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

Carlos A. LÓPEZ-GONZÁLEZ and Alberto GONZÁLEZ-ROMERO
Instituto de Ecología, A. C., km 2.5 Antigua Carretera a Coatepec, Apdo. Postal 63, 91000, Xalapa, Veracruz, MEXICO

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).

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 5 ½ 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

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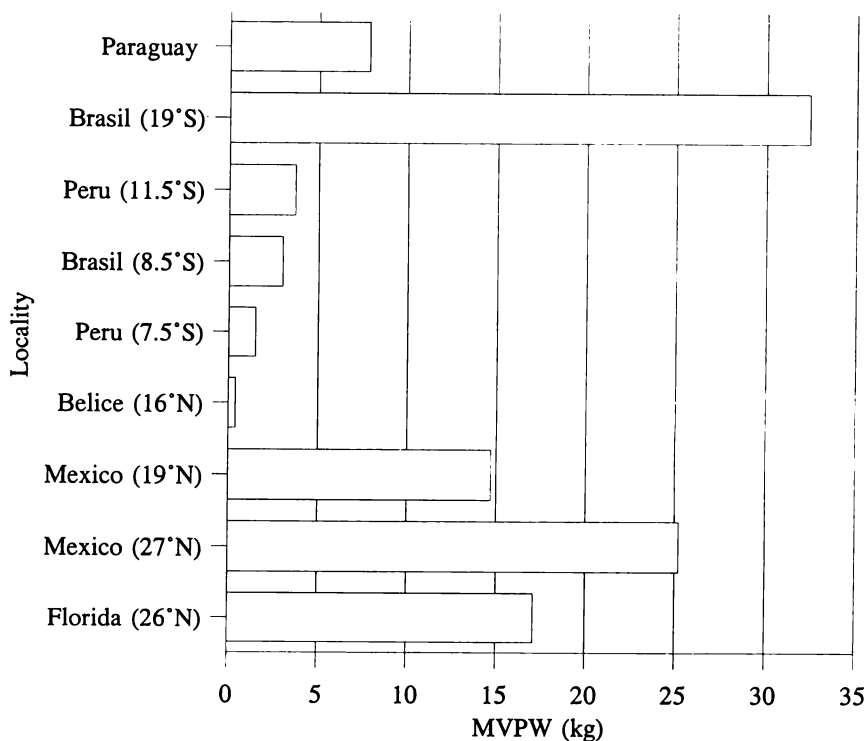
Figure 1
Comparison of mean vertebrate prey weight (MVPW) used by pumas through tropical America (Data from Iriarte *et al.* 1990, Lopez-Gonzalez *et al.* 1996, Olmos 1993, Romo 1995)

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

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

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

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 nemionus*, 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 occurring 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

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.

LITERATURE CITED

Ackerman, B.B., F.G. Lindzey & T.P. Hemker. 1984. Cougar food habits in southern Utah. *J. Wildlife Manage.* 48(1): 147-155.

_____. 1986. Predictive energetics model for cougars. pp.333-352. *In*: Miller S.D. & D.D. Everett (eds). *Cats of the World: Biology, Conservation, and Management.* Proc. Second International Symposium, Kingsville, TX. 1982.

Allen, J.H. 1906. Mammals from the State of Sinaloa and Jalisco, Mexico, coll. by J.H. Batty during 1904 & 1905. *Bull. Amer. Mus. Ñat. Ecol. Hist.* XXII. Article XII: 191-262.

Anderson, A.E. 1983. A critical review of literature on puma (*Felis concolor*). *Colorado Division of Wildlife Special Report* No. 54. 91 pp.

Anderson, A.E., D.C. Bowden & D.M. Kattner. 1992. The Puma on Uncompahgre plateau, Colorado. *Technical Publication* No. 40. 116 pp.

Aranda, M. & V. Sanchez-Cordero. 1996. Prey spectra of jaguar (*Panthera onca*) and puma (*Puma concolor*) in Tropical Forests of Mexico. *Studies in Neotropical Fauna and Environment* 31: 61-64.

Beier, P., D. Choate & R.H. Barrett. 1995. Movement patterns of mountain lions during different behaviors. *J. Mammal.* 76(4): 1056-1070

Beier, P. & S.C. Cunningham. 1996. Power of track surveys to monitor population trend. *Proceedings of the Fifth Mountain lion workshop.* San Diego California. pp. 3.

