

Mountain Lion

Puma concolor

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NOMENCLATURE

COMMON NAMES. Mountain lion, puma, panther, catamount, and cougar
SCIENTIFIC NAME. *Puma concolor*

TAXONOMY

Mountain lions have a complicated taxonomic history. Numerous subspecies have been described, largely based on morphometric differences. For example, Young and Goldman (1946) listed a total of 30 subspecies, and Culver et al. (2000) noted that 32 named subspecies existed. Of those listed by Young and Goldman (1946), at least 13 occurred in Canada or the United States (and adjacent Mexico); the remainder had geographic distributions restricted to Mexico, Central America, or South America.

The mountain lion was first described from a specimen collected in Brazil (Marcgrave 1648); Linnaeus reclassified the mountain lion as *Felis concolor* in 1771. Jardine (1834) placed the species in the genus *Puma*, where it remains (Wozencraft 1993). The historical taxonomy of the mountain lion was reviewed in detail by Young and Goldman (1946) and Currier (1983).

Based on molecular and morphological investigations, the mountain lion is thought to have evolved from an ancestor in common with the cheetah (*Acinonyx jubatus*) and jaguarundi (*Herpailurus yagouaroundi*) (Van Valkenburgh et al. 1990; Janczewski et al. 1995; Johnson and O'Brien 1997; Pecon-Slattery and O'Brien 1998). Mountain lions are represented in the North American fossil record dating back 300,000 years (Turner 1997). Based on an extensive analysis of mitochondrial DNA haplotypes and microsatellite alleles from throughout the geographic range of *Puma concolor*, Culver et al. (2000) speculated that a mass extinction during the Pleistocene (Martin 1989), which eliminated the majority of large mammals in North America, was followed by a colonization of mountain lions of South American stock. Furthermore, Culver et al. (2000) concluded that mountain lions (north of Nicaragua) today represent a single subspecies, *Puma concolor cougar*, in lieu of the 15 that formerly were recognized. Five other subspecies of *Puma concolor* are recognized throughout their southern range (Culver et al. 2000).

DESCRIPTION

Although the sexes are similar in appearance, male and female mountain lions are dimorphic in size. Gay and Best (1995) examined specimens from throughout the range of mountain lions and reported that males were significantly larger than females in 14 cranial and 5 mandibular measurements. In California, mean body weight of adult (≥ 2 years of age) males was $\bar{X} = 53.4$ kg (± 8.5 kg [*SD*]). Adult females weighed 30–40% less ($\bar{X} = 35.8 \pm 7.7$ kg) (Charlton et al. 1998). Based on a sample of 1076 specimens from Oregon, Kohlmann and Green (1999) reported that males averaged about 50% heavier than females of equivalent age. Gay and Best (1995) found no evidence that sexual dimorphism among mountain lions varied geographically. Data compiled by Anderson (1983) show that similar degrees of sexual size dimorphism occur

among mountain lions throughout their range. Although the degree of sexual dimorphism did not vary geographically, the size of mountain lions generally increased with an increase in latitude (Kurten 1973; Iriarte et al. 1990).

The dorsal pelage of a mountain lion is tawny, and they generally are white on the ventral surface (Fig. 37.1). Slight variation in color is common, and their coats can have reddish, yellowish, or grayish tinges. There are no obvious contrasting markings on the coats of adult lions, other than black markings at the base of the vibrissae on the muzzle, on the dorsal surface of the ears, and on the tip of the tail. In Latin, the specific epithet *concolor* means "single color."

In contrast to adults, young mountain lions have darker facial markings and are heavily spotted at birth (Fig. 37.2), but that pattern fades as kittens mature. The spotted pelage of kittens becomes less obvious at about 9 months of age. By the time young are approximately 2 years old, the spotting has largely disappeared (Russell 1978). The eyes are closed at birth, but open by 2 weeks of age (Young and Goldman 1946). Logan and Sweanor (1999) reported that the light blue eye color of kittens changes to the amber color typical of adults when kittens are as young as 5 months.

Despite the large difference in body weight typical of adult males and females, distinguishing the sexes from a distance can be difficult. Unless males are in an older age category, with well-developed shoulder, neck, and facial musculature, body conformation of young adult males can be confused with that of older adult females. Genders can be distinguished by observing the genitalia, but male lions frequently are misclassified as females, even by professional wildlife biologists and law enforcement personnel, because the scrotum and penis are not obvious to the untrained observer. Dark coloration is associated with hair surrounding the penis sheath of males, and is an important clue to the gender of lions (Logan and Sweanor 1999).



FIGURE 37.1. Adult mountain lion (*Puma concolor*). SOURCE: Photo by Becky M. Pierce.



FIGURE 37.2. Three-week-old mountain lion (*Puma concolor*) kittens in the birth nursery. SOURCE: Photo by Becky M. Pierce.

As with all felids, except cheetahs, mountain lions have retractable claws (Fig. 37.3) at the terminus of each digit. These claws function primarily to grasp prey, rather than as an aid in locomotion (Dixon 1982). The rostrum of felids is short and the orbits are large (Fig. 37.4) compared to those of canids. These skull adaptations allow for a more powerful bite, and felids are more dependent on sight than are canids to detect prey (Vaughan et al. 2000). The adult dental formula is I 3/3, C 1/1, P 3/2, M 1/1.

DISTRIBUTION

Although they occur at low densities, mountain lions are the most abundant large felid occupying North America and are second in size only to the jaguar (*Felis onca*) (Russell 1978). Historically, mountain lion distribution encompassed most of the western hemisphere (Young and Goldman 1946). They occurred from the Atlantic to the Pacific oceans and from approximately 50° N to 50° S latitude, and from near sea level to about 4000 m elevation (Young and Goldman 1946). In essence, mountain lions ranged from approximately the Cassiar Range of northern British Columbia to southern Chile and Argentina, and from ocean to ocean on the continents of North and South America.

In North America, the distribution of mountain lions has been reduced by as much as two thirds of its historical range (Fig. 37.5), largely because of conflicts with humans as settlers migrated westward (Ross et al. 1997). Currently, mountain lions occur in suitable habitat throughout Mexico, in the majority of the western United States, and in western Canada; a small population also occurs in southern Florida

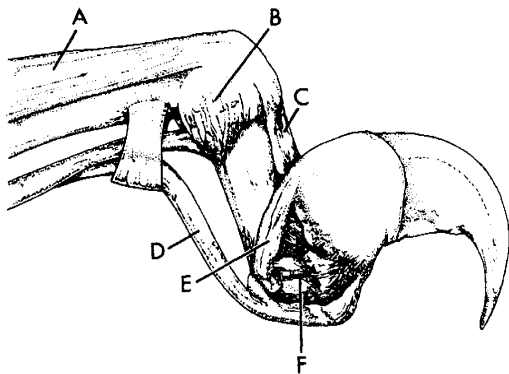


FIGURE 37.3. Retractable claw mechanism of the mountain lion (*Puma concolor*). A, Extensor expansion; B, middle interphalangeal joint; C, extensor tendon; D, flexor digitorum profundus tendon; E, lateral dorsal elastic ligament; F, distal interphalangeal joint. SOURCE: Adapted from Gonyea and Ashworth (1975).

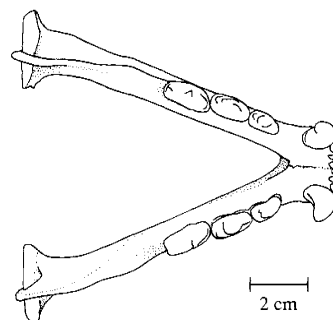
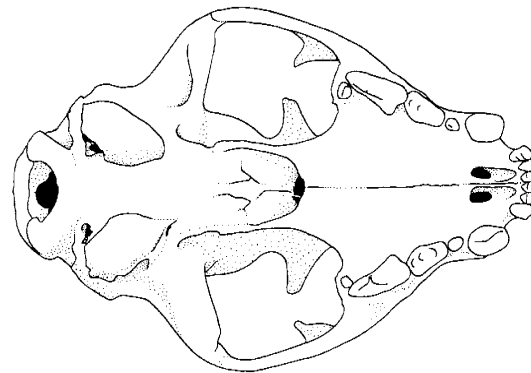
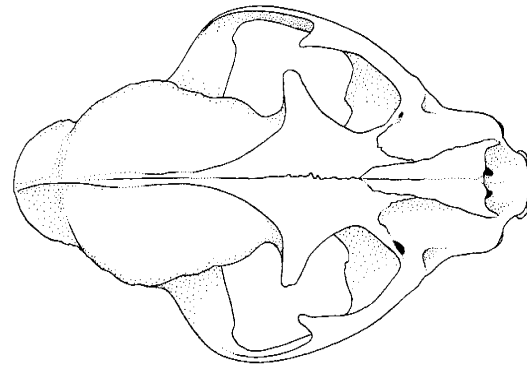
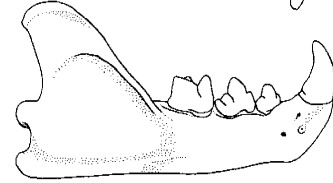
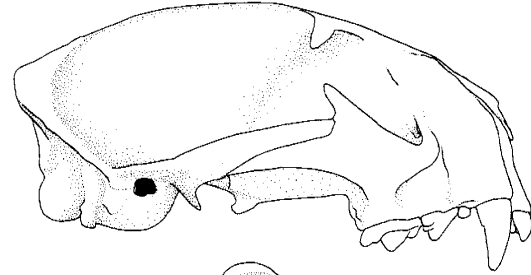


