensions:

$$Ne = \pi (2\sigma x 2\sigma y)\delta$$

where x and y are the standard deviations of dispersal distances in two dimensions and δ is the density, 1 individual per 100 km^2 as has been calculated for this study (Chapter II). After obtaining the population size we extracted the effect of density to estimate the dimensions of the protected area from the information generated with the formula. Once this procedure was completed, we calculated the area affected by dispersers, assuming all pumas had the same opportunity to reach the outer limits of the metapopulation.

We also calculated population area through three home range estimators: Minimum Convex Polygon (Mohr 1947, MCP joins the outer points of the polygon); the Harmonic Mean Method (HMM, Dixon and Chapman 1980), and the Adaptive Kernel Method (AKM, Worton 1989). These last two methods rely on probability to construct the use of an area utilized by an animal, in this case the population. The three methods were compared at the 50, 75, 95, 100% contour intervals to determine how different the results were with each method, and to determine which may better fit the requirements for our objective regarding preserve size and shape. Calculations were performed using the computer program CALHOME (Kie et al. 1994).

The USDA (Bailey 1995) classifies the study area as part of the Intermountain Semidesert Province, an ecoregion mainly dominated by sagebrush steppe (West 1996). To know if the dispersing pumas were moving along the same or several ecoregions, we used the classification proposed by Bailey (1995). We overlayed the final points of dispersal into a manually digitized 1:7,500,000 map of the ecoregions of the United States.

All data were tested for normality (Kolmorogov-Smirnov) and equal variance (Leven median) and reported as mean and circular standard deviation (White and Garrott 1990). We used Rayleigh's z (Zar 1974) to test for direction of dispersal with significance set at rejection level of 0.05. All statistic tests were performed with Sigmastat for Windows 2.0 (Jandel Corporation®), and Systat for Windows 2.0, following Zar (1974).

RESULTS

Dispersers characteristics

Twenty four kittens (8 females and 16 males) reached dispersal age. Age of independence for females averaged 14.5 months (SD=3.25, range 9-17), and for males 16.31 months (SD=3.25, 13-24). The age of all subadult dispersal/independent pumas was between 9 and 24 mo. (Mean=15.34 mo, SD= 2.72, Figure 1). The sex ratio for kittens reaching dispersal age was of 2M : 1F ($z=2.14$, $P<0.05$). Actual dispersers sex ratio was 5 M: 1F ($z=1.07$, $P<0.05$). Philopatry was detected in five females, they did not change residency and remained within their natal home areas. The final destination of ten of the 19 dispersing pumas is known, one female and nine males ($z= 1.23$, $P<0.05$). One male dispersed within the study area to a distance of 1.44 home ranges.

Fifteen animals dispersed in a westerly direction, 2 dispersed to the east, one to the N and another to the NE, with no records for the S or SE. For the 10 dispersal pumas that either settled or died, dispersal bearing from natal home range was 286.9° ± 85.9 (angular deviation), we tested the data for random or directional movements, finding no mean direction ($z= 3.23$, $P<0.05$).

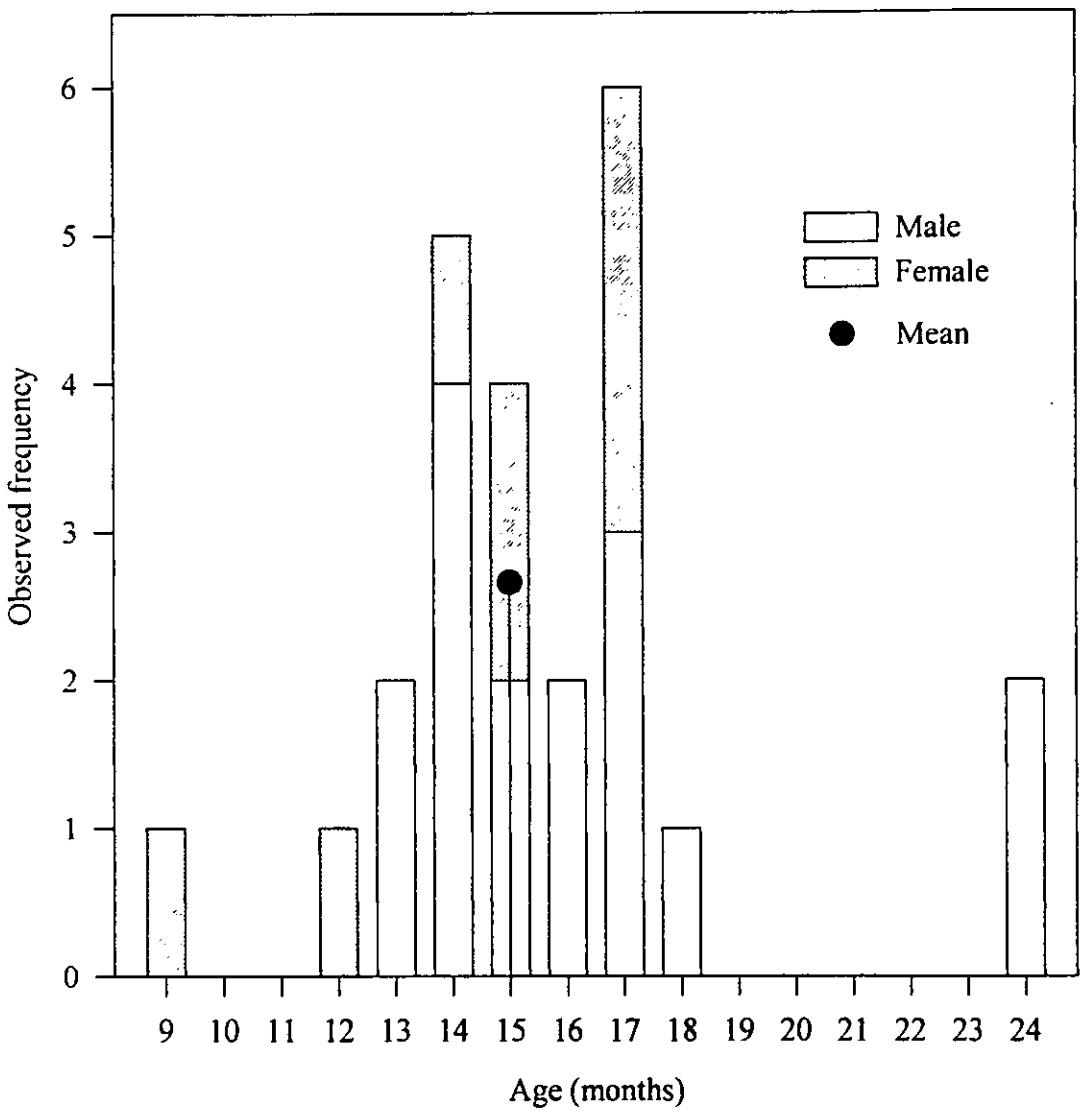

Figure 8.- Age at dispersal time for 24 pumas on the study area.

The mean distance dispersed was 192.1 km (SD=130.8, range 25.8 to 420.2 km, Figure 2). The average dispersal distance of males (197.6 km) was greater than that for the female (142.2 km). We tested this data with a one sample test, and did not find significant differences (t = ??, df =8, P<0.05). Most (n = 8) of the dispersal distances were ≤220 km. Eight of 10 dispersers whose history was known achieved the social status of resident adult and two remained non-residents. The female was still alive at the end of this study (Nevada Dept. of Wildlife, pers. com.) and one male is currently monitored by another puma study within the surrounding area of Pocatello, ID (Carl Anderson Idaho Fish & Game, pers. com.).

Dispersal distances, including philopatric females, differed from the distribution expected from the competition hypothesis (Kolmorogov-Smirnov 2-sample test = 0.708, P< 0.05).

Average age at time of death (or end of the study) for dispersal animals is 37.3 months (SD=12.85, range 19 to 60). To determine if age had an effect on the distance traveled, we compared distance traveled by resident animals (>4 years old) and non resident animals (< 4 years old), and found that there was not a significant difference between the two groups (t= 1.25, df= 8, P>0.0982).

For the 10 animals with ending points, two male siblings (WIL and LER) dispersed in opposite directions with a difference of 185° and dispersal distances differed by 25 km. Three males (ZEK, PAN, and JAS) of different litters, but progeny of the same female, went to different directions and distances.