Berger, J. & J.D. Wehausen. 1991. Consequences of a mammalian Predator-Prey Disequilibrium in the Great Basin Desert. *Conservation Biology* 5(2): 244-248.

Bisbal, F. 1989. Distribution and habitat association of the carnivores in Venezuela, Pp. 339-362. *In*: Eisenberg J. (ed). *Advances in Neotropical Mammalogy.* The Sandhill Crane Press Inc.

Bleich, V.C., B.M. Pierce, J.L. Davis & V.L. Davis. 1996. Thermal characteristics of mountain lion dens. *Great Basin Nat.* 56 (3): 276-278.

Branch, L.C. 1995. Observations of predation by pumas and Geoffroy's cats on the plains vizcacha in semi-arid scrub of central Argentina. *Mammalia* 59(1): 152-156.

Branch, L.C., M. Pessino & D. Villareal. 1996. Response of pumas to a population decline of the plains vizcacha. *J. Mammal.* 77(4): 1132-1140.

Brown, E.M., A.F. King & D.B. Houston. 1988. Natural mortality of a cougar. *The Murrelet* 69: 38.

Cashman, J.L., M. Pierce & P.R. Krausman. 1992. Diets of mountain lions in Southwestern Arizona. *Southwest. Natur.* 37(3): 324-326.

Chinchilla-Romero, F.A. 1994. La dieta del jaguar (*Panthera onca*), el puma (*Felis concolor*), el manigordo (*Felis pardalis*) (Carnivora, Felidae) y dos metodos de evaluacion de su abundancia relativa en el Parque Nacional Corcovado, Costa Rica. Ms. Thesis. Universidad Nacional Heredia, Costa Rica. 49 pp.

Crawshaw, P.G. 1995. Comparative ecology of ocelot (*Felis pardalis*) and jaguar (*Panthera onca*) in a protected subtropical forest in Brazil and Argentina. PhD Dissertation. University of Florida. Gainesville, Florida, USA. 189 pp.

Crawshaw, P.G. & H.B. Quigley. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *J. Zool. London* 223: 357-370.

Cumberland, R.E. & J.A. Dempsey. 1994. Recent confirmation of a cougar, *Felis concolor*, in New Brunswick. *Can. Field-Natur.* 108(2): 224-226.

Currier, M.J.P. 1983. *Felis concolor*. Mammalian Species No. 200. Pp. 1-7

Dixon, K.R. 1981. Mountain lion *Felis concolor*. pp. 711-727 *In*: Chapman, J.A. and G.A. Feldhamer (eds). *Mammals of North America*. John Hopkins University Press.

Eaton, R.L. & K.A. Velander. 1977. Reproduction in the puma: biology, behavior and ontogeny. pp. 45-70 *In*: Eaton, R.L. (ed). *The World's cats*, Vol. 3, No. 3. Carnivore Research Institute. Nurke Museum, Univ. Washington, Seattle.

Eisenberg, J.F. 1989. An introduction to the Carnivora. pp 1-9 *In*: Gittleman, J.L., ed. *Carnivore behavior, ecology and evolution*. Cornell University Press, 620 pp.

Eisenberg, J.F., M.A. O'Connell & P.V. August. 1979. Density, Productivity, and Distribution of Mammals in two Venezuelan Habitats. pp. 187-207 *In*: Eisenberg J.F. (ed.), *Vertebrete Ecoloy in the Northern Neotropics*. Smithsonian Inst. Press, Washington, D.C.

Emmons, L.H. 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behav. Ecol. Sociobiol.* 20: 271-283.

_____. 1990. *Neotropical rainforest mammals: a field guide*. University of Chicago Press, Chicago. 390 pp.

Enders, R.K. 1935. Mammalian life histories from Barro Colorado Island, Panama. *Bull. Mus. Compar. Zool. (Harvard)* 78(4): 385-502.

Fuller, T.K. 1994. An international review of large carnivore conservation status. *Proc. Intern. Wildlife Manag. Congr.* 410-412.

Gaumer, G.F. 1917. *Mamíferos de Yucatán*. Depto. Talleres Graficos, Secretaria de Fomento. México, 331 pp.

Gay, S.W. & T.L. Best. 1995. Geographic variation in sexual dimorphism of the puma (*Puma concolor*) in North and South America. *Southwest. Natur.* 40(2): 148-159.

Hall, E.R. 1981. *The Mammals of North America.* John Wiley and Sons, New York. Vol. 1: xv + 1-600 + 90 and 2: vi + 601-1181 + 90.