FIGURE 37.4. Skull of the mountain lion (*Puma concolor*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

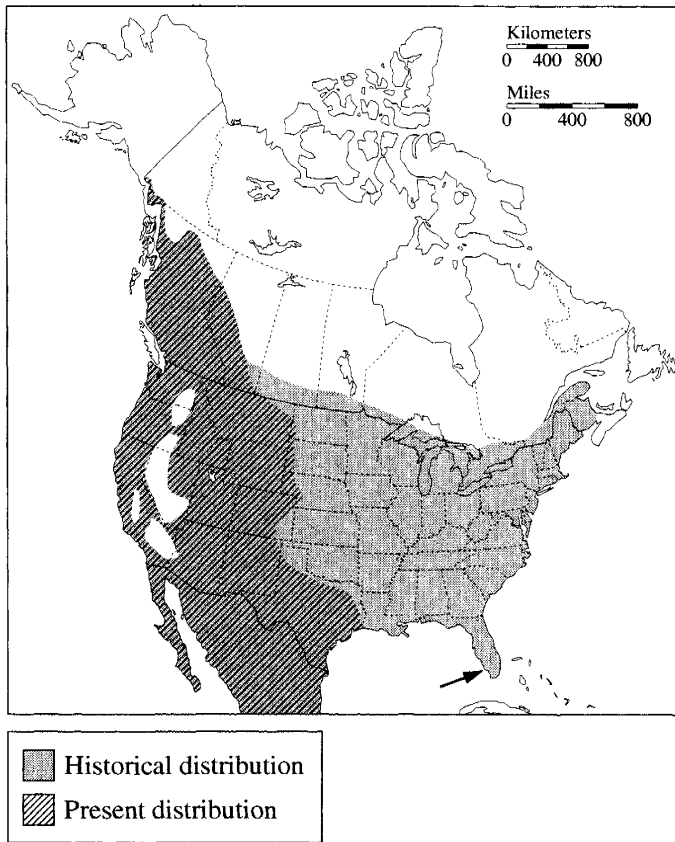


FIGURE 37.5. Past and present distribution of the mountain lion (*Puma concolor*).

(Fig. 37.5). Recently, mountain lions have been observed in southeastern Alaska and southwestern Minnesota (Nowell and Jackson 1996), and they inhabit western North Dakota (Jensen 2001) and Nebraska (Genoways and Freeman 1996) and are thought to be colonizing previously occupied habitat in Oklahoma (Pike et al. 1997). Recent evidence of a mountain lion in New Brunswick, Canada, was indisputable, but it could not be ascertained whether the animal had escaped from captivity (Cumberland and Dempsey 1994). The persistence of mountain lions in the maritime regions of Canada and the United States remains speculative (Hansen 1992). Anderson (1983) provided a detailed compilation of distributional records for mountain lions in the United States and Canada.

PHYSIOLOGY

There has been a paucity of information on blood parameters for free-ranging mountain lions. Anderson et al. (1992) sought to rectify this by providing hematological and biochemical reference values for ≤ 7 adult mountain lions from Colorado. Prior to that, information was limited to reports by Currier and Russell (1982) or Hawkey and Hart (1986). Paul-Murphy et al. (1994) provided serum biochemical reference ranges for 19 free-ranging mountain lions from throughout California, and concluded that the values were similar to those in domestic cats and captive exotic felids. Dunbar et al. (1997) described hematological and serum biochemical values for mountain lions from Florida. Most values were consistent with those established for mountain lions in Colorado (Currier and Russell 1982) and California (Paul-Murphy et al. 1994), but some differences were apparent (Table 37.1).

Dunbar et al. (1997) attributed higher packed cell volume, hemoglobin, and red blood cell values reported by Currier and Russell (1982) to the higher elevations in Colorado than in Florida. They also reported higher values for these three parameters within one "population" of

Florida panthers compared to a nearby "population," and speculated that differences could be a result of generalized differences in health and nutritional status between the two groups. It may prove useful for mountain lion researchers to examine hematological and serological data from their study animals, given differences reported within localized areas as well as among widely separated populations (Dunbar et al. 1997). For example, mountain lions that use high-elevation passes to follow migratory prey (Pierce et al. 1999b) may exhibit differences that are not evident in mountain lions from the same population(s) that do not use high-elevation habitats. Further, data on hematological and serological parameters may reflect the general health status of mountain lions existing under different nutritional regimes (e.g., abundant vs. uncommon primary prey) that may occur as lion populations fluctuate with populations of mule deer (*Odocoileus hemionus*).

Mountain lions, like most cats, are well adapted to approaching prey closely and then rushing forward quickly to subdue their intended target (Guggisberg 1975). As such, they are not adapted to running long distances. Harlow et al. (1992) investigated the effects of pursuit on mountain lions. Animals responded physiologically to stresses experienced during pursuit by a depression in adrenal responsiveness. They suggested that frequent pursuit could result in deleterious physiological changes and urged caution by wildlife agencies in setting pursuit seasons until more information becomes available.

BEHAVIOR

Activity Patterns. Most felids are nocturnal predators (Kitchener 1991), and mountain lions are most active during crepuscular periods (Ackerman 1982; Hopkins 1989; Sweanor 1990). That pattern appears to shift to a more nocturnal pattern for mountain lions in the proximity of human disturbance (Van Dyke et al. 1986). Mountain lions will

TABLE 37.1. Blood serum biochemical values for free-ranging mountain lions from California ($n = 19$) and Florida ($88 \leq n \leq 94$)

Parameter	Units	Location ($\bar{X} \pm SD$)	
		California	Florida
Albumin	g/dl	3.13 ^a \pm 0.32 ^b	3.70 \pm 0.36
Alanine aminotransferase	IU/L	58.8 \pm 16.7	60.2 \pm 35.0
Alkaline phosphatase	IU/L	22.6 \pm 11.3	35.4 \pm 38.6
Aspartate aminotransferase	IU/L	—	73.4 \pm 77.8
Calcium	mg/dl	9.53 \pm 0.66	9.92 \pm 0.66
Carbon dioxide	mEq/L	12.53 \pm 1.75	14.33 \pm 4.00
Cholesterol	mg/dl	155.1 \pm 29.9	147.9 \pm 26.7
Chloride	mEq/L	—	115.5 \pm 4.3
Creatine phosphokinase	IU/L	—	515.6 \pm 415.1
Creatinine	mg/dl	2.05 \pm 0.45	1.84 \pm 0.54
Gamma glutamine transferase	IU/L	—	1.6 \pm 1.4
Globulin	g/dl	3.45 \pm 0.41	—
Glucose	mg/dl	110.6 \pm 37.3	154.4 \pm 51.0
Inorganic phosphorus	mg/dl	5.66 \pm 1.15	5.77 \pm 1.51
Iron	μ g/dl	—	65.1 \pm 33.5
Lactate dehydrogenase	IU/L	—	269.7 \pm 173.2
Potassium	mEq/L	—	4.60 \pm 0.48
Sodium	mEq/L	—	152.6 \pm 3.4
Total bilirubin	mg/dl	0.30 \pm 0.25	0.26 \pm 0.61
Total protein	g/dl	6.58 \pm 0.67	7.35 \pm 0.67
Triglycerides	mg/dl	—	54.9 \pm 103.4
Urea nitrogen	mg/dl	32.9 \pm 6.4	37.7 \pm 14.1
Uric acid	mg/dl	—	0.55 \pm 0.59

SOURCE: Data have been adapted from Paul-Murphy et al. (1994) and are reported directly from Dunbar et al. (1997).

^aThe number of digits to the right of the decimal point has been reduced, by rounding, for consistency with the data reported by Dunbar et al. (1997) for mountain lions from Florida.

