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CHAPTER 1

Introduction and Background

What carnivores eat, their hunting behavior and habitat use, and how they survive is not only a function of their predatory nature but also hinges on the pivotal role other large carnivores play in the lives of less dominant ones—by competing with them for food, by preying on them, or both (Creel 1998; Ballard et al. 2003; Caro and Stoner 2003). In some instances, competition for resources determines whether one predator is even allowed to live where another predator exists, which can have important implications for carnivore management and conservation (Donadio and Buskirk 2006; Murphy and Ruth 2010). For instance, rare African wild dogs do not fare well where African lion and spotted hyena densities are high (Creel and Creel 1996, 2002). Competition with coyotes (*Canis latrans*) reduces survival of endangered San Joaquin kit foxes (*Vulpes macrotis multica*), although kit foxes reduce some of this predation mortality by avoiding coyote-dominated shrub habitats (Cypher and Spencer 1998; Nelson et al. 2007). Hence, along with predation, competition between carnivores for resources has important implications for the structure and function, as well as conservation, of ecological communities (Schoener 1982; Palomares and Caro 1999; Linnell and Strand 2000; Creel et al. 2001; Caro and Stoner 2003).

At the time of European settlement of North America, cougars (*Puma concolor*), wolves (*Canis lupus*), black bears (*Ursus americanus*), and brown bears (*U. arctos*) were widely distributed, occupying diverse habitats (Wilson and Ruff 1999; Laliberte and Ripple 2004). Such extensive distribution meant that many carnivores were regionally sympatric, and during their co-evolution, interspecific interactions and competition may have been one of several evolutionary forces contributing to the structure of assemblages of carnivores in the various environments (Schaller 1972; Mills 1990; Caro 1994; Durant 1998). As human settlement increased, particularly in the 1800s and early 1900s, people altered habitats and drastically changed carnivore distribution and abundance. In most of the United States, the complex system of interactions between these species was altered or eliminated. Large carnivores now occupy remnants of their former distribution—grizzly bears persist in roughly 45 percent of their historical range and cougars and wolves in about 60 percent of theirs (Laliberte and Ripple 2004: 126).

Although scientific research has advanced our understanding of carnivores substantially since the early 1970s, we are still learning how to live with cougars and wolves and how best to understand their management and conservation needs in the various states where they remain or are becoming restored (Mech and Boitani 2003a; Hornocker and Negri 2009; Jenks 2011). During the time we were writing this book, wolves in Idaho and Montana reached numbers that met federal goals for recovery from endangered status; they were frequently in the news, and their status was haggled over in and out of the courts. Wolves were delisted from endangered status in 2008, quickly relisted after litigation, and delisted again in 2009. They were hunted in Idaho and Montana in the winter of 2009–10, relisted as endangered in August 2010, and then fully delisted, with hunting resumed in both states in late 2011 (Idaho Department of Fish and Game 2012). Later, on September 30, 2012, Wyoming assumed management authority for wolves (Wyoming Game and Fish Department 2013). Meanwhile, cougars were in the news as they worked their way eastward, showing up on remote cameras, shot in farmers' fields, or killed along highways in Nebraska, Missouri, Michigan, Wisconsin, and other midwestern states (Cougar Network 2012).

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Questions concerning how species within the large carnivore guild interact, how they partition resources, and what enables or hampers their coexistence are pertinent to management and conservation of these large species as they are restored in our human-dominated landscape. However, in most ecosystems in North America, little information has accumulated regarding such interspecific interactions. This is the case for several reasons. Sustaining long-term ecological studies of large carnivore populations is challenging and expensive because they necessitate working at large spatial scales (Hobbs 1996; Garrott and White 2009). In addition, the rarity of multi-species carnivore assemblages has made investigation of communities of carnivores less common than the single-species approaches that have thus predominated in conservation efforts for these large species. Hence it is not surprising that much of what we have learned about cougars has occurred in the absence of wolves, their main natural competitors.