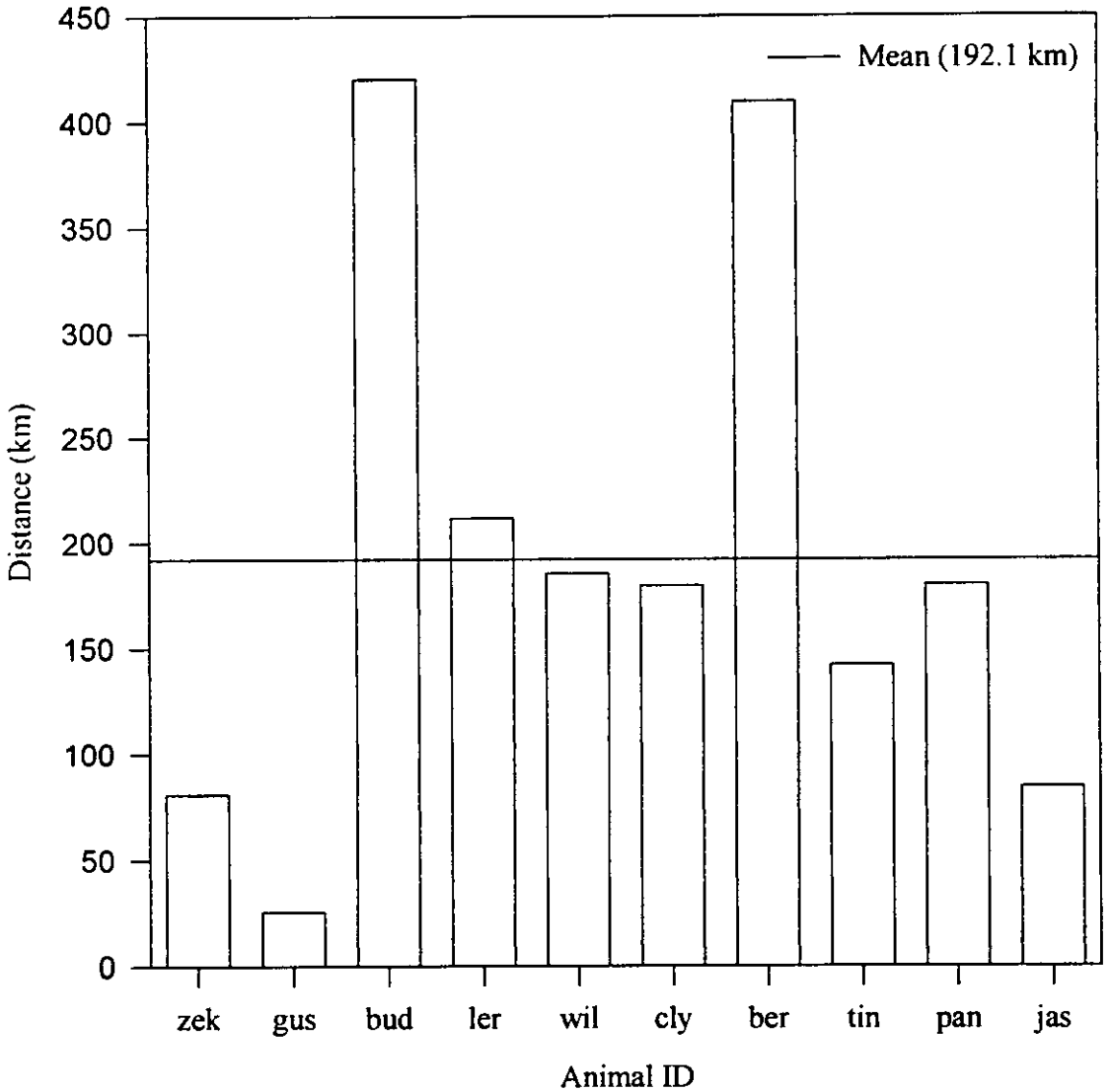

Figure 9- Puma dispersal distances from natal centers of activity.

Dispersal Area

The population size (Ne) calculated, totaled 1125.7 (1126) resident pumas, which when multiplied by 100 km² per puma, translated into an elliptical neighborhood size of 112,570 km². Using the known percentage of resident males (17.5%) females (35.0%), kittens (33.3%) and transients (14.2%) in this population (unpublished data), and a 1M: 2F sex ratio. We calculated 376 adult male residents and 750 female adult residents, 319 transients and 713 kittens for a total of 2133 pumas.

The area calculated through the neighborhood size formula with the three home range estimators is shown in Table 1, and Figure 3. The AKM area was 6.6 larger than HMM and 7.9 larger than the MCP at the 50% level. At the 100% level AKM was still larger than the other two by 4.67 and 2.88 times respectively. From the three comparisons, MCP gives the closest estimate to the Ne formula with a difference of 12,000 km², and probably reflects a better and more realistic shape of the metapopulation. The HMM always seemed to underestimate the size affected by dispersal animals and the AKM seemed to overestimate it.

When the final dispersal points of the 10 animals were overlaid on the Ecoregion map (Figure 4), six of the dispersers ended within the original ecoregion. One ended in the ecoregion called Southern Rocky Mountain steppe-open woodland-coniferous forest-alpine meadow province. Two dispersers finalized their travel at the Nevada-Utah Province semi-desert-coniferous forest-alpine meadow province. Finally one ended in the Intermountain Semidesert and Desert Province.

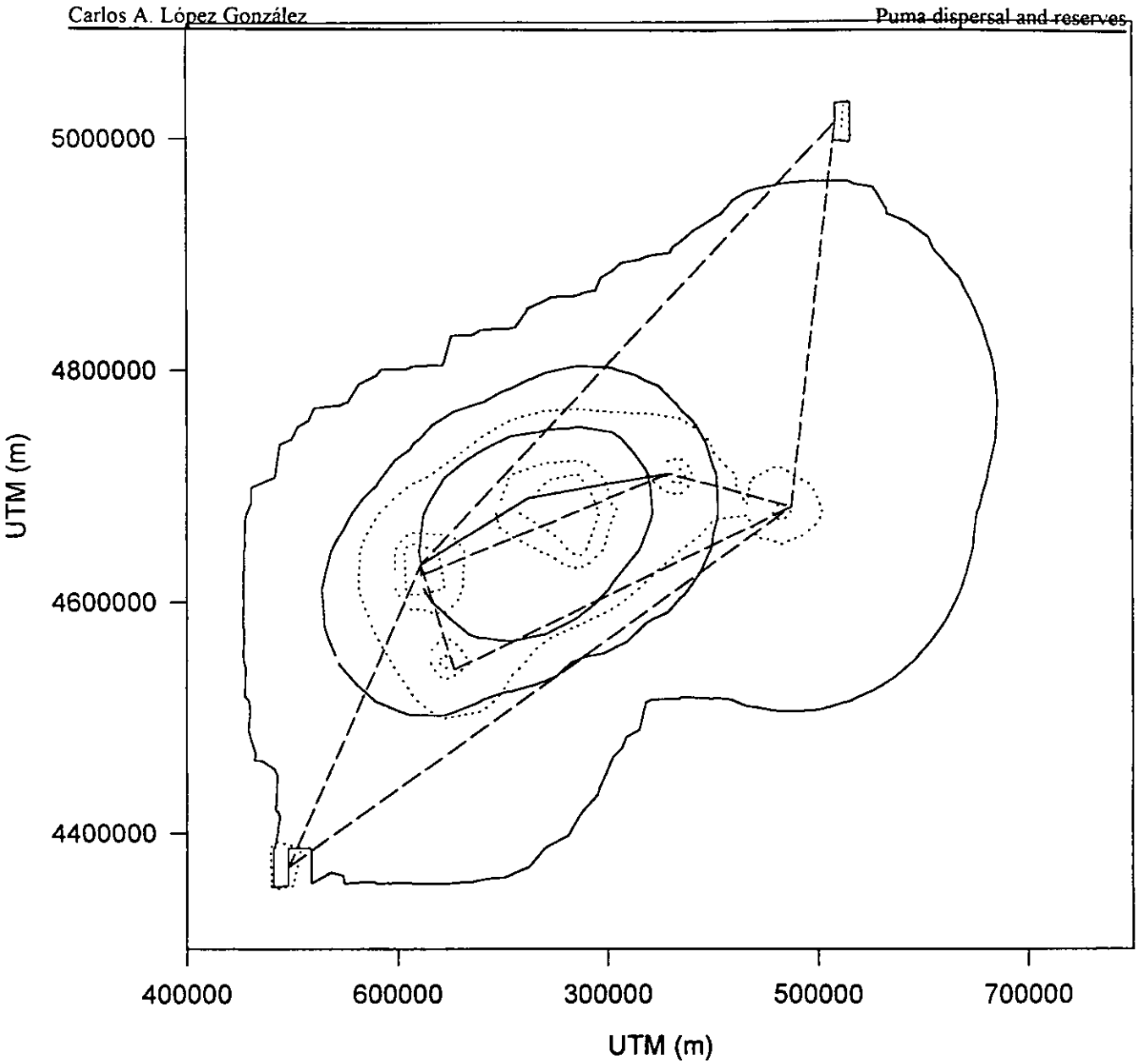

Figure 10.- Area of influence of dispersal *Puma concolor* via 3 home range (estimates at 50,75,95%) contour intervals:——Adaptive kernel ·····Harmonic mean — — — Minimum convex polygon.