^bPaul-Murphy et al. (1994) reported means and two standard deviations for serum biochemistry values. Standard deviations reported here were calculated by halving, and rounding as appropriate, data from Paul-Murphy et al. (1994) for mountain lions from California.

repeatedly move and wait in ambush during the night when hunting (Beier et al. 1995), but that behavior is suspended when cached prey is available (Beier et al. 1995; Pierce et al. 1998). Movement to prey caches at night occurs earlier for females with small young than for other social categories of mountain lions (Pierce et al. 1998). That behavior could be a strategy to avoid adult males, a response to greater energetic needs of the mother, or a tendency to kill prey closer to the daytime resting location of the young. Female mountain lions without young cover more area and make longer movements than females with young (Sweaner 1990). Males make the longest movements (Sweaner 1990; Beier et al. 1995), cover the greatest area (Seidensticker et al. 1973; Logan et al. 1986a; Pierce et al. 1998), and are more likely to leave a prey cache before it is completely consumed (Ross 1994). The more extensive movements of males likely are necessary to monitor as many females as possible and result in large home ranges.

Adult mountain lions spend a majority of time resting during a diel cycle (Beier et al. 1995). The long periods of rest exhibited by most felids may reduce energy expenditure for a species that often kills prey as large as or larger than itself and frequently has prey caches available. Mountain lions will gorge when a large amount of food is available (Danvir and Lindzey 1981; Ross 1994) and move more frequently when they are unsuccessful at making a kill (Beier et al. 1995). Mountain lions also inhabit regions of extreme temperatures: resting may be the most efficient way to prevent overheating in desert environments or conserving fat stores in extremely cold climates. The negative relationship between mass-specific metabolic rate and body size likely influences the behavior patterns of large carnivores (Robbins 1993) and accounts for long periods of inactivity by mountain lions.

Communication. Mountain lions are the largest felid that make the low rumbling noise called a "purr." Purring, chirping, and whistling vocalizations have been described for adult females when they return to their offspring (Logan et al. 1996). Defensiveness and aggression are expressed by a suite of similar behaviors shared among felids (Kitchener 1991): ears layed down in a flattened position, growling, opening the mouth wide while making a hissing sound, tail twitching, and piloerection. Female mountain lions in estrus make a loud "caterwauling" vocalization to advertise their condition to males, and this behavior continues throughout any resulting mating association (Rabb 1959; Padley 1991; Beier et al. 1995; Logan et al. 1996).

Home range areas of mountain lions are marked by scrapes made by pawing the ground in a backward motion, drawing dirt and ground litter into a small pile behind two parallel grooves (Seidensticker et al. 1973). Males make scrapes more frequently than females (Cunningham et al. 1995), and scrapes often have feces or urine deposits associated with them (Smith 1981; Logan et al. 1996). Scrapes occur most frequently in locations where topography funnels a number of mountain lions into the same area (Smith 1981) and may facilitate mutual avoidance among individuals with overlapping home ranges (Hornocker 1969). Mountain lions display a Flehman response when smelling urine deposits in scrapes (Seidensticker et al. 1973). Females may scrape only when in estrus (Maehr 1997) and, if so, such scrapes may be used by males to monitor the reproductive cycles of females as well as home range occupancy. Mountain lions also scratch logs and trees repeatedly with their front claws. Scratch marks may serve the purpose of marking home range areas (Schaller 1972), but may simply be for sharpening claws (Seidensticker et al. 1973). In addition, felids have glands in the cheek, which often are rubbed against objects and family members as another means of communication (Macdonald 1985).

Hunting and Feeding. Mountain lions can jump vertically ≥ 3 m (Anderson 1983) and are capable tree climbers (Hornocker 1970). When pursued by canids, mountain lions may seek refuge in trees or rocks (Hornocker 1970; Seidensticker et al. 1973; Davis et al. 1996). Most reports of mountain lions ambushing prey have described them stalking from the ground (Koford 1946; Hornocker 1970; Wilson 1984; Beier et al. 1995) with very few instances of attacking prey from an elevated perch (Connolly 1949). The effect of hunting by humans on the behavior of mountain lions is unknown. Pursuit of mountain lions with

hounds for research does not appear to cause changes in home range use or abandonment of prey caches in most instances (Seidensticker et al. 1973; Maehr 1997; Pierce et al. 1998, 1999b). Mountain lions remain close to human activity directly after being pursued, captured, and then released for research purposes (Seidensticker et al. 1973; Beier et al. 1995). However, they also may avoid areas where they are repeatedly harassed (Hebert and Lay 1997; Janis and Clark 2002).

Mountain lions move quietly and low to the ground when hunting and stalking prey (Koford 1946; Wilson 1984; Bank and Franklin 1998). Ears also may be lowered to reduce detection while they move slowly and deliberately, frequently freezing in position while waiting to approach closely enough to ambush the intended prey (Leyhausen 1979). When prey is within a suitable distance, they rush at the target. Pursuit of prey by mountain lions is relatively short compared to the long chases of coursing predators, such as wolves (*Canis lupus*). If prey is caught, it usually is attacked at or near the neck. When attacking ungulates, mountain lions most frequently grip the anterior ventral portion of the neck, delivering a crushing bite to the trachea and causing suffocation (Kitchener 1991). The dorsal portion of the neck also may be bitten, and the spinal cord can be severed. After killing prey, it is usual for mountain lions to open the body cavity of the carcass and remove the digestive tract (Hornocker 1970). Other internal organs including the heart, liver, and lungs often are consumed first (Danvir and Lindzey 1981). Gorging on the most nutritious tissues during the first day may be an important strategy for mountain lions that can lose food to scavengers (Danvir and Lindzey 1981) or need to move to locate mates (Ross 1994).

In an examination of hunter-killed mountain lions, Robinette et al. (1959) reported that 30% had empty stomachs. Mountain lions may consume >10 kg of meat during a single feeding (Hornocker 1970; Danvir and Lindzey 1981; Ackerman et al. 1986), with more being consumed during the first day than on consecutive days following the kill (Danvir and Lindzey 1981). Results of field sampling and trials with captive animals suggest that mountain lions consume an average of 4.4 kg of meat/day (Danvir and Lindzey 1981; Ackerman et al. 1986). In most instances, prey carcasses are dragged, sometimes >200 m, to locations with vegetative or topographic cover (Beier et al. 1995). When lions finish feeding, they usually conceal the prey by covering it with sticks, grass, and other material until the carcass is consumed or abandoned. Mountain lions normally consume 73–79% of a deer carcass (Danvir and Lindzey 1981; Ackerman 1982). Covering caches may slow decomposition of the meat and hide it from scavengers (Beier et al. 1995). Prey caches may be guarded to protect them from scavengers, but mountain lions can use day-beds several kilometers from kill sites, returning only at night to feed (Beier et al. 1995; Pierce et al. 1998, 2000b).

REPRODUCTION

Mountain lions are polygynous and males do not contribute to rearing young. Like all felids, except African lions (*Panthera leo*), adult mountain lions are solitary except when raising young, dispersing with siblings, or mating. Males tend to have relatively large home ranges, which overlap with those of more than one female (Seidensticker et al. 1973; Logan et al. 1986a; Pierce et al. 1999b, 2000b). Male and female mountain lions likely rely on auditory and olfactory signals to locate each other for mating (Currier 1983) (see Behavior).

Estrous cycles in females with overlapping home ranges may be synchronous (Padley 1990). Associations for mating generally last 2–5 days (Beier et al. 1995), during which time the pair may copulate up to 70 times a day (Eaton 1976). Female estrous cycles last approximately 8 days (Rabb 1959; Eaton and Vclander 1977) and gestation is 82–96 days (Young and Goldman 1946; Anderson 1983; Currier 1983). Mountain lions may reproduce during any season (Robinette et al. 1961; Ashman et al. 1983), but many studies have identified seasonal birth pulses (Robinette et al. 1961; Ashman et al. 1983; Barnhurst and Lindzey 1984; Logan et al. 1986a; Ross 1994). Timing of reproduction in mountain lions may be affected by climate or prey abundance (Logan et al. 1996; Pierce et al. 2000a).

Females have eight teats, but only six produce milk (Lechleitner 1969). The number of kittens born per litter typically ranges from two to four (Robinette et al. 1961; Ashman et al. 1983; Ross and Jalkotzy 1992; Logan et al. 1996), but this may vary with prey availability, demography, and population density. Females may average more offspring per litter during their first year of reproduction and fewer toward the end of their lives (Logan et al. 1996). Most studies of mountain lions have reported an equal sex ratio among young (Donaldson 1975; Anderson et al. 1992; Logan et al. 1996). Padley (1991), however, reported that for a population of mountain lions in California, with 12 adult females and seven litters, six of seven kittens whose sex he was able to determine were male. In that population, adult males were scarce, and estrous females were unable to locate an adult male with which to mate for almost a year.

Kittens are brought to kill sites by their mother as early as 8 weeks of age, but are not weaned until they are 2–3 months old. Canine teeth first appear between 20 and 30 days and molars at about 40 days of age. Some permanent teeth erupt at 5–6 months of age and permanent canines appear during the eighth month, when primary and permanent canines are present. At weaning, kittens may weigh 3–4 kg (Currier 1983) with little variation in weight between the sexes until about 30 weeks of age (Robinette et al. 1961).