Given limited funding and logistical support, many studies on cougars have lasted only two to four years—far short of the cougar's natural life span of twelve to fourteen years for females in the wild. However, more recently, a number of studies have provided continual investigation over eight years or more (Beier 1996; Logan and Sweanor 2001; Maehr et al. 2002; Beier et al. 2003; Laundré and Clark 2003; Laundré et al. 2007). In comparison, much greater numbers of short- and long-term research studies have amassed critical information on wolves and bears, both in and beyond Yellowstone National Park. But again, most of these studies, including the famous studies of wolves in Alaska and Michigan (see Mech 1970; Carbyn et al. 1995; Mech and Boitani 2003a), have occurred in the absence of cougars.

Today only a few relatively intact ecosystems remain where we can further our understanding of interactions among multiple large carnivores. With the restoration of wolves in 1995 and 1996, the Greater Yellowstone Ecosystem became one of these.

This book is about cougar ecology and how cougars responded to the restoration of their main competitors, wolves, on the Greater Yellowstone Northern Range. At its core, our research was directed toward understanding whether cougars and wolves would compete for certain resources directly and indirectly, how they might sort out the landscape as a result of competition and avoidance, and whether wolves negatively affected cougar population performance, including survival and reproduction. These questions encompass topics that have been of interest to the general public, hunters, agencies charged with management of these controversial top carnivores, and conservationists seeking to incorporate ecological and community information into long-term wildlife conservation.

The book is arranged in five parts consisting of eighteen chapters. This first part covers background on development of the project and includes the evolutionary history and taxonomy of cougars and wolves, describes the study area, highlights how we went about quantifying competition and coexistence, and describes our methods of studying cougars before and during wolf restoration. Prey selection, kill rates, and interactions at kills are the focus of part 2. Part 3 addresses whether the movement behavior and spatial-habitat use patterns of cougars changed after wolf restoration. In part 4 we assess whether reproduction, survival, and numbers of cougars have been negatively influenced by the presence of wolves. Finally, in part 5 we synthesize our findings and present our ideas for the management and conservation of cougars in the Greater Yellowstone Ecosystem and in states where cougars and wolves are now naturally being restored.

CO-EVOLUTION AND TAXONOMY OF COUGARS AND WOLVES

Up until the time they were eradicated by humans from much of their range, cougars and wolves shared a long evolutionary history across North, Central, and South America. At one time cougars had the broadest geographic distribution of any terrestrial mammal in the Western Hemisphere (Logan and Sweanor 2001; Cougar Management Guidelines Working Group 2005; Culver 2010).

Cougars, wolves, and other extinct and extant carnivores originated from a common ancestor between 65 million and 55 million years ago during the Miocene—from a tree-dwelling shrew-like predator called a miacid that scurried after insects (Ewer 1973; Macdonald 1992). At the base of the carnivores' story were two types of miacids, one that probably looked much like modern martens—vulpavines—and the other resembling modern genets—viverravines. These early arboreal carnivores gave rise to two main branches of the order Carnivora: the Canoidea arose from the vulpavines of the New World, and the Feloidea arose from the Old World viverravines (Ewer 1973; Kleiman and Eisenberg 1973; Macdonald 1992).

The teeth of the Canoidea and Feloidea exemplify the differences in skeletal structure that separate these two major divisions. In the canids, one of the lower carnassials retains a broad shelf (talonid) that provides a dual function—cutting at the front and crushing behind—which enables mastication of food; hence, digestion can begin in the mouth (Tedford 1994). As a result, dogs and their close relatives can process a variety of foods—meat, bone, sinew, invertebrates, plants—which provides great survival value because the wider range of food enables the canids to adapt to shifting resources as local conditions dictate. The dog branch diversified and gave rise to four caniform families: dogs (Canidae), bears (Ursidae), weasels (Mustelidae), and raccoons (Procyonidae). Members of the cat group, in contrast, lack the talonid shelf, and their molars are all specialized to cut meat and deliver the chunks whole to the stomach for digestion (Tedford 1994). Four feliform families sprouted from the cat branch: cats (Felidae), civets (Viverridae), hyenas (Hyaenidae), and mongooses (Herpestidae).