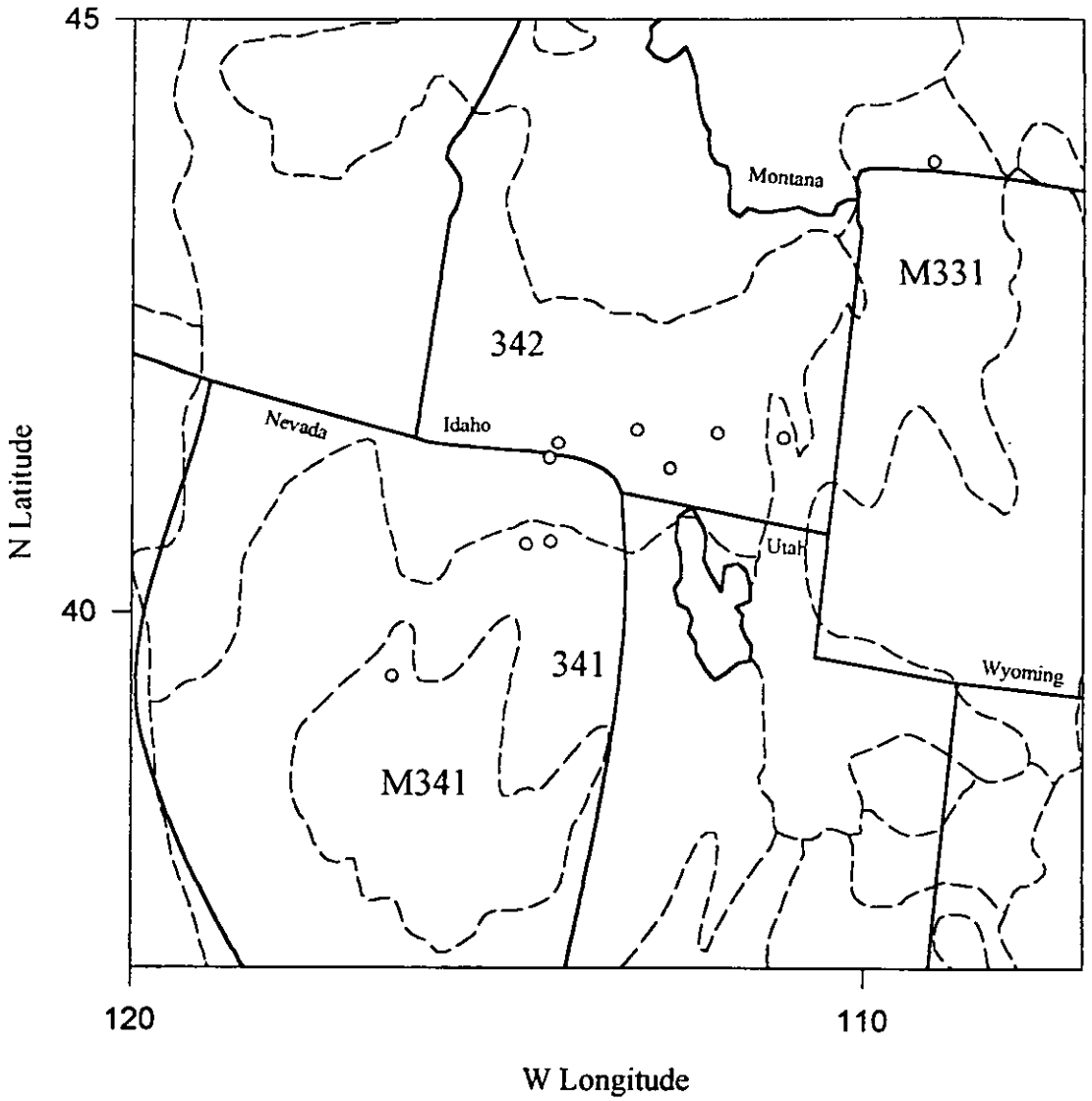

Figure 11.- Map of the States and Ecoregions showing ending points for dispersal pumas. Ecoregions are labeled with numbers. Southern Rocky Mtn. Steppe-Open woodland-Coniferous forest-Alpine Meadow Province (M331), Intermountain Semidesert and Desert Province (341), Intermountain Semidesert Province (342), Nevada-Utah Mountain Semidesert-Coniferous forest-Alpine Meadow Province (M341).

Corridors use by dispersal pumas

The most used corridor by pumas (n=7) is the one that connects the Albion Mountain range with the Raft River Mountains (Figure 5) located on the west side of the study area. Another important corridor (n = 2) joins the Black pine mountains with the Raft River Mountains; this one is located to the East of the last range. A third corridor (n = 1) is a creek that connects the northeastern side of the Jim Sage and the Cotterel Mountains with the Subblett Mountain range. This one is very important because is the only cover available for almost 60 km. One of the radio collared dispersers (CLY) used this corridor during the study, but at least two more (VIR and one non-collared) may have taken the same route on late winter of 1996. The radio collared one was first captured within the edge of the corridor on February of 1996.

DISCUSSION

Female phylopatry has been observed in other puma studies (Laing and Lindzey 1993) and has been attributed to density (Lindzey 1987). Males tend to disperse regardless of density. The age of dispersal found in this study lays well within the published records for the species elsewhere (see Anderson 1983, Anderson et al. 1992, Ashman et al. 1983, Beier 1995, Sweanor 1990). Most of the dispersal distances recorded for this study (8 of 10) were within published distances of travel for the puma (see Anderson 1983, Cunningham et al. 1995, Sweanor 1990). The other two records (409 and 420 km) and one unpublished distance of 483 km (Logan et al. 1996) are some of the longest dispersal distances recorded for the species.