Mountain lion dens generally are located in rocky terrain (Logan et al. 1996) or thick vegetation (Beier et al. 1995; Bleich et al. 1996). Dens are not elaborate, but do provide hiding cover (Ross 1994; Beier et al. 1995) and thermal benefits (Bleich et al. 1996). Females with kittens have restricted movement patterns until the young are old enough to travel away from the den (Beier et al. 1995). A mother may move her young to several different dens before they are weaned (Shaw 1989).

ECOLOGY

Habitat. The broad distribution of mountain lions attests to their ability to adapt to a wide variety of habitats. Because of their wide distribution (see Fig. 37.5), defining preferred habitat for mountain lions is limited to general characteristics specific to distinct regions, and tremendous variation occurs among populations. Despite the large range of habitats used by mountain lions, relatively few quantitative studies of habitat selection exist; many studies present descriptive information without reference to habitat availability. For those studies that quantified habitat selection, prey availability, vegetation, and topography are the general characteristics that determine suitability for mountain lions. Within regions where a variety of habitat types occurs, structure of the vegetation and topography appear to be the most important criteria for determining habitat use (Lindzey 1987).

Most studies of habitat selection for mountain lions in western North America suggest that vegetative and topographic cover, in addition to steep slopes and higher elevations, are preferred resting, hunting, and denning sites, whereas open agricultural lands, sagebrush (*Artemisia tridentata*) grasslands, and open meadows and pastures are avoided (Murphy 1983; Logan and Irwin 1985; Laing 1988; Lindzey et al. 1989). Ashman et al. (1983) suggested that thermal characteristics cause mountain lions to select north-facing slopes at high elevations, with more vegetation and cooler temperatures, in the summer. South-facing slopes with little snow cover were selected in winter. Those habitats were strongly correlated with the density of deer. Rugged or steep terrain, with adequate vegetative cover, may be critical for stalking and catching prey (Ashman et al. 1983; Logan and Irwin 1985; Laing 1988) or for providing hiding cover and protection from thermal extremes for young at denning sites (Belden et al. 1988; Ross 1994; Bleich et al. 1996).

Dense hiding cover is preferred by mountain lions for hunting (Russell 1978; Beier et al. 1995). Indeed, mountain lions were more successful hunting pronghorn (*Antilocapra americana*) that inhabited rugged terrain with more vegetation than pronghorn that occurred in open prairie habitat (Ockenfels 1994). Mountain lions, however, can inhabit open or sparsely vegetated habitats, such as the plateaus of

Patagonia (Wilson 1984; Bank and Franklin 1998) and the deserts of the southwestern United States (Cunningham et al. 1995; Logan and Sweaner 2001), by successfully using the limited available cover to catch prey. In addition, Pierce (1999) noted that mountain lions were more successful killing mule deer in relatively open habitat compared to that in which deer foraged. The pursuit of deer by mountain lions likely began in areas with vegetative cover, but deer that fled into more open areas without obstacles during the chase were more likely to be caught than those that remained in heavier vegetation.

Mountain lions can thrive in extremely dry climates with limited rainfall (Shaw et al. 1987; Cunningham et al. 1995; Logan et al. 1996; Pierce et al. 2000a); however, the severely cold temperatures of northern Canada and Alaska may limit their distribution despite the availability of ungulate prey. Mountain lions may avoid human disturbance when possible (Van Dyke et al. 1986), but can persist near human development (Beier et al. 1995; Torres et al. 1996).

Laing (1988) suggested that habitat use by mountain lions did not differ significantly during a 24-hr cycle, but that pattern may depend on the availability of habitats. When habitat used by mountain lions for denning or for caching prey is different than that used for resting, then they will use different habitats during a diel cycle. Beier et al. (1995) reported that mountain lions with young hunted throughout the night, but returned to the den during the day. Den sites were located in nearly impenetrable vegetation. Pierce et al. (1998) found that mountain lions fed on cached prey primarily after sunset and often rested long distances from the cache site during the day. In addition, Beier et al. (1995) reported that, in some instances, mountain lions rested >4 km from their cached prey. This behavior also was consistent with the reported use of high-elevation cliffs during the daytime and use of lower elevations with flatter terrain for hunting deer at night (Pierce et al. 1998, 2000b).

Several studies have described seasonal changes in elevation and habitat use associated with changes in home range for mountain lions preying on migrating populations of deer and elk (*Cervus elaphus*) (Rasmussen 1941; Seidensticker et al. 1973; Ackerman 1982; Ashman et al. 1983; Murphy 1983; Anderson et al. 1992; Pierce et al. 1999b). Indeed, differences in forage availability associated with seasonal ranges of prey leads to potential differences in the tradeoff between foraging benefit and predation risk for deer and elk. Consequently, there may exist differences in the effects of mountain lion predation on the seasonal foraging behavior and habitat selection of those large ungulates (Pierce 1999).

Dispersal. Young remain with their mother for 12–18 months. Dispersal may result from the mother abandoning the young (Seidensticker et al. 1973), but it is likely that there is some aggression by the mother directed toward the young to prevent them from following her (Hansen 1992). Dispersal of young from the mother is coincident with the female coming into estrous; adult males will kill young (Young and Goldman 1946; Ackerman et al. 1984; Spreadbury 1989; Logan and Sweaner 2001). During the period of dispersal, mountain lions are often referred to as “transients” (Hornocker 1970). Transients, as opposed to “residents,” are individuals that do not have a defined home range area within a population.

Dispersal is a relatively risky period during the life cycle for many species (Baker 1978), and survivorship likely declines for mountain lions during the dispersal period (Logan and Sweaner 2001). Transients are more likely than resident mountain lions to be involved in depredation incidents or conflicts with humans, as they attempt to locate food without the advantage of an established home range (Torres et al. 1996). Males are more likely to disperse from their natal ranges than are females, and males tend to disperse further (Anderson et al. 1992; Sweaner et al. 2000).

Mountain lions can disperse nearly 500 km from their natal home range (Logan and Sweaner 1999). Consequently, mountain lion habitat throughout North America is considered almost contiguous on a large scale, with the exception of the isolated populations in southeastern Florida. Nevertheless, mountain lion populations can be isolated by

residential development or geographic features such as desert basins. Reduction in the size of habitat "islands" for populations of any species increases the chance of extirpation for that population (MacArthur and Wilson 1967).

Sweaner et al. (2000) described a metapopulation structure (Levins 1970) for mountain lions living in basin and range habitats of the Southwest. Mountain ranges provide islands of suitable habitat that support semi-isolated populations of mountain lions. Those populations are maintained through immigration by dispersers (primarily male) from other mountain ranges and recruits (primarily female) from within the population. The basins between the mountains are not considered suitable mountain lion habitat (Germaine et al. 2000) and act as barriers that may limit gene flow. Protecting source populations and habitat stepping stones may be exceptionally important in conserving subpopulations of mountain lions that exist in a metapopulation structure (Sweaner et al. 2000). Although concerns about habitat fragmentation and interruption of gene flow are legitimate, Ernest et al. (2003) have cautioned that it has not been demonstrated that mountain lions conform to the assumptions inherent in basic metapopulation models.

Survivorship of adults likely varies within most populations on an annual basis (Lindzey et al. 1988), but can be affected significantly by hunting (Anderson 1983). Destruction of habitat also can have large impacts on the demography of mountain lion populations. For example, fragmentation of habitat can inhibit dispersal and increase competition for resources (Beier et al. 1995; Maehr 1997). Furthermore, real estate development may limit prey populations, increase depredation events (Shaw 1980; Cunningham et al. 1995; Torres et al. 1996), and increase collisions with automobiles (Maehr 1997; Beier et al. 1995).

Disease and Parasites. Anderson (1983) suggested that the widely held opinion that mountain lions are relatively free of parasites and diseases reflected a lack of specific research rather than reality. For example, based on his literature review, Anderson (1983) reported the occurrence of feline panleukopenia virus was low, but Paul-Murphy et al. (1994) detected titers to the virus in nearly 100% of the animals that they tested. Furthermore, Adaska (1999) reported the first case of coccidioidomycosis detected in a mountain lion, and Jessup et al. (1993) documented the first occurrence of feline leukemia virus infection in a free-ranging mountain lion. Evermann et al. (1997) reported on the occurrence of puma lentivirus specifically in mountain lions in the state of Washington. Yamamoto et al. (1998) found overall seroprevalence of bartonellosis in 26 of 74 mountain lions they examined from California, among the first evidence of this condition detected in wild felids. Hence, it appears that Anderson's (1983) admonition was insightful.

Mountain lions potentially are susceptible to many infectious agents that affect domestic cats (Paul-Murphy et al. 1994) as well as to other diseases (summarized by Anderson 1983). Some of these, including feline panleukopenia virus, have the potential to affect morbidity and mortality (Paul-Murphy et al. 1994), may limit growth of wild populations (Anderson 1983), and have implications for the conservation and persistence of a viable population of the endangered Florida panther (Roelke et al. 1993). Foley (1997) concluded that epizootic diseases likely are not a primary threat to populations of mountain lions in the western United States. From a human health perspective, rabies has been detected among mountain lions (Storer 1923) and should be of concern in all cases involving attacks on humans (Kadesky et al. 1998).