Harrison, S. 1989. Predation rates of cougar within the junction Wildlife Management Area. Proceedings of the Third Mountain Lion Workshop. Dec 6-8, 1988. Prescott, Arizona. Arizona Chapter, *The Wildlife Society-Arizona Game and Fish Department*. pp. 48.

Hast, M.H. 1989. The larynx of roaring and no-roaring cats. *J. Anat.* 163: 117-121.

Hemker, T.P., F.G. Lindzey, & B.B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. *J. Wildlife Manag.* 48: 1275-1284.

Hershkowitz, P. 1972. The recent mammals of the Neotropical region: A zoogeographic and ecological review. pp 311-421 *In*: Keast, A., F.C. Erk, and B. Glass (eds.), *Evolution, Mammals, and Southern Continents*. State University of New York Press.

Holt, D.W. 1994. Larder hoarding in the cougar, *Felis concolor. Can. Field-Natur.* 108(2): 240-241.

Hornocker, M. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho primitive area. *Wildlife Monographs* No. 21. 39 pp.

Iriarte, J.A., W.L. Franklin, W.E. Johnson & K.H. Redford. 1990. Biographic variation of food habits and body size of the America puma. *Oecologia* 85: 185-190.

Jardine, W. 1834. *Naturalist's Library*. Vol. 2., Mammals, Felidae: 266 pp.

Johnson, W.E., W.L. Franklin, & A. Iriarte. Sympatric felid and canid predators of Torres del Paine National Park, Chile. *In*: Franklin W.L. (ed). *Patagonia Gem: the ecology and natural history of Torres del Paine National Park, Chile.* (In press)

Jorgenson, J.P. & K.H. Redford. 1993. Humans and big cats as predators in the Neotropics pp. 367-390 *In*: N. Dunstone and M.L. Gorman, (eds.) *Mammals as predators.* Sympopsium of the Zoological Society of London No. 65. Oxford Science Publications.

Kiltie, R.A. 1984. Size ratios among sympatric neotropical cats. *Oecologia* 61: 411-416.

Koehler, G.M. & M.G. Hornocker. 1991. Seasonal resourse use among Mountain lions, bobcats and coyotes. *J. Mammal.* 72(2): 391-396.

Kurtén, B. & E. Anderson. 1980. *Pleistocene mammals of North America.* Columbia University Press. New York. 443 pp.

Lindzey, F.G. 1987. Mountain lion. pp. 657-668 *In*: Novak, M., J.A. Baker, M.E. Obbard, and B. Malloch, (eds.) *Wild furbearer management and conservation in North America.* Ontario Trappers Association, North Bay.

Lindzey, F.G., W.D. Van Sickle, S.P. Liang & C.S. Mecham. 1992. Cougar population response manipulation in Southern Utah. *Wildlife Soc. Bull.* 20: 224-227.

Lindzey, F.G., W.D. Van Sickle, B.B. Ackerman, D. Banhurst, T.P. Hemker & S.P. Laing. 1994. Cougar population dynamics in Southern Utah. *J. Wildlife Manage.* 58(4): 619-624.

Logan, K.A., L.L. Irwin & R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. *J. Wildlife Manage.* 50(4): 648-654.

Logan, K.A., L.L. Sweanor & M. Hornocker. 1996. Cougars population dynamics, Chapter 3. pp. 22-113. *In*: Logan, K.A., L.L. Sweanor, T.K. Ruth and M.G. Hornocker. *Cougar of the San Andres mountains, New Mexico.* Federal Aid in Wildlife Restoration Project W-128-R for New Mexico Departament of Game and Fish, Santa Fe, New Mexico.

_____. 1996. Cougars and desert bighorn sheep, Chapter 6. Pp. 230-249. *In*: Logan, K.A., L.L. Sweanor, T.K. Ruth & M.G. Hornocker. *Cougar of the San Andres mountains, New Mexico.* Federal Aid in Wildlife Restoration Project W-128-R for New Mexico Departament of Game and Fish, Santa Fe, New Mexico.

López-González, C.A. 1994. Ecologia y comportamiento del puma (*Puma concolor*) en un habitat fragmentado. Master in Science thesis. Facultad de Ciencias, UNAM. 64 pp.

López-González, C.A., E. Martínez-Meyer, J.W. Laundre, B. Miller, & A. Gonzalez-Romero. 1996. Contribution to the natural history of pumas (*Puma concolor*) in the tropical dry forests of western Mexico. *Proceedings of the Fifth Mountain lion workshop.* San Diego California. pp. 14.