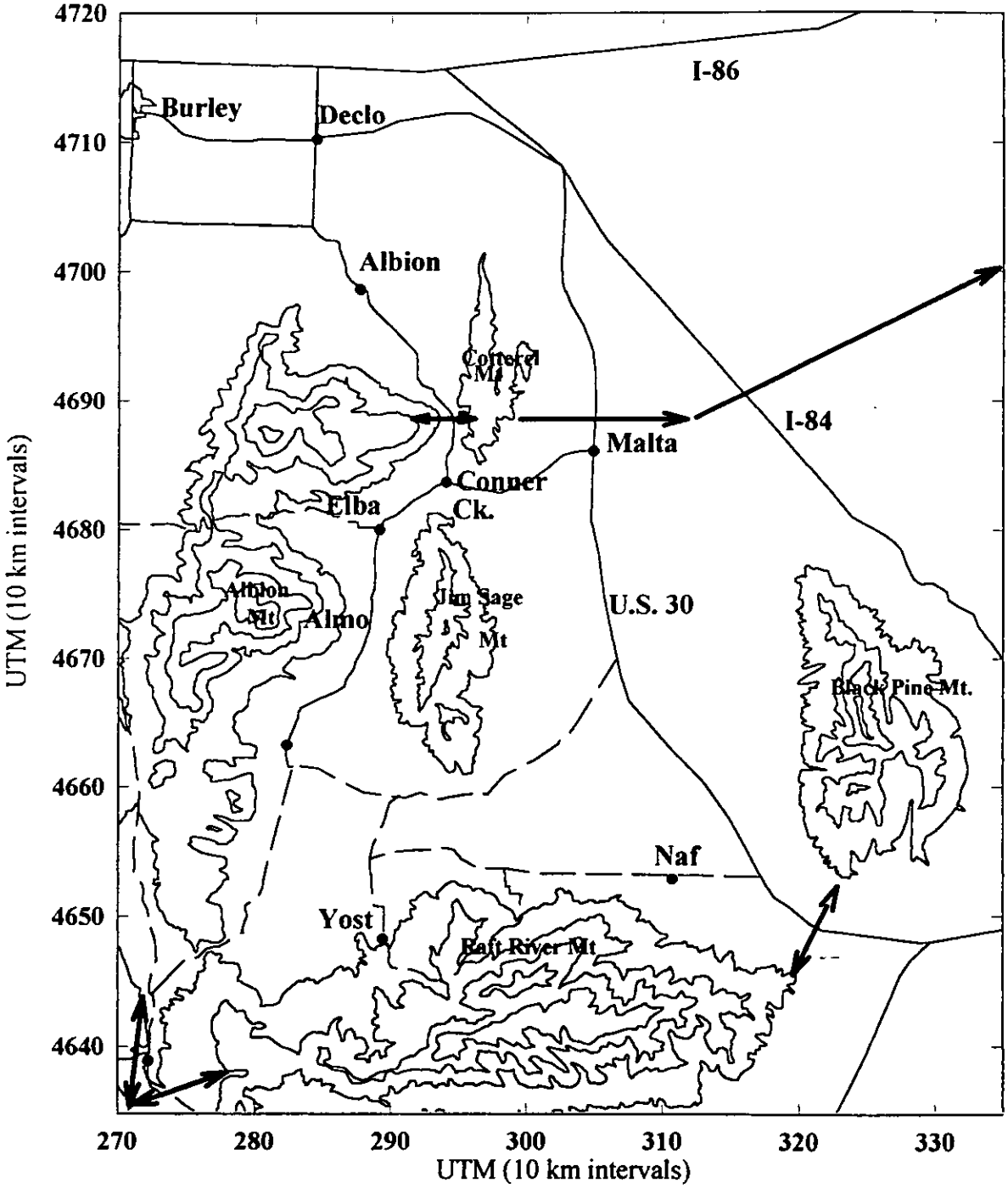

Figure 12.- View of the study area showing the location of corridors identified from 1987 to 1995. Contour lines lay 300 m apart and start at 1800 masl. (Corridors are shown with arrows).

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In this study as in many others, the straight line of dispersal does not reflect the actual distance the animal traveled to its final destination. These long distance movements have been related in other studies to pressure from dominant resident male competitors and lack of free space to settle down (Sweanor 1990).

An ecologically similar area to our study area exists in North-eastern Nevada (Ashman et al. 1983). In Nevada, the longest dispersal movement did not exceed 100 km, nevertheless several of our pumas dispersed to this area. The short dispersal behavior in Ashman et al.'s study could be explained by heavy exploitation of the population at the time which in turn may have produced several vacant areas. The Nevada study (Ashman et al. 1983) and the Aravaipa-Klondike region of Arizona (Cunningham et al. 1995), have one of the highest published removal rates of pumas.

Another important difference between the Nevada study area and our study area is road density. The site in Nevada has a large roadless wilderness area (364.66 km^2), and therefore human presence is less constant. This less accessible area could serve as a feeding subpopulation that would favor short distance dispersal into vacant areas.

Longer movements could be the result of less available space in natal areas where carrying capacity is almost reaching an asymptote. Another possible factor influencing dispersal in large strict carnivores is prey biomass availability. More productive environments will result in shorter dispersal distances (i. e. *Panthera onca,* Quigley and Crawshaw 1992, *Panthera tigris,* Smith 1993, *Panthera pardus,* Sunquist 1983, Bailey 1993) but also reduced habitat availability (*Leopardus pardalis*, Laack 1991, pers. obser). In wild dogs (*Lycaon pictus*) dispersal has been atributed to a higher pup survival (Burrows 1995).

Dispersal patterns can be grouped into directional and nomadic movements (Mech 1987). Both of these patterns have been recorded for pumas, with a smaller incidence of nomadic movement. We are relating this to the less vagile capacity by the cougar compared to more cursorial species, such as wolves *(Canis lupus,* Mech 1987) or coyotes (*Canis latrans,* Harrison 1992).

It has been speculated that finding a mate or a vacant area would be easier by making circular excentric movements away from their natal area (Mech 1987). Nonetheless these kind of pattern is not really present in nature. Large predators are likely cued on geomorphological features to disperse, looking for areas similar to where they were raised. Mountain lions usually live in forested and/or covered habitats (Koehler and Hornocker 1991, Laing and Lindzey 1991, Lopez Gonzalez 1994,Van Dyke et al. 1986) and they probably try to remain with these features when dispersing, although some juveniles may be pushed into lower quality habitat (McIvor et al. 1995, Van Dyke et al. 1986). Most dispersal in our study area occurred in late winter, thus it is possible for animals to cue on forested patches of mountainous islands when these places are covered with snow. Nevertheless in places where snow is not present other habitat characteristics such as color, sun intrusion, cover; should favor patch recognition.

In smaller mammals, interpatch movements increases the chance of mortality from predation or environmental stochastic events (Dippendorfer et al. 1995). Large predators usually do not have to be concerned about predation, instead the pressure is higher due to intraspecific competition, males killing subadult males or females (Anderson et al. 1992, Sweanor 1990). That situation however may change in areas where wolves and grizzly bears are present (i.e. Montana,

Ruth and Hornocker 1996) or in tropical areas, where jaguar *(Panthera onca)* may prey upon pumas (Quigley 1987). Off added importance is human related mortality, where 74% of large carnivore around protected areas was caused human caused (Woodreffe and Ginsberg 1998.

The area affected by dispersal animals encompasses the States of Idaho, Montana, Nevada, and Utah; likely, Wyoming should also be included because the movements of the animal killed in Montana probably took him through the Rockies in western Wyoming. The study area lays between the limits of two puma subspecies, *P. c. hippolestes* and *P. c. kaibabensis* (Young and Goldman 1946). Dispersing animals have influence on those geographic races and also *P. c. missoulensis.* One finding from this study is that the area of influence encompasses the geographical distribution ranges of two other subspecies of pumas. This finding tends to support a recent proposal to reduce in the number of puma subspecies from 31 to 18 (Nowell and Jackson 1996). A point of support of this comment is that spatial heterogeneity in population genetic structure is probably not relevant for large carnivores that range widely (Miller et al. 1999).

Minimum areas for the conservation of pumas have been estimated by computer simulation for southern California's Mediterranean environment (Beier 1993). The result was a minimum area of 2200 km² to avoid extinction of the population. The core area that we calculated is 3880 km², 76% increase in the computer calculated number. It is of note that 50% of the final locations encompassed an area less than double in size of the original study area, but an increment to 75% gives a 7 fold increase over the area calculated at the 50% level, and finally incorporating the last quarter gives almost a 26 fold increase over the 50% level. The configuration of an area proposed to preserve a metapopulation of pumas can be drawn from the Figure 3. In this figure

we can see that the general shape of the preserve would follow a NE to SW direction on a generally elliptical shape. Using the 50% contour line we can define a core area or nucleus of such a preserve. An obvious difference between Beier (1993) and our study is that our study is using actual field data. Another difference is the more productive nature of the southern California habitat. Beier (1993) suggests that an immigration of 1 to 4 pumas within a decade, increases the probability of persistence of a population. Placing our study area within this scenario, successful dispersal (n=10) occurred within three years. Using this criteria we can state that our population is not yet isolated and constant gene movement is occurring.

All the biotic provinces, where our dispersed pumas either settled or killed, are relatively similar. Lower altitudes hold sagebrush and higher altitudes hold conifers and Alpine meadows, and all provinces belong to the dry domains of the western United States. The study area has potential to be designated a core area for a biosphere reserve. It contains one of the few protected lands within south central Idaho, City of Rocks National Preserve where pinyon-juniper lands represent almost half of the area (≈ 50 km^2). It also has land considered "protected", namely Forest Service and Bureau of Land Management Land (Caicco et al. 1995). Other protected areas located within the area influenced by dispersal animals are listed in appendix 1. From the total, 10 are Wilderness areas and two are Biosphere Reserves with a size of ≥ 500 km^2. Only Yellowstone National Park is >8,000 km^2. Using the calculated density for this study (1/100 km^2) a minimum of 5 resident adults would be present in those wilderness areas and potentially 80 in Yellowstone.

Suitable protected areas to maintain a population of pumas within the sagebrush steppe are limited and not legally interconnected with each other. Almost 29,900 km^2 are protected

within the area, and that could possibly be affected by dispersal pumas out of our study population (IUCN 1993, see Appendix 1). Most of the protected areas rest within the State of Wyoming, specifically the Greater Yellowstone Ecosystem (GYE, 67.93%). They are well connected, but not all of the habitat is available for pumas, and only the northern portion of the GYE has a stable population (Hornocker et al. 1989). The protected areas of Idaho listed in Appendix 1, only represent 12.49% of the total. Five of the seven protected sites contemplated here (Appendix 1), have a size smaller than 100 km², including the City of Rocks National Preserve. Only the INEL has a considerable area but habitat is xeric and flat which lacks quality both for good numbers of ungulates and puma.