Parasitic infections among mountain lions are not uncommon; Anderson (1983) listed ≥ 40 species of parasites that have been collected. Forrester et al. (1985) and Waid (1990) listed additional internal parasites not noted by Anderson (1983). The majority of parasites recorded have been internal (protozoans, trematodes, cestodes, or nematodes), but mites, ticks, and insects are known to parasitize mountain lions. Pence et al. (1987) noted a high degree of overdispersion (i.e., a few mountain lions harbored the majority of parasites collected and most had few or no parasites) in helminth species collected from the viscera of mountain lions in Texas. In general, mountain lions have been described as remarkably free of external parasites (Currier 1983), but our experience has been that ticks are commonly encountered during handling.

FEEDING HABITS

Mountain lions kill and eat vertebrate prey almost exclusively (Lindzey 1987). Vegetation often is ingested because it adhered to a carcass or to help with passage of parasites and hair from the gut (Robinette et al. 1959; Anderson 1983). The historical distribution of mountain lions throughout North America coincided with the distribution of their primary prey—deer. Most studies in North America identified deer as the most frequent prey in diets of mountain lions (Hornocker 1970; Shaw 1980; Ackerman 1982; Logan et al. 1996; Ross et al. 1997; Pierce et al. 2000a).

Despite the congruence of deer and mountain lion distributions in North America, lions are generalist predators (Anderson et al. 1992; Logan and Sweaner 1999). They do prey on other large ungulates including moose (*Alces alces*; Ross and Jalkotzy 1996), elk (Hornocker 1970), feral horses (*Equus caballus*; Turner et al. 1992), feral pigs (*Sus scrofa*; Harveson 1997; Sweitzer 1998), and wild sheep (*Ovis canadensis*; Cronmiller 1948; Harrison 1990; Wehausen 1996; Ross et al. 1997; Schaefer et al. 2000). Mountain lions also feed on smaller prey such as lagomorphs (Shaw 1980; Ackerman et al. 1984); ground squirrels (*Spermophilus* spp.; Seidensticker et al. 1973); beavers (*Castor canadensis*; Padley 1991); porcupines (*Erethizon dorsatum*; Sweitzer et al. 1997); small carnivores including raccoons (*Procyon lotor*), gray foxes (*Urocyon cinereoargenteus*), and skunks (Cashman et al. 1992; Beier et al. 1995); and birds such as wild turkeys (*Meleagris gallopavo*), grouse, and quail (Ashman et al. 1983; Ackerman et al. 1986; Maehr et al. 1990). Currier (1983) listed 41 nondomestic species of vertebrates identified in the feces of mountain lions from North and South America. Domestic sheep, goats, cattle, horses, dogs, and cats also are consumed when populations of mountain lions are in proximity to livestock operations or areas of human habitation (Shaw 1980; Torres et al. 1996). Attacks on humans by mountain lions are rare (Beier 1991); however, in most instances, victims of fatal attacks were treated as prey and either dragged to cover or partially consumed (Beier 1991; J. Banks, California Department of Fish and Game, pers. commun., 1996). Remains of bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and other competing carnivores occasionally occur in feces of mountain lions. Also, species that scavenge on lion kills, including eagles and turkey vultures (*Cathartes aura*), can be killed by mountain lions guarding a prey cache. Although intraspecific aggression leading to death in mountain lions may occur as a result of competition for resources or mating opportunities (Robinette et al. 1961; Hornocker 1970; Sweaner 1990; Pierce et al. 1998), instances of cannibalism by mountain lions, in which the carcass has been largely consumed, have been reported frequently (Lesowski 1963; Donaldson 1975; Ackerman et al. 1984; Spreadbury 1989).

Selection of Prey. Numerous authors have described the sex, age class, and condition of prey killed by mountain lions. Hornocker (1970), Spalding and Lesowski (1971), Shaw (1977), Ackerman (1982), Ackerman et al. (1984), and Murphy (1998) all suggested that vulnerability of individual prey may be the most important factor in their selection by mountain lions. Those investigations identified individuals in younger or older age classes or in poorer condition as being selected by mountain lions. Among adult deer and bighorn sheep, mountain lions also may prey on males selectively (Hornocker 1970; Ackerman 1982; Harrison 1990), especially when males are in a weakened condition following the rut (Robinette et al. 1959; Shaw 1977; Harrison 1990) or during drought conditions (Logan and Sweaner 2001). Studies of prey selection, however, require comparisons with availability of prey. Most studies of prey selection by mountain lions have been limited by lack of information on availability of prey or by biases in detecting prey.

Anderson (1983) attempted to compare sex and age ratios of deer killed by mountain lions to the estimated ratios in the populations of deer for six study areas, and concluded that the sampling methods used in those studies prevented clear testing of any hypothesis regarding prey selection. Since then, Ross et al. (1997) reported selection for young bighorn sheep by mountain lions. Pierce et al. (2000a) reported that mountain lions selected deer in young and old age classes, and that females were selected among adult deer. Preference for females among

adult mule deer also has been reported for other populations of mountain lions (Bleich and Taylor 1998). More recent investigations suggested that mountain lions do not select prey in poor condition (Kunkel et al. 1999; Pierce et al. 2000a); however, bone marrow fat has been the primary index used to determine prey condition by most investigators. Although percentage bone marrow fat was not related to prey selection by mountain lions (Kunkel et al. 1999; Pierce et al. 2000a), they selected for older animals. Thus, percentage marrow fat may not adequately reflect other forms of weakness detected by mountain lions (Pierce et al. 2000a).

Kunkel et al. (1999) determined that mountain lions killed deer with shorter diastemae than those killed by wolves or hunters, but values of marrow fat did not differ between deer killed by mountain lions and wolves. Size of prey also appears to affect selection by mountain lions. They selected deer over elk, and elk over moose in Montana (Kunkel et al. 1999). Ross and Jalkotzy (1996) reported that male mountain lions were more likely to kill moose than were females. Body size, however, did not appear to be important for selection of mule deer preyed on by mountain lions when compared with those killed by coyotes during winter, when young deer were unavailable (Pierce et al. 2000a).

Sex and age of mountain lions likely affect their diet. Solitary mountain lions may be more likely to eat smaller prey than do females with kittens (Ackerman 1982). Ackerman suggested that killing large prey to provide for their offspring would be a necessary strategy for mothers, and that populations of mountain lions could not exist in areas devoid of large ungulate prey. Pierce et al. (2000a), however, reported that female mountain lions with kittens (≤ 6 months old) were significantly more likely to kill young deer (< 1 year of age) than were single adult females or males. Birth pulses of mountain lion populations often coincide with the birth pulse of their primary prey (Logan and Sweanor 2001; Pierce et al. 2000a), suggesting that timing of reproduction in mountain lions may be dependent on the availability of vulnerable, young prey. Adult females that are lactating may not be able to fast for extended periods between unsuccessful attempts to catch larger prey (Pierce et al. 2000a).

Latitude correlates strongly with size of prey selected by mountain lions (Iriarte et al. 1990; Maehr et al. 1990). In temperate zones, they tend to kill larger ungulates, whereas mountain lions in tropical environments have a higher frequency of small prey in their diet. The complicating effect, however, of competition with the jaguar on this pattern of latitudinal prey variation is unknown. Additionally, variation in prey selection is notable for some populations of mountain lions as vulnerability or availability of prey changes. During the wet season in coastal California, mountain lions increased predation rates on feral

pigs (Craig 1986) and, in Utah, they killed twice as many black-tailed jackrabbits (*Lepus californicus*) during winter (Ackerman et al. 1984) than during summer. Adult male deer may be taken at a higher rate during winter when they are in weakened condition from the rut (Robinette et al. 1959; Shaw 1977). The vulnerability of newborn calves results in high depredation rates on cattle in Arizona (Shaw 1977; Cunningham et al. 1995).

POPULATION DENSITY AND DYNAMICS

Mountain lions coexist in a system of individual home ranges with varying amounts of overlap (Seidensticker et al. 1973; Hemker et al. 1984). Mean home range size and distribution of mountain lions can be affected by sex (Seidensticker et al. 1973) or availability of resources such as prey (Pierce et al. 1999b, 2000a). Anderson et al. (1992), however, concluded there was no relationship between prey density and frequency of use by mountain lions of areas inhabited by deer and elk. They felt that other factors, such as suitable habitat for hunting, may affect prey availability independently of prey density (Kruuk 1986) and may ultimately affect the home range size necessary for mountain lions to be successful.