Maehr, D.S., J.C. Roof, E.D. Land & J.W. McCown. 1989. First reproduction of a panther (*Felis concolor coryi*) in southwestern Florida, U.S.A. *Mammalia* 53(1): 129-131.

Maehr, D.S., E. Darrell-Land, J.C. Roof & J.W. McCown. 1989. Early maternal behavior in the Florida panther (*Felis concolor coryi*). *Amer. Midland Natur.* 122(1): 34-43.

Maehr, D.S., R.C. Belden, E. Darrell-Land & L. Wilkins. 1990. Food habits of panthers in souhwest Florida. *J. Wildlife Manage.* 54(3): 420-423.

Maehr, D.S., E. Darrell-Land & J.C. Roof. 1991. Social Ecology of Florida Panthers. *National Geographic Research and Exploration* 7(4): 414-431.

Maehr, D.S., E. Darrell-Land & M.E. Roelke. 1991. Mortality patterns of panthers in Southwest Florida. *Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies* 45: 201-207.

Maehr, D.S., J.C. Roof, E.D. Land, J.W. McCown, & R.T. McBride. 1992. Home range characteristics of a panther in south central Florida. *Florida Field Natur.* 20(4): 97-103.

Mazzolli, M. 1993. Ocorrência de *Puma concolor* (Linnaeus) (Felidae, Carnivora) em áreas de vegetação remanescente de Santa Catarina, Brasil. *Rev. Brasil. Zool.* 10(4): 581-587.

McBride, R.T. 1976. The status and ecology of the mountain lion *Felis concolor stanleyana* of the Texas-Mexico border. M.S. thesis. Sul Ross State University, Alpine, Texas. 160 pp.

Nowell, K. & P. Jackson. 1996. Wild Cats: Status, survey and conservation action plan. IUCN/SSC Cat Specialist Group. 382 pp.

Nuñez, R. & B.J. Miller. 1997. Ecología de jaguares y pumas en el Oeste de México. Reporte Final CONABIO. México, 25 pp.

Olmos, F. 1993. Notes on the Food habits of Brazilian "Caatinga" Carnivores. *Mammalia* 57(1): 126-130.

Oliveira, T.G. 1994. *Neotropical cats: Ecology and conservation.* EDUFMA (Univ. Fed. do Maranho) San Luis, Brazil. 245 pp.

Padley, W.D. 1990. Home ranges and social interactions of mountain lions in the Santa Ana Mountains, California. M.S. thesis. California State Polytechnic University, Pomona. 65 pp.

Paine, R.T. 1966. Food web comlexity and species diversity. *Amer. Natur.* 100: 65-75.

_____. 1969. A note on trophic complexity and community stability. *Amer Natur.* 103: 91-93.

Patton, S., A. Rabinowitz, S. Randolph, & S. Strawbridge-Johnson. 1986. A survey of paratises in wild felines. *J. Parasit.* 72(4): 517-520

Rabb, G.B. 1959. Reproductive and vocal behavior in captive pumas. *J. Mammal.* 40:616-617.

Rabinowitz, A. & B.G. Nottingham, Jr. 1986. Ecology and behavior of the Jaguar (*Panthera onca*) in Belize, Central America. *J. Zool. Lond.* 210: 149-159

Redford, K.H. & J.F. Eisenberg. *Mammals of the Neotropics*, Vol. 2: the southern cone. Chicago University Press. 430 pp.

Robinette, W.L., J.S. Gashwiler, & O.W. Morris. 1959. Food habits of the cougar in Utah and Nevada. *J. Wildlife Manage.* 23(2): 261-273.

_____. 1961. Notes on cougar productivity and life history. *J. Mammal.* 42(2): 204-217.

Roelke, M.E. 1990. *Florida panther biomedical investigation: health and reproduction.* Final Perf. Rep. Fla. Game and Fresh Water Fish Comm. Tallahassee. 176 pp.

Romo, M.C. 1995. Food habits of the Andean fox (*Pseudalopex culpaeus*) and notes on the mountain cat (*Felis colocolo*) and puma (*Felis concolor*) in the Rio Abiseo National, Peru. *Mammalia* 59(3): 335-343.

Ross, P.I. & M.G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in Southwestern Alberta. *J. Wildlife Manage.* 56(3): 417-426.