Tracing the diversification of modern felids and canids is not easy (Ewer 1973; O'Brien and Johnson 2007). Fortunately, advances in DNA sequencing have allowed mapping of the genomes of various species, which made it possible to construct the first resolved family tree for cats (Culver 1999; O'Brien and Johnson 2007) and an improved tree for the dog family (Wayne and Vilà 2003).

Evolutionary History of Cougars and Wolves

Before modern carnivore families appeared, the dog and cat branches evolved separately in the New World and the Old World. When the Bering land bridge opened up between America and Eurasia roughly 30 million years ago, representatives of each branch made the crossing, and dogs and cats came face to face (Macdonald 1992).

The cougar belongs to the extremely old puma lineage, members of which originated from a common North American ancestor roughly 7 million to 8 million years ago (Culver 2010). The puma lineage also includes the cheetah (*Acinonyx jubatus*) and jaguarondi (*Puma yaguarondi*), with the cheetah first to diverge from the common felid ancestor about 5 million to 8 million years ago, making it the second closest relative of the cougar (Johnson and O'Brien 1997; Turner and Antón 1997; Culver 2010). Later, the jaguarondi and cougar diverged around 4 million to 5 million years ago, making them the closest relatives in the puma lineage (Janczewski et al. 1995; Johnson and O'Brien 1997; Johnson et al. 2006; Culver 2010).

Fossil evidence in North America suggests that cougars or an ancestor may have evolved in North America and migrated to southern continents approximately 2 million to 4 million years ago (Patterson and Pascual 1968; Webb 1976; Logan and Sweanor 2001; Culver 2010). But more recent research using genetic tools finds disagreement between the fossil record and the molecular data. Specifically, molecular analyses indicate that the oldest cougar population inhabits Brazil and Paraguay, the North American population is the most recently founded, and cougars as a species are ~0.39 million years old (Culver et al. 2000). Around 10,000–17,000 years ago, during the late Pleistocene, the North American cougar population experienced a demographic contraction event, or "bottleneck," persisting as a small population while many other large mammals went extinct (Driscoll et al. 2002). Descending from a "founder event" involving this small number of individuals, modern North American cougars then expanded from the south, where populations remained stable, to the north, where populations had been extirpated (Culver et al. 2000; Culver 2010). This relatively young age for cougars in North America is directly related to the lack of genetic diversity and differentiation observed in extant North American cougars (Culver 2010: 33). Providing further evidence to support expansion from south to north, molecular genetic data show higher levels of genetic variation among cougars in California and Arizona–New Mexico than among cougars residing farther north (Ernest et al. 2003; McRae et al. 2005).

Wolves arose at about the same time cougars did. By the Pliocene, *Canis* had diversified and become widespread in both the Old World and North America, with wolf-like canids diverging from a common ancestor approximately 2 million to 3 million years ago (Nowak 1979; Wayne et al. 1995). A related branch of small canids entered South America and began an entirely separate evolutionary lineage (Nowak 1979; Kurtén and Anderson 1980; Tedford et al. 1995). It is likely that wolves arose from some population of those small early canids and that the ancestral line also led to coyotes (Nowak 2003). Wolf and coyote lineages diverged between 2.5 million and 1.8 million years ago, not long after divergence of the cougar and jaguarondi lineages (Kurtén 1974; Nowak 1979).

The emergence of modern wolves occurred sometime between 300,000 and 130,000 years ago (Nowak 1979; Wayne et al. 1995). An ancestor to today's wolves probably arose in North America and crossed via the Bering land bridge into Eurasia, where it evolved in the direction of *C. lupus*, the gray wolf (Nowak 2003). The gray wolf is thought to have developed fully in the Old World and then reinvaded the New World in the Pleistocene by once again crossing the Bering land bridge (Nowak 1979; Kurten and Anderson 1980; Brewster and Fritts 1995). Wolf populations of the Old and New World show varying degrees of genetic subdivision, and this, in combination with the extremely high mobility of wolves, suggests the effect of multiple invasions following the numerous glacial advances and retreats of the Pleistocene (Wayne et al. 1992; Forbes and Boyd 1996, 1997; Vilà et al. 1999a).