Home ranges of mountain lions are delineated by visual and olfactory marking behaviors, and adult males tend to have larger home ranges than females (Seidensticker et al. 1973; Logan et al. 1986a; Pierce et al. 1998) (Table 37.2) (see Behavior). Male home ranges often overlap those of several females but have limited overlap with those of other males (Seidensticker et al. 1973; Murphy 1983; Logan and Sweanor 2001), whereas the home ranges of adult females often overlap those of other females extensively (Seidensticker et al. 1973; Sweanor et al. 1996; Pierce et al. 1999b, 2000b; Logan and Sweanor 2001). Extensive overlap among male home ranges (Anderson et al. 1992; Sweanor 1990) and limited overlap of female home ranges (Harrison 1990) also have been reported. Additionally, mountain lions may avoid each other temporarily, a behavior termed "mutual avoidance" (Hornocker 1969), but no investigations have tested for the dominance reversal necessary to demonstrate true territoriality in mountain lions (Kitchen 1974).

Hornocker (1969, 1970) and Seidensticker et al. (1973) suggested that mountain lion populations were self regulating (see Predator-Prey Dynamics). They described social behaviors such as mutual avoidance, territorial marking, and cannibalism as mechanisms that limited densities of mountain lions. Transient mountain lions were unable to secure permanent home range areas unless the home range area of a resident adult became vacant. This pattern occurred independently of prey densities. Lindzey et al. (1994) also concluded that the density of a mountain

TABLE 37.2. Estimated home range size and average density of mountain lions from North American studies using the minimum convex polygon method (Mohr 1947)

Study	Location	Males		Females		Lions/100 km ²
		n	Range (km ²)	n	Range (km ²)	
Ross and Jalkotzy 1992	Alberta	6	334	21	140	1.9 (RA, H), 4.2 (T)
Cunningham et al. 1995	Arizona	5	196	2	109	— (H)
Beier and Barrett 1993	California	2	767	12	218	1.1 (RA)
Hopkins 1989	California	4	199	7	84	3.6 (T) ^a
Anderson et al. 1992	Colorado	6	256	7	309	1.1 (RA, H)
Maehr et al. 1991	Florida	8	558	10	191	—
Seidensticker et al. 1973	Idaho	1	453	3	233	0.6 (RA ^b , H)
Ashman et al. 1983	Nevada	7	574	6	178	— (H)
Logan et al. 1996	New Mexico	23	187	29	74	1.7 (RA)
Murphy 1983	Montana	2	462	5	202	7.1 (RA, H)
Pittman et al. 2000	Texas	6	349	5	206	0.4 (RA, H)
Pence et al. 1987	Texas	1	628	5	143	—
Hemker et al. 1984	Utah	1	826	4	685	0.4 (T)
Logan 1983	Wyoming	2	320	2	73	1.5 (RA, H), 3.9 (T)

NOTE: RA, Density of resident adults; T, density of total population; H, hunted population.

^aFrom Anderson et al. (1992), Table 23.

^bEstimated from Seidensticker et al. (1973), Table 6, Fig. 16.

lion population in Utah was independent of the density of their primary prey, mule deer, because the population of mountain lions did not increase at the rate predicted by the increase in prey. Nonetheless, the population of mountain lions did increase by one third after an increase in the deer population. Long time lags between fluctuations in prey populations and responses in mountain lion populations make determining the true relationship between predator and prey difficult (Schaller 1972), and emphasize the need for long-term research when working with large carnivores (Pierce 1999).

To invoke social regulation for a population (Hornocker 1969, 1970; Seidensticker et al. 1973), it must be demonstrated that the population is not limited by competition for resources (Watson and Moss 1970). Mutual avoidance does not prevent passive competition for resources. Pierce et al. (2000b) demonstrated that competition for prey by mountain lions occurred in a pattern that would be expected for nonterritorial species that do not exclude each other from prey resources. Furthermore, if mountain lions engaged in a territorial system that excluded individuals from resources beyond what would be expected for a population limited by competition, such costly behavior could have evolved only if it maximized reproduction for individuals that were territorial and, ultimately, would not lead to population limitation (McCullough 1979). Hemker et al. (1984) concluded that population size of mountain lions was primarily limited by the population of prey, a conclusion supported by Pierce et al. (2000b) and Logan and Sweanor (2001).

The density of males may be limited by intraspecific aggression to maximize access to females, but mountain lion populations on a whole likely are not limited by social behavior. In addition, dispersal by young mountain lions appears to be independent of population density (Seidensticker et al. 1973; Hemker et al. 1984; Ross and Jalkotzy 1992; Logan et al. 1996), and mountain lion population numbers parallel their prey populations (Lindzey et al. 1994; Logan et al. 1996; Cox and Stiver 1997) (Fig. 37.6). Furthermore, Logan and Sweanor (2001) reported a pattern of density-dependent growth for a mountain lion population, providing additional evidence that competition is an important factor affecting their population dynamics.

PREDATOR-PREY DYNAMICS

Few long-term studies of predator-prey dynamics have been conducted that include mountain lions. Unfortunately, many studies have

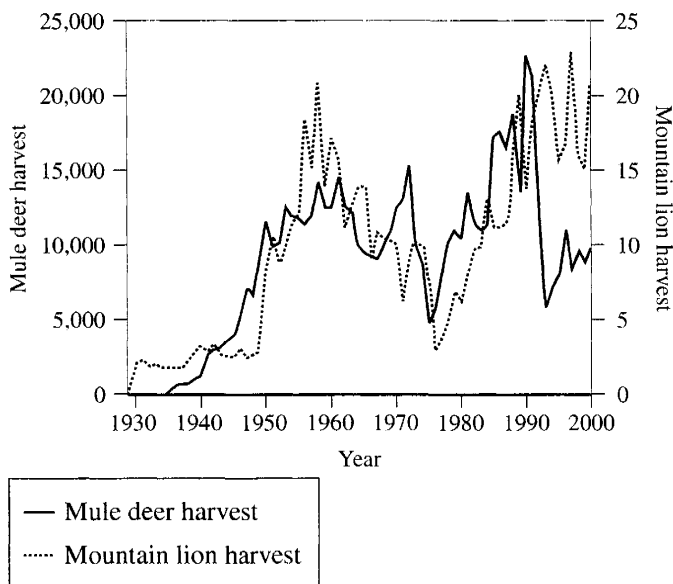


FIGURE 37.6. Harvest of mule deer (*Odocoileus hemionus*) and mountain lions (*Puma concolor*) in Nevada. Mule deer harvest shown includes males only. Mountain lion harvest shown includes depredation removals and sport hunting (sport hunting estimated to 1967). SOURCE: Data from S. Stiver, Nevada Department of Wildlife, pers. commun., 2001.

independently focused on either the predator or the prey, thereby limiting conclusions that can be drawn about interspecific effects (Pierce 1999). In most instances, viable populations of mountain lions are dependent on populations of large ungulate prey (Ackerman 1982; Anderson 1983). Most ungulates that are preyed on by mountain lions, including deer, elk, and moose, are affected by density-dependent processes (McCullough 1979; Boyce 1989; Bowyer et al. 1999; Keech et al. 2000). Therefore, determining the effect of predation by mountain lions on the population dynamics of their prey requires an understanding of those density-dependent processes and all factors potentially limiting the population including weather, resources, and other predators.

In the ecological systems that mountain lions inhabit, both exploitative and interference competition with other predators likely occur. Niches of wolves (Kunkel et al. 1999), coyotes (Pierce et al. 2000a; Harrison 1990), bears (Murphy 1998), bobcats (Koehler and Hornocker 1991), and jaguars (Iriarte et al. 1990) overlap extensively with that of mountain lions. Niche partitioning via habitat use and prey selection may allow for coexistence of mountain lions with those other carnivores. In some instances, scavenging of their food caches requires mountain lions to increase predation rates (Harrison 1990). In addition, mountain lions often kill smaller species of carnivores, such as bobcats, without feeding on them (Koehler and Hornocker 1991). Conversely, mountain lions have been killed by packs of wolves (White and Boyd 1989; Boyd and Neale 1992). Those observations also suggest that competition is an important factor affecting the predator-prey dynamics of multipredator systems that include mountain lions.

Mountain lions are an important limiting factor for some ungulate species (Hornocker 1970; Shaw 1980). Shaw (1980) estimated that lions annually removed 15–20% of the mule deer population on the Kaibab Plateau in Arizona. Anderson et al. (1992) estimated that mountain lions annually killed 8–12% of the mule deer population on the Uncompahgre Plateau, Colorado. In Alberta, a single mountain lion killed 8.7% ($n = 11$) of the early-winter bighorn sheep population and 26.1% ($n = 6$) of the young (Ross et al. 1997).