At a larger scale we can provide insight to explain the shape of the area that can be proposed as a reserve. The study area is surrounded by natural and artificial barriers. To the North and Northeast, the Snake River plain offers little cover. With the exception of a small window, this area is almost an agricultural landscape with human activity present most of the time. During winter time the landscape is large, open and bare, and that probably makes travel impossible for pumas. To the South it extends to the Salt Lake plains that are similar in character to the Northern barrier. This area exhibits little or no cover, a very reduced available prey base, and free water is scarce. Another barrier encountered to the Southeast is a major interstate highway (I-96) where many animals are killed (i.e. mule deer) during natural wintering migrations (Ken Jafek, Pers. com.).

One of the corridors identified is a creek that connects the northeastern side of the Jim Sage Mountains and the Cotterel Mountains with the Subblett Mountain range. It is probably very

important because it is the only natural cover available for almost 60 km. This corridor has patches of willows, and thick vegetation that may or may not act as a barrier. The width of such area is no more than 200 m in some parts but it is continuos. Corridor characteristics in the study area differ from the ones described by Beier (1995). There are a lower number of dwellings per km^2 in Idaho (<4/km^2, Lopez González estimation from U.S.G.S. maps), and this possibly explains why one corridor in Idaho was considerably longer and narrower than the limit of corridors to be designed for puma use (>400 m wide, 1 to 7 km length) by Beier (1995). More dwellings increases the need for secrecy.

CONSERVATION/MANAGEMENT IMPLICATIONS

The Rockies of central Idaho are connected to the Greater Yellowstone Ecosystem. As pointed out by Noss et al. (1996), grizzly bear (*Ursus arctos horribilis*) recovery areas in Idaho reveal lower potential to protect species of reptiles and invertebrates. The use of pumas as an umbrella species within the sagebrush steppe can actually provide the data necessary to designate a matrix of protected areas that could benefit the conservation of the Great Basin biodiversity. A crucial point evident from GAP analysis data (Kiester et al. 1996) and large carnivore management plans is that southcentral Idaho has the potential to act as a natural bridge not only for pumas but for other animals that still are in good numbers in the Great Basin area.

We are not proposing to either reduce or prohibit puma exploitation on the study area, but a conservation strategy should include feeding populations that can supply other managed/harvested areas.

Sociological and economic factors should be evaluated before any conservation action may be developed within this area of the western United States. People still believe that predators are good if they are dead, therefore the use of pumas as conservation flags may be taken in a wrong sense. Another political issue of importance is how to incorporate a system of protected areas that will not place undue burden on the traditional livestock husbandry and unduly limit personal freedom.

As recently pointed out by an Eastern Idaho rancher, the issue of preserving biodiversity is not really a question of species protection as much as it is about who will have the final say over the land and our actions upon it (Thomas 1996). Quoting Thomas: "The folks who want to regulate the ranchers into environmental protection and put western land users and other legitimate business into jeopardy with all the regulatory red tape of environmental fixes, are going at it the wrong way and will ultimately destroy the very thing they are trying to preserve".

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Table 1.- Area affected as calculated by different home range methods. Minimum Convex Polygon (MCP), Harmonic Mean Method (HMM), Adaptive Kernel Method (AKM). Measurements in km^2.

Method	50%	75%	95%
MCP	3,880	27,410	100,500
HMM	4,670	13,350	62,380
AKM	30,930	80,330	289,900

Appendix 2.- Protected areas within reach of dispersal pumas from South Central Idaho & NW Utah. The numbers express the size of the area in square km. Abbreviations are: Biosphere Reserve (br), National Monument (nm), National Park (np), National Wildlife Refuge (nwr), and Wilderness Area (wa),. Data is taken from IUCN (1993).

Idaho	
Bear Lake (nwr)	42.84
Camas (nwr)	72.69
Minidoka (nwr)	83.86
Craters of the Moon (wa)	216.69
Sawtooth Ntn'l Forest (wa)	878.53
Deer flat (wa)	45.62
INEL	2,315.00
City of Rocks Ntn'l Preserve	74.74
State total	**3,729.97**

Montana	
Lee Metcalf (wa)	1,007.44
Absaroka-Beartooth (wa)	3,724.45
Lee Metcalf (wa)	24.28
Red Rock Lakes (nwr)	140.50
State total	**4,896.67**

Nevada	
Santa Rosa Paradise Pk (wa)	125.45
Jarbridge (wa)	457.97
East Humboldt (wa)	149.33
Ruby Mountains (wa)	364.22
Ruby Lake (nwr)	152.30
Mount Moriah (wa)	26.04
Mount Moriah (wa)	331.84
Great Basin (np)	310.80
State total	**1,917.95**

Utah	
Mount Naomi (wa)	179.48
Wellsville Mountain (wa)	96.52
Bear River (nwr)	263.37
Mount Olympus (wa)	64.75
State total	**604.12**

Wyoming	
Jedediah Smith (wa)	499.59
Yellowstone (np)	8,991.39
North Absaroka (wa)	1,418.38
Teton (wa)	2,368.38
Washakie (wa)	2,850.11
Grand Teton (np)	1,241.40
National Elk Refuge (nwr)	99.89
Gros Ventre (wa)	1,161.45
Winegar Hole (wa)	43.36
Fossil Butte (nm)	32.80
State total	**18,706.75**

Grand Total	**29,855.46 km²**

CAPITULO IV

GASTO ENERGÉTICO DEL PUMA (*PUMA CONCOLOR*) DETERMINADO POR MEDIO DE LOS PATRONES DE ACTIVIDAD EN UN AMBIENTE FRAGMENTADO.

ENERGY EXPENDITURE OF THE PUMA (*Puma concolor*) AS DETERMINED BY ACTIVITY PATTERNS IN A FRAGMENTED ENVIRONMENT.

ABSTRACT

The energetic requirements of the puma were described with the use of two models. Predation rates were calculated for the non-winter time of the year and for two diets: ungulate and mixed (deer-porcupine-lagomorphs). These models merged basal metabolic rate and specific activities (time spent hunting, traveling and localized activities). Results from the two models had a 52% difference. Daily caloric expenditure was 2559 for females and 3588 for males in model I. For model II calories spent were 5326 and 7381 for females and males respectively. Model I predicted female and male pumas would kill 32 and 44 deer per year respectively. In model II the number of deer changed to 39 and 54. Average number of deer removed per year were 1510 and 1852 for model I and II respectively. Biomass removed with model I was 21.1 kg/km^2 and for model II 25.9 kg/km^2. These figures are both within or above calculated energy expenses or kill rates. Model I seems to perform a better calculation.

RESUMEN

Los requerimientos energéticos del puma son descritos por medio de dos modelos, del mismo modo la tasa de depredación se calculó para la época no invernal del año, para dos dietas diferentes: ungulados y mixta (venado-puercoespines-lagomorfos). Estos modelos juntan las tasas metabolicas y actividades específicas (tiempo utilizado para la cacería y el desplazamiento así como actividades localizadas). Los resultados de los dos modelos tienen una diferencia del 52%.

El gasto energético diario fue de 2,559 y 3,588 calorías para hembras y machos respectivamente para el modelo I. En el modelo II el gasto fue de 5,326 y 7,381 en hembras y machos. El número de venados cazados utilizando el modelo I fue de 32 para las hembras y 44 para los machos. Para el caso del modelo II fueron 39 y 54 para hembras y machos respectivemente. El número promedio de venados anuales que son removidos por la población de pumas es de 1,510 y 1,852 para el modelo I y II respectivamente. La biomasa que es removida por los pumas es de 21.1 kg/km² y por el modelo II es de 25.9 kg/km². Los datos obtenidos reflejan valores similares o superiores a los calculados anteriormente y/o por diferentes métodos. El modelo I al parecer refleja mejor las condiciones reales.

INTRODUCTION

The metabolic requirements of a predator species should be considered for any conservation/management plan. Energetic requirements can be transformed into minimum numbers of prey items necessary to maintain a population of predators within a management area.

Basal metabolic rate (BMR) is defined as the rate of energy metabolism of a nongrowing organism at rest under postabsorbative conditions in a thermoneutral environment (Ricklefs et al. 1996). BMR for many mammals have been determined in laboratory conditions and have been extrapolated to the field. When possible, isotopes, specifically doubled labelled water, are used to calculate the daily energy expenditure or field metabolic rate (FMR, Koteja 1991, Nagy 1987), but for most large mammals, especially carnivores, this process can be considerably harder to accomplish. BMR is usually lower than FMR (Koteja 1991). Nevertheless a very robust

correlation between basal metabolic rate and field metabolic rate has been found for mammals (Ricklefs et al. 1996).