Regardless of their exact point of origin, cougars and wolves fared well after the late Pleistocene extinctions when the demise of mega-herbivores led to the demise of many of the larger carnivores (Macdonald 1992). Five species of carnivorous mammals disappeared from North America at the end of the Pleistocene: giant short-faced bear, American lion, American cheetah, sabertooth, and dire wolf (Pielou 1991). As many of the larger carnivores went extinct, interspecific competition would have declined somewhat, and the midsized cougar was well adapted to subsist on the smaller, soft-skinned grazers as well as on a wide range of other prey in various habitats (Logan and Sweanor 2001). After the extinction of their dominant competitor, the dire wolf (*C. dirus*), about 8,000 years ago, gray wolf populations grew and remained abundant until they were all but exterminated by modern hunters (Pielou 1991). Along with cougars and wolves, several other midsized to large North American carnivores survived the extinctions: grizzly and black bears, wolverines, coyotes, badgers, red and gray foxes, lynxes and bobcats, and polar bears (Pielou 1991). Thus, in addition to wolves, cougars still had to contend with a few formidable competitors.

Taxonomy

From the mid-1700s to the mid-900s—using morphological characteristics, habitat, and general geographic distribution—biologists described thirty-two distinct subspecies of the cougar, distributed throughout North and South America (Young and Goldman 1946). The cougar was originally named *Felis concolor* by Linneaus in 1771 (Wozencraft 1993; Culver 2010) and later renamed *Felis (Puma) concolor* when Jardine (1834) recognized *Puma* as a subgenus of *Felis*. Although *Puma* was recognized as a separate genus as recently as 1973 (Ewer 1973), *Felis* remained the more commonly referenced genus until the mid-1990s. By then, taxonomy could draw upon molecular genetics to examine the accuracy of generic and subspecific divisions. When cougar DNA was analyzed from blood and tissue samples collected throughout the Americas, Culver and colleagues (2000) determined that there were six groups of cougars, not thirty-two, across their range. One cougar subdivision occurred from Nicaragua northward and five subdivisions existed south of Nicaragua. Apparently, cougars had been breeding with each other, wandering great distances to do so and even swimming substantial bodies of water, over much larger areas than originally thought. In South America a high level of genetic diversity was found in cougars, whereas Central and North American cougars, north of Nicaragua, had only moderate levels (microsatellite DNA) to no variation (mitochondrial DNA). Culver and co-workers (2000, 2011) eventually proposed taxonomic revisions to include the six subspecies: in North America *Puma concolor cougar*, Central America *P. c. costaricensis*, northern South America *P. c. concolor*, eastern South America *P. c. capricornensis*, central South America *P. c. cabrerae*, and southern South America *P. c. puma*.

Worldwide, the gray wolf has also been divided into as many as thirty-two subspecies (Hall and Kelson 1959; Wayne and Vilà 2003). But in contrast to the situation for cougars, the rates of gene flow and geographic variation among North American wolf populations are high. Rather than populations partitioned into discrete geographic areas, geographic variation in the wolf is distributed along a continuum (Nowak 2003; Wayne and Vilà 2003). Thus the division of wolves into discrete subspecies and other genetic units may be somewhat arbitrary (Wayne and Vilà 2003), although Forbes and Boyd (1996) found a limited pattern of genetic differentiation with increasing geographic distance. Now biologists consider the gray wolf part of a single monophyletic clade (Wayne et al. 1995; Wayne and Vilà 2003). In fact, all species in the genus *Canis*, as well as the dhole and the African hunting dog, possess identical numbers of chromosomes (Wayne et al. 1978a, 1978b; Wurster-Hill and Centerwall 1982).

Hounds from Wolves: The Path to Hunting Cougars

The extant species most closely related to the gray wolf is the domestic dog (*C. l. familiaris*; Tsuda et al. 1997; Vilà et al. 1997, 1999a; Leonard et al. 2002; Savolainen et al. 2002). Using mitochondrial DNA, Savolainen and colleagues (2002) concluded that domestic dogs had a single origin about 15,000 years ago in East Asia. Early wolf-dogs probably associated with humans primarily for food, and imprinting on humans from an early age would have facilitated the domestication process (Mech 1970; Olsen 1985). The dogs of the Western Hemisphere derive from the domesticated descendants of these Old World wolves that trekked with humans over the Bering land bridge (Leonard et al. 2002). Some of these early dogs also accompanied humans to western Asia and Europe, where they played a role in founding some of today's breeds (Leonard et al. 2002; Kerasote 2007).