Mountain lion predation may reduce the severity of fluctuations in prey populations (Hornocker 1970) by slowing the growth rate and reducing overshoots of resource-based carrying capacity (K). Limitation and regulation, however, are distinctly different mechanisms. Limitation implies that the number of prey is reduced through decreased production or increased loss, and therefore any source of predation is limiting (Sinclair 1989; Boutin 1992). Limitation slows the increase of a population from the growth rate it would have achieved in the absence of the predator. However, if the prey population continues to increase, the proportion of prey removed by the predator is reduced. Consequently, prey populations limited by predators can continue to grow, although at a slower rate than in the absence of predation, until they reach K .

Regulation implies that rate of removal by the predator changes with the population of prey; as prey numbers increase, so does the rate at which predators kill prey. This phenomenon results from an increase in the number of predators (numerical response), the case with which they find and kill prey (functional response), or a combination of both (Holling 1959). Regulation by a predator eventually stops the increase of the prey population and causes a decline to lower densities, which ultimately results in lower predation rates. Such feedback mechanisms can cause a prey population to fluctuate between low- and high-density equilibria, both of which are below K . This multiple-equilibria scenario is frequently termed a "predator pit" (Haber 1977; Bergerud et al. 1983; Messier and Crete 1985). Functional responses of the predator may ultimately determine whether a species has the capacity to regulate a prey population (Messier 1994). Nonetheless, determining the functional response curve for a species requires an unbiased measure of predation rate throughout the range of population densities of the prey, and controlled removal studies are necessary to determine the conditions that may cause multiple equilibria (i.e., regulation) to occur in predator-prey systems (Van Ballenberghe and Ballard 1994).

Attempts to measure predation rates of mountain lions have been made for static populations of prey. Using an energetics model, Ackerman et al. (1986) estimated that adult male mountain lions would kill

a deer every 8–11 days, adult females would kill every 14–17 days, and a female with three juveniles would kill every 3.3 days. Connolly (1949) reported that an adult mountain lion killed one deer every 9.7 days. Predation rates on bighorn sheep and mule deer by females with kittens ranged from 0.7 to 2.1 ungulates/week (Harrison 1990). Beier et al. (1995) determined that mountain lions killed 48 large and 58 small mammals/year. Rate of predation by mountain lions can vary extensively (Ross and Jalkotzy 1996), and is dependent on a number of factors including the number and age of young (Ackerman et al. 1986), season (Pierce 1999), and extent of competition from other predators (Kunkel et al. 1999) or scavengers (Harrison 1990). Those studies give insight into the behavior of mountain lions and their possible effects on prey populations, but the question of whether mountain lions can independently regulate a prey population remains unanswered.

Mountain lions have been implicated as regulating a wild horse population (Turner et al. 1992), and are thought to have caused populations of porcupines to decline through predation (Sweitzer et al. 1997). In addition, some bighorn sheep populations may have declined due to avoidance of high-quality forage in response to predation risk by mountain lions (Wehausen 1996). In those instances, mule deer were the primary prey for mountain lions. Systems with multiple predators and multiple prey are more likely to be regulated by predation and to produce predator pits (Gasaway et al. 1992). Mule deer populations can keep mountain lion numbers high. If populations of alternative prey increase, mountain lions encounter those species more frequently and predation rates may increase, causing alternative prey to decline. Bleich et al. (1997) noted, however, that unless female mountain sheep were killed in significant proportions, predation by mountain lions probably is not an important factor in the population dynamics of those ungulates.

Several studies examining the population dynamics of deer and mountain lions suggest that mountain lions do not determine the ultimate size of deer populations. Instead, other factors (especially forage resources) appear to be more important determinants of deer populations. For example, Logan and Sweanor (2001) determined that mountain lions were not responsible for the decline of mule deer in New Mexico, but that a lack of forage resources because of drought was responsible. Pierce et al. (1999a) came to a similar conclusion for a population of mule deer in the eastern Sierra Nevada of California. In that study, mountain lion numbers declined precipitously as did the deer numbers, but with a lag of 8 years. Long time lags between changes in prey populations and responses in mountain lion populations increase the difficulty of determining the relationships between mountain lion populations and prey populations (Schaller 1972), and emphasize the need for long-term studies (Pierce 1999).

MANAGEMENT AND CONSERVATION

Management Techniques. Demographic information is difficult to obtain for populations of large, cryptic predators like mountain lions. Track surveys have been a traditional method of determining presence or absence of mountain lions as well as establishing estimates of relative abundance. Various investigators have attempted to distinguish among lions using track characteristics unique to individual animals (Currier et al. 1977; Fitzhugh and Gorenzel 1985; Van Dyke et al. 1986) or track measurements (Currier et al. 1977; Shaw 1983; Fitzhugh and Gorenzel 1985) to recognize individuals. None of these investigators believed it was reliable to distinguish among individual mountain lions using only tracks.

Smallwood and Fitzhugh (1993) used a sophisticated statistical technique (multiple group discriminant analysis) in an attempt to develop a method to discriminate among individual animals based on measurements and characteristics of tracks. However, Grigione et al. (1999) determined that Smallwood and Fitzhugh (1993) had used an inappropriate method. Based on additional analyses, they concluded it was unlikely that individual mountain lions could be detected using discriminant analysis. Furthermore, Grigione et al. (1999) concluded that the most commonly used measurement (width of heel pad) for distinguishing among mountain lions based on their tracks was also the least

variable, calling into question the utility of that measurement. Despite the problematic nature of discriminating among individual lions, Beier and Cunningham (1996) conducted several detailed analyses. They felt it is possible to detect changes in relative abundance of mountain lions using tracking techniques at the local level. Nonetheless, the migratory nature of some mountain lions makes it problematic to define populations (Pierce et al. 1999b), with serious implications for the use of track surveys for estimating changes in population size. Track surveys could be useful for estimating relative use of a specific geographic area by mountain lions, but inferences about population size over time are confounded because it is difficult to define an open population. The use of track surveys over large geographic scales to index relative abundance of mountain lions (Smallwood 1994; Smallwood and Fitzhugh 1995) has been attempted, but likely does not provide the power necessary to detect such changes.

Mountain lions frequently are captured to allow attachment of radiotransmitters. Capture techniques often involve the pursuit of animals with hounds, followed by chemical immobilization (Logan et al. 1986b; Jessup et al. 1986). Physical retrieval of immobilized animals (Hornocker 1970) is necessary if they are sedated in a location high above the ground. McCown et al. (1990) described a portable cushion that lessened the probability of injury to mountain lions falling from trees. Davis et al. (1996) developed a method to safely lower immobilized mountain lions from trees and cliffs. Foot snares have been used safely and successfully by some investigators (Logan et al. 1999; Pierce et al. 2000a), and are advantageous in some situations.

Radiotelemetry has been used extensively to determine the distribution of mountain lions in numerous studies, from which density estimates have been inferred. Capture and recapture methods also have been used to estimate population densities. Reliability of estimates obtained with those techniques is variable (Logan and Sweanor 1999), but densities have been estimated at 0.3–2.2 adult mountain lions/100 km². Pierce et al. (2000b) estimated the abundance of mountain lions by maintaining an intensive and constant effort to capture and radio-collar all lions detected on a mule deer winter range. They then used aerial telemetry to estimate the number of mountain lions present per aerial-telemetry day, and were able to determine their absolute abundance from year to year. Smallwood (1997) noted that most variation in densities of mountain lions can be attributed to the spatial extent of individual study areas, and suggested that field studies would be more meaningful if they spanned larger areas, a variety of land uses and habitats, and greater periods of time than most conventional studies.

Molecular techniques have been developed that allow investigators to identify individual mountain lions using DNA obtained from blood, tissue, or hair samples (Ernest 2000a, 2000b) and from feces (Ernest et al. 2000). These techniques depend on obtaining good-quality DNA, which is more difficult when using feces (Ernest 2000a). Fecal DNA has been used to identify individual lions occurring within certain geographic areas (Ernest et al. 2000) or associated with particular kill sites for large mammals (Hayes et al. 2000). Use of this technique to determine the absolute number of mountain lions occurring in a particular geographic area is subject to biases associated with their distribution and frequency in the area. Although it is possible to estimate minimum numbers of individuals present, the probability of detecting all individuals using molecular techniques is a function of sampling effort.

The literature is replete with estimates for home range sizes of mountain lions that have been determined using land-based or aerial telemetry. However, global positioning system (GPS) technology raises questions regarding previous studies. Bleich et al. (2000) described the results from GPS collars on two adult male mountain lions. Patterns of movement were vastly different and home ranges were much larger than were estimates from simultaneous aerial telemetry flights conducted on a weekly basis. Some GPS collars incorporate switches (Bleich et al. 2000) that have the potential to be useful in predicting mountain lion activity; Janis et al. (1999) described and quantified the use of traditional very high frequency transmitters equipped with tip switches to estimate activity of mountain lions.