The puma energetic requirements were modeled 10 years ago (Ackerman et al. 1986). These authors addressed the metabolic needs of the species on their study area through activity patterns based on the number of pulse changes during one minute intervals. These authors classified the activities into three categories. Point out that with their sampling technique, they were probably underestimating activities such as movement, traveling, play and feeding, and overestimating sleep and resting time. Ackerman et al. (1986) calculated the number of large prey, namely mule deer (*Odocoileus hemionus),* needed by sex and social status of a population of pumas during a year.

Recent puma studies have pointed out more specific activity patterns. Beier et al. (1995) discussed puma behavior on a suburban interface of southern California, describing travel while hunting during periods of up to 6 h. Typical travel speed was 0.7 km/h. A sharp crepuscular-nocturnal pattern was displayed by pumas in this study. Nevertheless, a predator's nocturnal activity pattern has been related to the time when their main prey is active, but they are also known to react to human related activities/intrusion (Beier et al. 1995, Van Dyke et al 1986). The one color coat of the puma has been related to a diurnal hunting pattern (Ewer 1973). In our study area, pumas can be active any time of the day (López-González 1994). Activity for the purpose of this study will be classified into four categories: non-active (resting), locally active (feeding, grooming, playing), traveling and hunting.

Predation rates for pumas have been described for several different studies (Anderson

1983), with estimates varying from 4 to 13 days between kills. In California, Grinell et al. (1937) estimated 36 to 52 deer/year. Robinette et al. (1959) estimated 36 to 91 deer/year. In the primitive area of Central Idaho these are estimates of 26 to 36 deer and 5 to 7 elk/year (Hornocker 1970). Conolly (1949) estimated 52 porcupines and 36 deer/year.

In Southern California, a single puma killed 48 large mammals and 58 small mammals per year (Beier et al. 1995). In a tropical deciduous forest of western Mexico, Nuñez (1999) calculated (from scat analysis) that pumas may kill 80 white-tailed deer (*Odocoileus virginianus*), 11 collared peccaries (*Tayassu tajacu*), and 13 armadillo (*Dasypus novemcinctus*). In southeastern Arizona (Cunningham et al. 1995), it was theorized that pumas killed between 35 - 40 deer, 17 - 19 calves, 21-24 collared peccary, and 7-9 rabbits.

We wanted to know what are the potential energetic requirements of the puma population in our study area, in light of new information obtained on activities and activity patterns; we are expecting predation rates to be higher than published estimates, we will compare these results with others and explain the possible differences.

Our objectives were: (1) to describe a model of daily energy expenditure using activity patterns of adult male and female pumas, and (2) to determine the rate of predation for pumas and the potential impact on prey populations for South Central Idaho and Northwestern Utah.

METHODS

Pumas were captured as described elsewhere (Chapter II, Lopez Gonzalez 1994) and were fitted with a radio-transmitter equipped with an activity switch (Wildlife Materials Inc.®), the

pumas were located and monitored for 24 h diel sessions from semi-permanent and mobile stations using a null-peak antenna system (AVM Instruments®). Location error was assessed by Lopez Gonzalez (1994) as 0.09 ± 0.12 km² ($\bar{x} \pm \sigma$). During a 24 h session, animals were relocated each 30 minutes, data produced was: location (from fixed or mobile telemetry stations, by one or more observers), distance traveled and number of pulse changes variable rate from mercury switch radio transmitters. Activity patterns were drawn from 88 diel (24 h) radio-tracking sessions, 29 for males and 59 for females.

Pooled data for each sex averaged by each animal were used to build a graphic relationship between distance traveled and number of pulses per unit. These data were transformed into a dummy variable and centered against the mean. Results were segregated into four categories (Table 1) using the following criteria:

I Sleeping (no/small movements and no/few pulse changes, this activity includes error area in telemetry locations).

II Localized activites such as feeding, grooming, playing (involved a high number of pulse changes but little or no movement).

III Travel (distance traveled with no/few pulse changes).

IV Hunting (distance travel with a high number of pulse changes).

Why did we relate distance travel with pulse change? It has been shown by López González (1994) that there is a weak positive relationship between these two variables ($r=0.489$, $df=47$, $p<0.001$), and field observations have confirmed that when animals are just traveling the number

of pulse changes is low or null. A high number of pulse change reflects an intense "head movement" and consequently has been related to hunting.

Once these results were obtained the number of 30 minute blocks were added to obtain the total time of the day devoted to each activity section of the pattern. This procedure was carried out for both sexes.

Five basic processes were calculated (Moen 1973, Schaller et al. 1985): basal metabolic rate (BMR), standing (S), walking (C, includes level and downhill), walking in a slope >30° (Cl), and feeding (F). Basal metabolic rate is present at all times and corresponds to activities I-IV of the upper classification. Both, standing and walking are related to activities III and IV. Feeding takes place during activity II.

Model I

In this model, basal metabolic rate (BMR) was calculated following Kleiber's (1961) formula:

$$BMR = 70(W^{0.75})/24$$

where W is the average weight (kg) of the puma, and 70 is a factor which increases BMR (Moen 1973). The number 24 is the number of hours within a day.

The amount of energy expended standing (S) is about 9% of the BMR (Moen 1973), therefore the formula to calculate the cost of standing was:

$$S = (1.1BMR/24)*T$$

where T is the number of hours spend traveling and hunting.

The cost of walking (C) was calculated following the formula proposed by Moen (1973):

$$C = 0.59W(D)$$

where 0.59 is a constant reflecting the number of kcal spend when traveling a km. And D is the number of km traveled on level ground or downhill.

The cost of walking up a slope >30° (Cl has been calculated ≈10 fold over walking on level ground (Moen 1973 and references listed there). We used the following formula to calculate energy spent by pumas traveling on steep terrain:

$$Cl = 6.45\ W(D)$$

Finally, foraging can be related to the number of kilograms the animal weights:

$$F = 0.54\ W$$

Constants associated with the formulas were taken from Moen's review (Moen 1973) and as with many models they are approximations.

Daily energy expenditure (DEE[1]) for females can be calculated by adding the following:

$$DEE = BMR + S_{10h} + C + Cl + F_{4.5h}$$

and for males:

$$DEE = BMR + S_{11.5h} + C + Cl + F_{5h}$$

DEEa = 50% level walking/50 up slope, DEEb = 75% level/25 up slope, and DEEc = 90% level/ 10% up slope.

[1]Although other activities are not really considered here, like playing or running or courtship, we are assuming that they are included one way or another into the model, either considering them during ascending slopes or as feeding time.

Model II

For this model, basal metabolic rate (BMR) was calculated following Kleiber 's formula (1961) but we will incorporate the multiples found by Corts and Lindzey (1984) for the different sexes:

$$BMR_m = [1.1(70W^{0.75})]/24 \quad BMR_f = [1.2(70W^{0.75})]/24$$

where W is the average weight (kg) of the puma, and 70 is a factor which increases BMR (Moen 1973), "m" stands for male and "f" for female.

The amount of energy expended standing (S) is about 9% of the BMR (Moen 1973), therefore the formula to calculate the cost of standing was:

$$S = (1.1BMR/24) * T$$

The cost of walking (C) was based on the work of Corts and Lindzey (1984). These authors found that male and female pumas traveling 1 km/h spend 4.7 kcal and 4.81 kcal respectively. In order to calculate the daily energy expended during one hour:

$C_m = 4.7\ W$ (distance travel in km per 24 h) $C_f = 4.81\ W$ (distance travel in km per 24 h)

Finally, foraging can be related to the number of kilograms the animal weighs:

$$F = 0.54\ W$$

Constants associated to the formulas are taken from Moen's review (Moen 1973) and are approximations.

Daily energy expenditure (DEE[1]) for females can be calculated by adding the following:

$$DEE = BMR + S_{10h} + C + F_{4.5h}$$

and for males:

$$DEE = BMR + S_{11.5h} + C + F_{5h}$$

Predation rate

Assuming the sample of diel cycles represents the observed distribution of activity for pumas in the study area, we transformed the data into proportions and extrapolated them to a 275 day interval (average non winter days on a given year). We wanted to do this to obtain the overall energy expenditure for this interval and then obtain a daily that may reflect the variability that a living organism has in a landscape where food is on the move and therefore resource patch predictability is low. We did not want to include winter days in the model for several reasons. First, it has been shown that activity patterns may change during winter, with animals being more active at daytime and distances traveled (based on snow-tracking) during a diel cycle are probably smaller, since large prey are more concentrated in winter yards (Trout 1963, Hornocker 1970).