Most hound breeds are descendents of the bloodhound, the most ancient breed of hound. Thought to have originated in France or England, bloodhounds have been put to work for hundreds of years tracking humans and other animals. Historical accounts of bloodhounds provide little evidence for how far back the origins of the breed reach, but many authorities believe the breed was known throughout the Mediterranean countries long before the Christian era (Brough 2007). Although no evidence exists, some claims indicate that the bloodhound ancestors referenced in English writing in the mid-fourteenth century were brought over from Normandy by William the Conqueror after the conquest of 1066 (Barwick 2006; Bloodhounds UK 2011). Scottish and English records from the fourteenth century also suggest that the rebel William Wallace (popularized in Mel Gibson's film *Braveheart*) was tracked by sleuth hounds, which many believe to be the same as the bloodhound. What is clear is that by the mid-fourteenth century, the English had a large, keen-scented hound that, similar to wolves, was adept at tracking, pursuing, and keeping at bay raccoons, bears, and cougars and other felid species.

The danger-avoidance behavior known as treeing—a trait that is common to cougars, bobcats, and black bears—evolved solely for the purpose of reducing interference competition with pack-living wolves and other dominant carnivores, including grizzly bears (Herrero 1978). The persistence of this instinctive behavior, even in areas where for over a century cougars did not need to avoid competition from wolves, exemplifies the "ghost of competition past" (Connell 1980). Although wolves did not operate as the selective force for this trait for fifty to sixty years, pursuit of cougars by hunting hounds in many states has perhaps helped maintain selective pressure for treeing as an advantageous survival trait. Thus, houndsmen who enjoy watching their dogs trail a cougar or bobcat, and researchers who use hounds to capture and mark cougars for study purposes, can link the hounds' fine tracking abilities to their ancestor, the wolf (fig. 1.1).

FIGURE 1.1. *Buck (left) and Cooter doing their job during the capture of adult female F125. Photo by Tony Knuchel, Hornocker Wildlife Institute.*

DEVELOPMENT OF OUR FOURTEEN-YEAR RESEARCH STUDY

A growing public desire to prevent the loss of threatened wildlife finds expression today in legislation as well as calls for federal and state agencies to form management and conservation strategies that incorporate the latest and best scientific information (e.g., Florida panther and black bear, Alvarez 1993). However, with the exception of game species, endangered species, or those with greatest conservation need, federal and state resource agencies typically are not funded or structured to conduct the intensive long-term biological research necessary to further the management-conservation process for large carnivores. Nonprofit conservation organizations have frequently played a successful role in filling this gap, and one such nonprofit was the impetus behind the fourteen-year study resulting in this book.

Guided by founder and director Dr. Maurice Hornocker, the Hornocker Wildlife Institute was a small, effective organization with a record of providing new information to agencies and the public by investing in long-term scientific studies. During its tenure, the institute supported long-term studies of cougars, brown and black bears, jaguars, tigers, and snow leopards as well as shorter-term studies of other carnivores (Koehler and Hornocker 1989, 1991; Quigley and Crawshaw 1992; Miquelle et al. 1995, 1996a, 1996b; Murphy 1998; Ruth 2004a; Ruth et al. 1998; Logan and Sweanor 2001; Kerley et al. 2003; Seryodkin et al. 2003; Costello 2008; Costello et al. 2008, 2009; Goodrich et al. 2008).