Translocation of mountain lions as a technique for managing "problem" lions (i.e., animals that have preyed on livestock or that occupy areas adjacent to human habitation) is controversial and is inconsistent with management policies in some states because of potential liabilities. Generally, survival of translocated lions is very low. For example, Ruth et al. (1998) described an experiment in which 14 animals were moved and released different distances ($\bar{X} = 477$ km) from their locations of capture. Nine of those individuals died and, overall, survival was lower than that of reference animals that remained within their original home ranges (Ruth et al. 1998). They concluded that translocation was most successful when mountain lions were 12–27 months old. Translocation as a management technique for mountain lions is not widely implemented, but may become increasingly important as a result of changing attitudes toward predator control (Hancock 1980) and loss or fragmentation of habitat (Nowell and Jackson 1996).

Conservation. Conservation of a large carnivore that preys on other large mammals, frequently is involved in the killing of domestic livestock, and occasionally is a threat to human safety presents challenges that seem overwhelming in contemporary times. The primary prey of mountain lions require large tracts of open and undeveloped land, both of which are becoming increasingly uncommon. Mountain lions themselves similarly depend on large tracts of land to meet their needs. Indeed, the conservation and management challenge for the future will be to assure the presence of mountain lions and their prey, despite the certain loss of habitat and increases in human numbers and activity (Torres 1997).

In western North America, mountain lion populations generally remain healthy (Hornocker 1992), but conservationists will be faced with the task of maintaining large, contiguous tracts of suitable habitat that are linked to other such areas. Populations of mountain lions may occur in a metapopulation structure (Sweaner et al. 2000; but, see Ernest et al. 2003). Islands of habitat suitable for supporting permanent populations sometimes are separated by vast areas of habitat that are not permanently occupied, but instead provide opportunities for movement between habitat islands. Thus, habitat fragmentation is a major concern. Beier (1993) and Beier et al. (1995) described a situation where mountain lion habitat in the Santa Ana Mountains of southern California had become isolated from other suitable areas and immigration likely was reduced as a result of human development. Immigration and emigration of individuals are necessary for the maintenance of genetic diversity. Further, opportunities for recolonization must be provided in the event of extirpations from islands of suitable habitat. Maintaining adequate space for mountain lions and their prey as well as linkages between such areas clearly is a pressing issue that must be addressed if mountain lions are to retain their current status.

Depredations on livestock and other domestic animals likely will increase in frequency, especially as the human population expands (Torres 1997). Depredation may be coincident with increases in lion populations (Torres et al. 1996), but may also be a function of declines in populations of primary prey (Pierce et al. 1999a, Kamler et al. 2002). Whatever the cause, management of depredating mountain lions will remain an important issue. Current management of depredating individuals usually involves killing of the offending animal, a strategy unlikely to change in the immediate future. Even in densely populated areas, such events are relatively uncommon (Torres 2000), and such removals likely do not present a threat to existing populations of mountain lions.

Mountain lion populations apparently have expanded during recent years, and there has been increasing concern about the potential for an increase in human encounters. Indeed, such concerns have resulted in publication of pamphlets and books (Torres 1997) designed to minimize the probability of such incidents. Young mountain lions, dispersing between areas of suitable habitat, may be most apt to encounter humans; indeed, the majority of attacks on humans have involved subadult or apparently underweight lions (Aune 1991; Beier 1991). As human populations increase and expand into currently occupied lion habitat, the rate at which such encounters occur may be expected to increase. Meeting human safety objectives while simultaneously providing habitat for

viable populations of mountain lions will become increasingly important (Torres 1997).

Sport hunting of mountain lions occurs in the majority of states that have viable populations of mountain lions, and harvest is a method by which wildlife managers attempt to control lion numbers. Increasingly, however, the concept of sport hunting has come under criticism, and hunting of mountain lions has been eliminated in California, and made extremely difficult in other states such as Oregon and Washington by restrictions on the use of hounds to bring animals to bay. Nonetheless, carefully regulated sport hunting remains an important recreational pursuit and is employed as a method of sustaining mountain lion populations at viable levels in a majority of western states (Logan and Sweaner 1999).

Conservation of mountain lions has a long and varied history, and has been couched largely in terms of political expediency (Torres 1997). Efforts to control or eliminate these obligate carnivores by unrestricted harvest and bounty systems were unsuccessful throughout much of the United States, but their efficacy has been attested to by the absence of mountain lions from much of their historical range. In those areas, such as western North America, where large tracts of essential habitat remained in relatively pristine conditions, intensive methods of controlling mountain lions gave way to regulated sport hunting, with an emphasis on ensuring viable populations with the capability of maintaining a sustainable harvest. Selective removal of individual lions that have preyed on livestock or domestic animals has been compatible throughout much of the range of mountain lions during the recent past. Elimination of lions involved with human safety incidents largely has achieved public acceptance.

RESEARCH NEEDS

Mountain lions occur at low densities and are secretive and cryptic; thus, they are among the most difficult large mammals to study. Furthermore, costs of research associated with the study of large carnivores are great, confounding efforts to obtain meaningful answers to difficult questions. Although many aspects of the ecology of mountain lions have been investigated, few authors have conducted the long-term investigations necessary to begin to understand the relationships among habitat, prey densities, and the dynamics of the populations of these secretive predators and their prey.

Mountain lions have been implicated as factors important in the dynamics of some populations of mountain sheep (Kamler et al. 2002), including two population segments (Wehausen 1996; Hayes et al. 2000) listed as endangered by the federal government. Impacts of lion predation on mountain sheep populations are most probable where mule deer and mountain sheep occur sympatrically (Schaefer et al. 2000; Kamler et al. 2002). Nonetheless, clear linkages among the dynamics of populations of primary prey (mule deer), mountain lions, and secondary prey (mountain sheep) are yet to be established, and warrant serious investigation. Such investigations must, however, be conducted over a temporal scale adequate to elucidate changes in habitat quality and resultant responses among prey and predators in such systems (Pierce 1999). As a result, population modeling may become an even more useful predictive tool, (Beier 1993) with more potential for application than currently recognized.

The genetic structure of populations of mountain lions has been examined only recently (Walker et al. 2000; Ernest et al. 2003), and additional opportunities to define populations from a genetic perspective are needed. Furthermore, the spatial structure of lion populations has been reported only on a local scale (Germaine et al. 2000; Sweaner et al. 2000), and landscape-level efforts to more clearly define populations of mountain lions clearly are warranted. Moreover, the potential metapopulation structure (Sweaner et al. 2000) of mountain lions warrants further investigation, and has important implications for the conservation of these large felids (Ernest et al. 2003). GPS technology can be incorporated into telemetry collars for investigations of mountain lion movements and habitat selection (Bleich et al. 2000; Anderson and Lindzey 2003) and can be combined with sophisticated genetic

analyses (Ernest 2000a; Ernest et al. 2000) to enhance the probability of obtaining meaningful results in landscape-level investigations of lion ecology.

Efforts to improve methods of estimating relative numbers of mountain lions in specific geographic areas should continue. Although investigators have developed a number of indirect methods of assessing abundance (Germaine et al. 2000; Pierce et al. 2000b) and some of these are robust (Beier and Cunningham 1996), they are not without problems associated with the definition of populations (Pierce et al. 1999b). Moreover, methods that rely on indirect evidence, such as tracks to identify individuals, are problematic and subject to statistical vagaries (Grigione et al. 1999). Efforts to determine relationships between indirect evidence of mountain lion abundance and genetic evidence from individuals known to be present in specific geographic areas (Ernest et al. 2000) may be a productive field of endeavor, and should be initiated.

As the human population increases, encounters between humans and mountain lions will occur more frequently (Torres 1997). The potential development of nonlethal methods to decrease such encounter rates has implications for the conservation of mountain lions in urbanized areas as well as for some endangered taxa on which they prey. Indeed, the question of aversive conditioning of mountain lions has not been adequately explored, and warrants investigation.

Preliminary findings (Foley 1997) have suggested that epizootic processes are not likely to affect populations of mountain lions in the western United States. Anderson (1983) felt that the relative absence of pathogens among wild mountain lions has largely reflected insufficient efforts to detect diseases, and the results of recent investigations have been consistent with that notion. Nonetheless, some diseases detected among mountain lions are similar to those affecting domestic cats, and further research is needed to determine whether they are the same as those carried by domestic cats or are endemic in wild populations.

Research on mountain lions has often been considered only in a management context, with publications limited to agency reports. Investigators have frequently failed to incorporate concurrent research on prey populations (Pierce 1999) or approach questions from the evolutionary perspective necessary (Pierce 1999; Bleich and Oehler 2000) to ensure that their findings have widespread applicability. The most meaningful knowledge provided by future investigations of mountain lion ecology will incorporate large-scale spatial and temporal components. Investigators will continue, however, to face challenges posed by the high costs and logistical constraints associated with working on a large, cryptic predator (Pierce 1999). Nonetheless, as mountain lions become a more significant and controversial management challenge, funding for the long-term, landscape-level research necessary to meet both proximate and ultimate conservation needs could be forthcoming. Investigators must be ready and willing to proceed along the most meaningful lines of endeavor.

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