We basically follow the procedure proposed by Ackerman et al. (1986) to estimate daily biomass consumed (DBC):

$$DB_LC = DEE/(0.87*cal*0.86)$$

$$DBcC = DEE/[0.75(0.87*1890cal*0.86)+0.2(0.87*1530\ cal*0.86)+ 0.05(0.87*1530cal*0.86)]$$

where 0.87 is equivalent to the fraction of energy derived from meat. The term *cal* stands for a value of 1,890 kcal/kg wet weight of deer meat (Davison et al. 1978) and 1,530 for small mammals (Litviatis and Mautz 1980). We used the deer value for medium size prey. The 0.86 value is the fraction of the energy remaining after digestion and assimilation (Ackerman et al.

1986). DB_LC is the value of a diet based upon deer. DBcC stands for a diet with a 75% deer, 20% porcupine (*Erethizon dorsatum*) and 5% jackrabbits (*Lepus* sp.).

Using the published weights of deer for the area (Trout 1963) and the data from deer killed by pumas in South Central Idaho and NW Utah (n = 18, López González 1994). The mean deer weight is 34.97 kg. We calculated a carcass consumption value of 75%, which is similar, but somewhat inferior than other studies have proposed (Ackerman et al. 1986, Hornocker 1970). Mainly hooves, pieces of large bones, skulls (sometimes the brain was eaten but the rest of the head was left), hides, rumens and intestines were left, concurrent with other studies (Anderson 1983, Beier et al. 1995, Hornocker 1970, Shaw 1979).

The number of prey items consumed within a day (NPD) was calculated by the formula:

$$NP_LD = DBC/(Wp*0.75)$$

where *Wp* is the weight of the prey species used.

We also calculated the NPD for a mixed diet including medium size mammals, and small mammals, specifically for porcupine (*Erethizon dorsatum*, $W \approx 8.2$ kg), the second species most frequently killed by pumas, jackrabbits and snowshoe hares (*Lepus spp*, $W \approx 3.0$ kg). The mean weights for the medium and small species were obtained from Hall (1981).

Although small prey items have been ranked as non important on pumas' diet in North America (Iriarte et al. 1990), they can be locally important (Ashman et al. 1983). Many times when finding kills, small prey items are usually consumed totally and consequently no evidence remains of such event (i.e. Iriarte et al. 1990).

Anderson's (1983) data on 619 stomachs, yield 26.7% (165) empty. The killing of a puma

with an empty stomach occurs more than expected by chance ($z=21.58$, $p>0.05$). However, if 70% of them had some content, it seems that starvation is more the exception than the rule. Irregular eating patterns of predators are determined by chance of encountering a prey item and that, increases the probability of finding an empty stomach.

RESULTS

Model I

The BMR value calculated was compared to the puma BMR calculated by McNab (1989) with a resulting difference of 0.07% and 7.97% for females and males respectively, which when calculating DBC and NPD was not sufficiently different than the values obtained with Moen's formula.

Using this model, female DEE varied from 2,559.03 to 4,304.24 kcal. Male DEE varied from 3,588.59 to 5,961.23 kcal. Most of the pumas followed presented a pattern of movement closer to the fifty/fifty ratio used for the DEEa. Therefore comparisons from now on will be made between this result and model II.

Biomass consumed per day as calculated with the model was 3.04 kg for the females and 4.21 kg for males. The number of deer killed per day was 0.116 for females and 0.16 for males. This in turn reflects a time between kills of 8.62 days for females and 6.25 for males. Thus a total number of deer killed by females is 32 and for males is 44.

Incorporating a varying number of kittens (1-4) into the model, and energy expenditure of the female increasing at a rate 0.6 per kitten will result in 19.2 more deer needed per kitten. Days

between kills of a female with kittens are 5.38 (1k), 3.91 (2k), 3.07 (3k), and 2.53 (4k). Therefore the number of deer per year will be 51 (1 kitten), 70 (2 kittens), 89 (3 kittens), and 108 (4 kittens).

The population of pumas on the study area (Lopez-Gonzalez et al. In preparation) can reach a maximum of 9 male residents, 15 female residents and potentially up to 6 transients with an average of four. The number of kittens can be potentially 30 in a given year, but to incorporate a more realistic number only 15 will be considered for the model. Females usually have a mean of 2.5 kittens but most of the litters are of two. Therefore a 15 kitten population each year sounds realistic considering a reproductive rate every 17 mo. or every other year.

A total of 1,510 deer need to be killed to fulfill the needs of the population, considering 396 for males, 480 for females, 64 for transients, and 570 for kitten maintenance. The total number of deer can be translated into biomass per area (2,500 km^2) consumed by the pumas, this number is 21.1 kg/km^2.

If we consider the mixed diet numbers of prey this resulted in 26.58 deer, 30.22 porcupine and 15.48 rabbits for the females. For the male the number was 36.81 deer, 41.85 porcupine and 21.45 rabbits. Female kill rate is 1 deer/7.75 days, 1 porcupine/1.81 days and 1 rabbit/0.88 days. In the case of the male, kill rate was 1 deer/5.49 days, 1 porcupine/1.31 days and 1 rabbit/0.64 days. Using these values the population of pumas will consume 1,268 deer, 1,434 porcupine and 735 rabbits, for a biomass density use of 23.32 kg/km^2.

Model II

Calculations using Model II, yield female pumas with an average DEE of 5,326.21 kcal

and male energy expenditure is 7,381.40. These results are different from model I by 20, 40, and 52 % in both sexes.

Daily biomass consumed was 3.76 kg for females and 5.21 kg for males. The number of large prey killed per day was 0.143 for females and 0.198 for males. This translates into an interval between kills of 6.99 days for females and 5.05 for males. The number of deer killed for females is 39 and for males 54.

Incorporating kittens into the model as I did before, translates into 64, 88, 112, and 137 deer with an increase in litter size from 1 to four. The number of days between kills is 4.25, 3.09, 2.43, and 2.

Incorporating the number of pumas in the study area will reflect a total of 1,852 deer killed by the pumas. A total of 486 for males, 585 for females, 76 for transients and 704 for kitten maintainance. The biomass per area for this model is 25.9 kg/km^2.

If we consider the mixed diet numbers of prey this resulted in 33.60 deer, 38.20 porcupine and 19.58 rabbits for the females. For the male the number was 45.58 deer, 51.83 porcupine and 26.56 rabbits. Female kill rate is 1 deer/6.01 days, 1 porcupine/1.44 days and 1 rabbit/0.70 days. In the case of the male, kill rate was 1 deer/4.44 days, 1 porcupine/1.06 days and 1 rabbit/0.51 days. Using these values the population of pumas will consume 1,586 deer, 1,803 porcupine and 934 rabbits, for a biomass density use of 29.21 kg/km^2.

DISCUSSION

Estimates of daily biomass consumed for this study were different from other studies. The

range of DBC estimated by Robinette et al. (1959) included my calculations (2.3-5.5 kg/day). Hornocker (1970) estimated a range of 1.8-2.7 kg/day or about half of the estimated biomass for the models used in our study. Ackerman et al. (1986) calculated a range of 2.2-2.7 kg/day for single adult female and 3.4 to 4.3 kg/day on males. The value for females lay below the calculated ones of this study by 12-18%. Male DBC values are included within the interval predicted, with a tendency to be on the higher side. Bailey (1993) estimated a male adult leopard (52.8 kg) consuming 3.5 kg/day and adult females (37.5) consuming 2.8 kg.

The predicted interval of days between kills for the study area rests within published studies for both sexes. Most studies do not make differences between sexes when displaying the days between kills. Young and Goldman (1946) proposed kill rate for a single adult as 1 deer/7days; and 1 deer/3 days for a female with cubs. Conolly (1949) says pumas are killing a deer every 9.7 days and one porcupine each 7.2 days. Hornocker (1970) propose 1 deer/ 10-14 days. Shaw (1977) propose 1 deer/calf every 10.4 days, and he says that a female with cubs kills one large prey per 6.8 days. Ackerman et al. (1986) calculated that a single female have to kill a deer every 14-17 days, a male every 8-11 days, and a female with three large cubs every 3.3 days. Harrison (1989) determined females with kittens a kill of one ungulate every 3.3 to 10 days. Most of these estimates are higher than those predicted by the models used in this study. Similarly-sized African leopards (*Panthera pardus*) on the Kalahari desert are killing one prey every 3 days for males and every 1.5 days for a female with cubs (Bothma and Le Riche 1986). Bailey (1993) estimated a kill rate of one impala every 6.9 days, but he points out that smaller prey could have been killed and not detected.