In the early to mid-1980s, as signs of cougars in Yellowstone National Park increased and plans to restore wolves were in development (US Fish and Wildlife Service 1978; National Park Service 1990; Varley and Brewster 1992), Hornocker realized there was a critical gap in information: how would wolf recovery influence cougar populations, predation by cougars, and existing conservation and management of the large American cat? He also recognized an opportunity: to conduct a long-term, intensive study on cougars that would take advantage of a natural experiment as wolf restoration became a reality in the Greater Yellowstone Ecosystem. A first step was to survey the Greater Yellowstone Northern Range and determine study feasibility. In cooperation with Yellowstone National Park and the Montana Department of Fish, Wildlife and Parks, the Hornocker Wildlife Institute conducted track surveys across the Northern Range of Yellowstone and adjacent lands north of the park boundary. Results of this survey, carried out in the winter of 1985–86, confirmed that a number of cougars did indeed inhabit the northern winter range, indicating recovery from very low numbers prior to cessation of poisoning and implementation of hunting regulations. Spurred by the track survey findings, Hornocker approached Superintendent Robert Barbee and John Varley, then director of the Yellowstone Center for Resources, about conducting a long-term study. The study goals were straightforward: to document the ecology of cougars in the northern Yellowstone system and lay the foundation of sound information on cougars prior to the planned restoration of wolves. This foundational work, from 1987 to 1994, was overseen by Hornocker and undertaken by Kerry Murphy through the University of Idaho, resulting in his doctoral dissertation, "The Ecology of the Cougar (*Puma concolor*) in the Northern Yellowstone Ecosystem: Interactions with Prey, Bears, and Humans" (1998).

The restoration of wolves to Yellowstone and Idaho's River of No Return Wilderness became a reality in 1995 and 1996, with the success of the restoration quickly surpassing expectations for wolf recovery (Fritts et al. 2001). With the restoration of wolves to the Greater Yellowstone Ecosystem, the four largest North American carnivores—wolf, grizzly bear, black bear, and cougar—were once again sympatric in the system. Prior to the restoration of wolves in Idaho, Montana, and Wyoming, the Northern Continental Divide Ecosystem—including Glacier National Park, which wolves had naturally recolonized in the late 1970s to early 1980s—was the only area supporting a complete assemblage of large carnivores in the contiguous forty-eight states (US Fish and Wildlife Service 1978; Apps et al. 2007). Noting the unmatched opportunities these two systems provided to gain knowledge about the influence of carnivores on one another and on ungulate prey, Hornocker initiated studies in the Glacier area in 1993 (Ruth 2004a) and later in Yellowstone, with a second-phase cougar study following the restoration of wolves. In late winter 1998, lead field scientist Toni Ruth began marking cougars, and soon afterward Polly Buotte joined the team to serve as geographic information specialist and coordinator of field crews quantifying cougar kill rates and displacement of cougars from their kills. In 2000 the Hornocker Wildlife Institute merged with the Wildlife Conservation Society, known for its international work to save wildlife and wild places. Our work continued under the Hornocker Wildlife Institute/Wildlife Conservation Society program through the end of our study in 2006.

Wolf restoration also led to other new multi-predator and multi-prey studies (Kunkel et al. 1999; Husseman et al. 2003b; Ruth 2004a; Kortello et al. 2007). These studies lasted two to four years and lacked data on cougars prior to wolf restoration, therefore relying on comparisons between cougar and wolf diets, selection of prey, spatial overlap, habitat use, and population dynamics to gain understanding of predatory roles and competition. Notably then, grounded in seven years of data on cougar ecology prior to wolves, our study was the first long-term investigation of cougar-wolf interactions and the first opportunity to conduct such research within the framework of a natural experiment—wolf restoration.

Fundamental to our investigation of species interactions and the large carnivore community in Yellowstone were: (1) committing to a long-term effort with a robust field presence and (2) forming strong collaborations with other established and committed research efforts on carnivores and prey. Including the work of Murphy (1998), our efforts translated into more than 7,000 person-days of fieldwork on cougars over sixteen years, 11,950 ground and aerial VHF locations, 19,530 GPS locations, 744 cougar kills, more than 22,500 kilometers of winter population tracking transects, and repeated blood, tissue, and hair samples from 163 cougars for disease and genetic studies. In addition, our efforts occurred in the midst of long-term studies and data accrued on bears (Interagency Grizzly Bear Study Team; see http://www.nrmsc.usgs.gov/science/igbst/detailedpubs for publications) and on wolves, coyotes, ungulates, and vegetation changes on the Greater Yellowstone Northern Range. Numerous graduate projects and publications have resulted from the diverse array of questions addressed within the system (see http://www.greateryellowstonescience.org for publications). As a result, we collaborated with other researchers and often had access to pertinent databases and expert knowledge from various federal and state agencies and university scientists that provided crucial insights into the strengths and weaknesses of the various sets of data (Ruth et al. 2003; Mao et al. 2005; White et al. 2007; Cross et al. 2009; see also Garrott et al. 2009b).