Ross, P.I., M.G. Jalkotzy, & P. Daoust. 1995. Fatal trauma sustained by Cougars, *Felis concolor,* while attacking prey in Southern Alberta. *Can. Field-Natur.* 109(2): 261-263.

Ross, P.I., M.G. Jalkotzy & M. Festa-Blanchet. 1997. Cougar predation on bighorn sheep in southewestern Alberta during winter. *Can. J. Zool.* 73(3): 771-775.

Ruth, T.K. 1990. *Mountain lion-human interaction in Big Bend National Park, Texas.* Texas A & M University, Kingsville TX 215 pp.

Ruth, T.K. & M. Hornocker. 1996. Interacions between cougars and wolves (and a bear or two) in the North Fork of the Flathead River, Montana. *Proceedings of the Fifth Mountain lion workshop.* San Diego California. pp. 22.

Saenz-Jimenez, Y. 1996. Estudio coprologico de parasitos en felinos salvajes de cautiverio en Costa Rica. Tesis de Licenciatura, Universidad Nacional de Heredia. 48 pp.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores, 164-182 pp. *In*: Gittleman, J.L. (ed). *Carnivore behavior, ecology and evolution.* Cornell University Press. 620 pp.

Schaller, G. & P.G. Crawshaw. 1980. Movement patterns of jaguar. *Biotropica* 12:161-168.

Schonewald-Cox, C., R. Azari, & S. Blume. 1991. Scale, variable density, and conservation planning for mammalian carnivores. *Conservation Biology* 5(4): 491-495.

Seidensticker, J.C., M.G. Hornocker, W.V. Wiles, & J.P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monogr.* 35:1-60.

Shaw, H.G. 1977. Impact of mountain lion on mule deer and cattle in Northwestern Arizona. pp. 17-32 *In*: Phillips R.C. and C. Jonkel (eds). *Proceedings of the 1975 Predator Symposium, Montana Forest and Conservation Experimental Station, Univ. Montana, Missoula.* 268 pp.

_____. 1989. *Soul among lions.* Johnson books, Boulder, Colorado. 144 pp.

Smallwood, K.S. 1993. Mountain lion vocalizations and hunting behavior. *Southwest. Natur.* 38(1): 65-67

_____. 1994. Trends in california mountain lion populations. *Southwest. Natur.* 39(1): 67-72.

Steger, G.N. 1988. Movement and survival of 14 month old orphaned Mountain lion kittens, pp. 73 *In*: Smith R.H. (ed). *Proceedings of the Third Mountain Lion Workshop.* Prescott, Arizona.

Stocek, R.F. 1995. The cougar, *Felis concolor,* in the maritime provinces. *Can. Field-Natur.* 109(1): 19-22.

Sweanor, L.L. 1990. Mountain lion social organization in a desert environment. M.S. thesis, University of Idaho, Moscow, 164 pp.

Taber, A.B., A.J. Novaro, N. Neris, & F.H. Colman. 1997. The food habits of sympatric jaguar and puma in the Paraguayan Chaco. *Biotropica* 29(2): 204-213.

Terborgh, J. 1990. The role of felid predators in Neotropical forests. *Vida Silvestre Neotropical* 2(2): 3-5.

Toweill, D.E. 1986. Notes on the development of a cougar kitten. *The Murrelet* 67: 20-23.

Turner, J.W., M.L. Wolfe, & J.F. Kirkpatrick. 1992. Seasonal mountain lion predation on a feral horse population. *Can. J. Zool.* 70: 929-934.

Van Dyke, F.G., R.H. Brocke, H.G. Shaw, B.B. Ackerman, T.P. Hemker & F.G. Lindzey. 1986. Reactions of mountain lions to logging and human activity. *J. Wildlife Manage.* 50(1): 95-102.

Van Pelt, A.F. 1977. A mountain lion kill in southwest Texas. *Southwest. Natur.* 22: 271.

Wade, J.G. 1929. Mountain lion seen killing a doe. *California Fish and Game* 15: 73-75.

Wozencraft, W.C. 1993. Order Carnivora, pp. 286-346. *In*: Wilson, D. and D.M. Reeder (eds). *Mammal Species of the world a taxonomic and geographic reference*, 2nd ed. Smithsonian Institution Press and The American Society of Mammalogists.

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

Young, S.P. & E.A. Goldman. 1946. *The puma, mysterious American cat*. The American Wildlife Institute, Washington D.C. 358 pp.