The number of deer, killed per puma per year on the study area using the first model exceeds two of the published estimates. Estimates using the second model are well above every study published. Nuñez (1999) estimates are also high, he estimated tha pumas only ate 1.5 nights per deer, where temperature appears to cause meat to dry faster than other areas. In central Idaho, 14-20 deer/year would maintain an adult puma (Hornocker 1970). In Arizona the calculated mumber of deer killed per year was 17-25 (Shaw 1977). In central Utah pumas need to kill 38 deer/year (Conolly 1949). In southern California Beier et al. 1995 estimated 48 large mammals and 58 small mammals were killed. This later study retraced the puma path on a diel cycle and estimated from successful hunts the number of times this pattern happened through the year. African leopards kill an average 45 impala per year (Bailey 1993).

A factor not really stressed in most published predation rates is the impact of scavenging. Harrison (1989) demonstrated that areas subject to coyote (*Canis latrans)* control reduced predation rates almost by half. This effect is probably more evident where complete carnivore assemblage are still present such as Glacier National Park or Yellowstone National Park (USA), or Manu National Park (Peru), South America.

Including smaller prey into the model, changes the intervals between prey kills (Bailey 1993), and therefore the number of prey items hunted on a yearly basis. This is important to consider, especially when thinking about the number of days a puma has to go without eating. Probably this finding is more relevant if we incorporate it into developing protected areas or game management for hunting. Between killing deer one can envision a puma killing smaller prey and this behavior may or may not be detected (Beier et al. 1995).

The time a small prey item will stay within the carnivore's body cannot be detected easily, as it has been reported that African leopards defecate after nearly 12.9 km of walking (Bothma and Le Riche 1994). The time that it takes a leopard to defecate a small prey is a day (Bothma and Le Riche 1994), this is probably true for the puma too as it has a high rate of metabolism suitable for feeding on vertebrate prey (McNab 1989).

It has been stated that pumas cannot survive completly on small prey, but a recent study in Argentina has shown that vizcachas (*Lagostomus maximus* ≈ 4.5 kg) are a reliable source food for pumas (Branch et al. 1996). This prey species will provide the predicted food intake proposed by this study and Ackerman et al. (1986). Reliance on porcupines as important prey items has been recently stressed as a synergistic effect in the Great Basin, where pumas + environmental conditions can provoke a collapse in a porcupine population (Sweitzer 1996).

The high percentage of empty stomachs in a puma sample (Anderson 1983) probably reflects that predicted kill rates are not usually met. Starvation is among natural mortality causes of pumas but is not the most important one (Anderson 1983, Lindzey et al. 1988, Shaw 1980, Sweanor 1990). It has been shown that nursing female cheetahs (*Acinonyx jubatus*) can provide enough growing material to kittens (n = 3) when killing 1.5 kg per day (Laurenson 1995). This is important when comparing it to the puma, because both cats are of similar size and closely related on a phylogenetic scale (Nowell and Jackson 1996). If a female cheetah can provide enough food both for the litter and herself, it is very likely pumas can survive with a similar amount of food on a daily basis (if so, this would reflect half of the consumption calculated by this study).

The model that we are using seems to perform close to "real" numbers published by Beier

et al. (1995). We say this because they include in their analysis activities similar to categories that we examined, such as walking and time spend hunting. Anderson (1983) has clearly stated the difficulty of homogenizing sampling techniques and that even with the best technology it is still hard to assess predation rates.

The biomass density removed in this study is approximately double the calculated biomass removed by pumas in the rainforest of Peru, and about 2/3 of the jaguar (*Panthera onca)* . Similar values develop when adding the biomass for both large cats, 24.66 kg/km² (Emmons 1987). This period of time probably accounts for the 33% difference in numbers of prey killed per year reported by Beier et al. (1995). Porcupine killing can be higher during this time of the year (Sweitzer 1996), both in numbers and biomass, because almost 30% of porcupine weight is lost during winter (Sweitzer and Berger 1993). Another difference is that spoilage of prey is reduced owing decreased environmental temperatures (Ackerman et al 1986). And finally, BMR increases as animals bear their lower critical temperatures (Mautz and Pekins 1989). Therefore, these conditions may well influence estimates for winter.

A final comment is that recent studies have determined individual puma behavior and consequently particular food preferences (Ross et al. 1997), therefore, estimates of consumption should be considered indicative of the potential impact of a puma population on a given area or prey populations.

For the Idaho portion of the study area, the average deer biomass removed by hunters during the length of this study (1987-1995) was 20.6 kg/km² (Data on deer harvest provided by Idaho Game and Fish Department, and transformation into biomass by Lopez Gonzalez), slightly

lower than the estimated amount removed by the total number of pumas on a given year (2.5% difference with Model I, 25.8% with Model II). This reflects the low impact that pumas are having on the deer population, but can potentially add to the herd productivity for the following year. Recent studies have shown that pumas coupled with environmental factors can reduce prey populations to minimal numbers (i.e. *Erethizon dorsatum* Sweitzer 1996, *Ovis canadensis* Wehausen 1996).

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Table 2.- Average time devoted to the different activity categories of adult resident pumas.

	Mean time spend in activity (h)	
Type	Male (n = 4)	Female (n = 13)
I [a]	7.5 (218)	9.5 (560)
II [b]	5 (145)	4.5 (266)
III [c]	4.5 (130)	5 (295)
IV [d]	7 (203)	5 (295)

[a]Sleeping (no/small movements and no/few pulse changes, this activity includes error area in telemetry locations), [b]localized activities such as feeding, grooming, playing (involved a high number of pulse changes but little or no movement), [c]travel (distance travel with no/few pulse changes), [d]hunting (distance travel with a high number of pulse changes). Numbers in parenthesis represent no. of radio locations for that given activity.

CONCLUSIONES GENERALES

A partir de los resultados obtenidos en este estudio y complementados con mi tesis de Maestría, se puede concluir que los pumas, en un ambiente fragmentado del desierto "Great Basin", tienen una tasa de reproducción baja pero constante donde las hembras producen de 2 a 3 camadas por vida. En donde la supervivencia de las hembras que permanecen dentro de la población es más alta que la de los machos que se llegan a dispersar. Aproximadamente el 30% de las crías que sobreviven se incorporan a la población residente, donde menos del 5% será de machos. El reclutamiento de las hembras al parecer está limitado por la capacidad de carga de este sistema. El número de pumas no se ve limitado por la organización social como se pensaba anteriormente y al parecer se ve limitada por la cantidad de recursos (tanto de habitat, como de alimento). La mortalidad por captura de alimento puede ser superior a la de encuentros agonistas. Las diferencias encontradas entre éste y otros estudios al parecer estan relacionadas con patrones cíclicos del medio ambiente, siendo en el área de estudio el ciclo poblacional de 16 años. Sin embargo no existe un programa de monitoreo para saber cuando va a ocurrir el próximo pico inferior en la población, la definición de este momento es importante debido a que sino se contempla el aumento en el número de pumas que se cacen, se podría provocar una extinción local debido a que la tasa de reemplazamiento es baja en esta población

La conectividad de la población estudiada con sitios en los Estados de Nevada, Wyoming y Montana se pudo identificar al encontrar pumas que se establecieron en estos sitios después de haberse dispersado. Al parecer el puma es una especie con gran potencial para proteger habitats importantes para la conservación de la biodiversidad de la región "Great Basin" reconocida como

parte de la estepa de *Artemisa*. La porción Sur-Central del Estado de Idaho tiene el potencial de ser utilizada como un corredor que comunique al "Great Basin" con las Rocallosas. Como resultado del análisis se propone la creación de áreas protegidas para mantener el germoplasma de pumas y permitir que los pumas esten surtiendo o reforzando a poblaciones que tengan cierto tipo de explotación. Donde el tamaño mínimo de estas áreas sobrepasa el de las ya existentes, por lo que es necesario tomar acciones para crear dichos refugios a la brevedad. Se juzga pertinente la evaluación social y económica de la región antes de llevar a cabo algún proceso orientado a la conservación.

Al evaluar los modelos de requrimientos energéticos se encuentra que tienden a ser más elevados que los publicados anteriormente, la diferencia aparentemente está relacionada con el uso de patrones de actividad obtenidos en el campo. Las tasas de depredación son, por la tanto, más elevadas, lo que puede tener implicaciones importantes ligadas a la creación de áreas protegidas. Un hallazgo importante es que al parecer el consumo de venados por toda la población de pumas presente en el área no sobrepasa la explotación realizada por los cazadores, por lo cual no deben autorizarse campañas específicas para el control de depredadores, ya que no se logrará incrementar la población del venado realizando esta acción, y se pondrá en riesgo la población del depredador.

Como comentario final se puede ver que no solo la dinámica poblacional, el área y distancia donde exitosamente llegan a dispersarse las crías, son importantes para la conservación, sino también el número de presas que necesita dicha población para mantener un tamaño que asegure su permanencia.