We were particularly fortunate to have two colleagues, Dr. Kerry Murphy and Dr. Doug Smith, employed at Yellowstone National Park during our study. In addition to Kerry's study on cougars prior to wolf restoration providing the groundwork and framework for our post-wolf restoration study, he also granted us access to his entire data set collected while he worked as a Hornocker Wildlife Institute scientist. Having such thoroughly collected data in hand is a wonderful thing. Yet we were limited in its use by the layers of details that do not come with paper or digital data records—details acquired through Kerry's experiences spending every day collecting data in the field (fig. 1.2). His knowledge of the individual animals he radio-collared and followed and of the landscape and climate at a particular time is his alone. Our privilege and benefit were to have his scientific background, ideas, and input on these hidden details throughout the post-wolf restoration study.

FIGURE 1.2. *Kerry Murphy uses radio-telemetry to locate a cougar on the Greater Yellowstone Northern Range. Kerry led the study on cougars prior to wolf restoration, providing the groundwork and data for comparing cougar ecology following the restoration of wolves. Hornocker Wildlife Institute photo.*

Doug Smith was in Yellowstone when the first wolves were brought into the soft-release pens and eventually released from those pens. He has coordinated population monitoring and numerous research studies as Yellowstone Wolf Project leader since 1995, resulting in well over ninety peer-reviewed publications (see http://www.greateryellowstonescience.org//search/apachesolr_search/wolf%20publications). Throughout our post-wolf restoration project, Doug was an enthusiastic, insightful, and supportive associate and collaborator. Field coordination, communication, and assistance with ground and aerial monitoring between our projects yielded valuable shared information on interactions between cougars and wolves. Kerry and Doug are contributing authors of chapters 5, 6, 11, and 15 of this book.

We also established a strong relationship with Chuck Schwartz and Mark Haroldson of the Interagency Grizzly Bear Study Team and, along with Yellowstone National Park Bear Management Specialist Kerry Gunther and Doug's wolf project, our three study teams addressed specific multi-carnivore questions coordinated through formation of the Large Carnivore Working Group in August 1998 (fig. 1.3). Led by Howard Quigley, the Large Carnivore Working Group focused on the Northern Range of Yellowstone National Park. This area was chosen because of the coexistence of

FIGURE 1.3. *To understand the interactions among cougars, wolves, and bears, the Large Carnivore Working Group formed in August 1998.* Left to right: *Mark Haroldson, Doug Smith, Polly Buotte, Steve Cherry, Chuck Schwartz, Howard Quigley, Kerry Gunther, Toni Ruth, and Dan Stahler (Haroldson and Schwartz—Interagency Grizzly Bear Study Team; Smith, Gunther, and Stahler—Yellowstone National Park; Buotte, Quigley, and Ruth—Hornocker Wildlife Institute/Wildlife Conservation Society; Cherry—Montana State University).*

grizzly bears, wolves, cougars, and black bears and the presence of our active field-based research and monitoring projects. With much of the single-species research already under way, the group concentrated on ways of integrating databases for a systems approach to natural resources management, giving added scientific and conservation value to individual projects by working together to understand the interactions among the large carnivores (e.g., Ruth et al. 2003).

Our intent in synthesizing our research in a book was to provide objective scientific data at the forefront of understanding cougars and large carnivore community structure and management issues in the Greater Yellowstone Ecosystem and elsewhere where wolves and cougars are being restored. We would like to emphasize that the findings presented apply to a particular period in a specific study area. Wildlife populations do not remain static, and ecosystems vary over time (Schaller 1972). As more studies investigate interspecific interactions and the role they play in various ecosystems, some of our findings may hold, others may be drawn into question, and new questions that advance our understanding of multi-species interactions in structuring communities will be answered.